Paper 11

[Accueil] [Remonter] [Intro 1] [Paper 2] [Paper 3] [Paper 4] [Paper 5] [Paper 6] [Paper 7] [Paper 8] [Paper 9]
[Paper 10] [Paper 11] [Paper 12] [Paper 13] [Paper 14] [Paper 15] [Paper 16] [Paper 17] [Paper 18]
[Paper 19] [Paper 20] [Paper 21] [Paper 22] [Paper 23] [Paper 24] [Paper 25] [Paper 26] [Paper 27]
[Paper 28] [Paper 29] [Paper 30] [Paper 31] [Paper 32] [Paper 33] [Paper 34] [Paper 35] [Paper 36]
[Paper 37] [Paper 38] [Paper 39] [Paper 40] [Paper 41] [Paper 42]

Genetic and biochemical analysis of aroma in Rice

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Abstract

Aroma in cultivated rice is more and more appreciated in Europe. Unfortunately, aromatic cultivars often show undesirable agronomic characters. Thus, breeders wish to develop high-yielding aromatic varieties adapted to European constraints. Many contradictory studies have been reported concerning the genetic control of aroma in rice. Thus, it was of interest to approach the problem using recently developed tools. The approach presented here involved a combination of two techniques. The first was quantification of volatile compounds in the cooking water of grains by gas chromatography. This technique allowed the analysis of grain aroma as a quantitative trait. The second technique was the construction of a genetic map using several types of molecular markers. Evaluations of aroma and mapping were performed using a population of doubled haploid (DH) lines derived from the F1 hybrid IR 64 x Azucena. Cosegregation between molecular markers and aromatic character was studied using a QTL detection approach. Segregation analysis allowed us to locate unambiguously on chromosome 8 the gene responsible for the presence of 2-acetyl-1-pyrroline (AcPy), the main compound associated with rice aroma. Estimations of recombination fractions on chromosome 8 were corrected for strong segregation distortion. Moreover, our results showed that AcPy concentration in plants may be regulated by at least 2 regions on chromosomes 4 and 12. We believe that our results could help understand why a gradient is observed in strength of aroma among scented cultivars. We discuss the implications of these results for rice selection. An immediate application of the tagging of aromatic gene(s) is their marker-assisted introgression into high yielding varieties.

Keywords

- Rice (Oryza sativa L.), aroma/fragrance/scent, grain quality, molecular mapping, gas chromatography, marker-assisted selection
- Europe.

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Introduction

In Europe as in many other regions, people tend to appreciate more and more aromatic or scented rice varieties. Thus, aroma represents a high value added trait. Also, high milling returns and good cooking quality are often associated with scented rice (Nagaraju et al., 1975 ; Tripathi and Rao, 1979). Unfortunately, scented cultivars often show undesirable agronomic characters, such as low yield, susceptibility to pests and diseases, strong shedding (Berner and Hoff, 1986). Moreover, except for the Basmati group, aromatic varieties are not well adapted to our temperate climates. Consequently, breeders wish to develop aromatic varieties adapted to European constraints.

To explore the possible ways of obtaining high-yielding aromatic varieties, many studies on genetic control of the aroma trait in rice have been undertaken (Ahn et al., 1992 ; Ali et al., 1993 ; Berner and Hoff, 1986 ; Lin, 1990 ; Nagaraju et al., 1975 ; Pinson, 1994 ; Raghuram Reddy and Sathyanarayanaiah, 1980 ; Sood and Siddiq, 1978 ; Tripathi and Rao, 1979 ; Yano et al., 1992). Some of the authors concluded that there was a monogenic inheritance of the trait, and others that two or three recessive or dominant genes participate in the determination of the trait. Thus, it seemed interesting to us to initiate a study of inheritance of aroma with tools permitting the chromosomal location of the gene(s) involved in the expression of this character.

Molecular markers represent a very powerful tool for analysing genetic models underlying qualitative or quantitative traits. Recently, Ahn et al. (1992) succeeded in locating a gene controlling aroma in rice on chromosome 8, in using molecular markers in combination with near isogenic lines (NIL's).

Buttery et al. (1983) identified 2-acetyl-1-pyrroline (AcPy) as the major component of rice aroma. This compound is present in all parts of the plant (stems, leaves, grains) except roots. At present, no linkage analysis between markers and AcPy as a quantitative trait was done in order to determinate the monogenic or polygenic nature of the trait. In the present study, the genetic mapping of aroma was improved in combining for the first time the two following approaches ::
1) a precise, quantitative and objective aromatic analysis using gas chromatography, permitted by the utilisation of doubled haploid lines and,
2) the genetic mapping by molecular markers, allowing the localisation of gene(s) involved in the expression of any character segregating in the studied population.

Materials and Methods

General strategy

A core rice genetic map was developed at IRRI, Philippines (Huang et al., 1994), on the basis of 145 RFLP (Restriction Fragment Length Polymorphism) markers. A core map consists of markers covering all the genome at middle density, i.e., with no gap larger than 20-25 centimorgans (cM). Therefore, there will be at least one marker sufficiently linked at 10 cM or less to the genes(s) underlying a trait. With this aim, a population of 135 doubled haploid lines was used. After evaluation for aromatic compounds of the DH lines by gas chromatography at ENSIAA, France, chromosome segments of interest were identified by Mendelian and QTL (Quantitative Trait Locus) analysis. A QTL may be defined as a locus (made of one or several tightly linked genes) explaining a fraction of the genetic variance of a quantitative trait. Saturation of the chromosome 8 region containing the major gene for aroma was then performed at ORSTOM, France, using different types of molecular markers.

Genetic mapping

The mapping population of doubled haploid (DH) lines was derived from the F1 hybrid IR 64 x Azucena through anther culture at IRRI (Guiderdoni et al., 1992). Azucena is a scented japonica land race from the Philippines, and IR 64 is a non-scented indica variety from IRRI. DNA was isolated from lyophilised leaves using the CTAB method (Murray and Thompson, 1980).

Several types of molecular markers were employed to complete the mapping work. We used the available information about

chromosomal location of some RFLPs and STSs (Sequence-Tagged Sites) to complete the map of chromosome 8 (Causse et al., 1994; Inoue et al., 1994). We also performed the Bulked Segregant Analysis (Michelmore et al., 1991) technique to find new RAPD (Random Amplified Polymorphic DNA) markers in the vicinity of the Aroma major gene. (See Lorieux et al. (1996) for more detailed information about molecular marker protocols.)

The molecular data were analysed using standard multipoint procedures (Lander et al., 1987). For chromosome 8, which showed strong segregation distortion in favour of the non-scented parent allele, an appropriate formula was derived to estimate the recombination fractions (Lorieux et al., 1995; Lorieux et al., 1996).

The QTL detection approach was based on quantitative evaluation of AcPy by gas chromatography. The interval mapping method (Lander and Botstein, 1989) was used. As AcPy was not normally distributed, ANOVA 1 and Kruskall & Wallis test were used to confirm results of interval mapping. In order to detect putative minor QTLs, interval mapping was redone on the scented DH lines only.

Evaluation of aroma

Sensitive evaluation of rice aroma by smelling leaves or smelling/chewing seeds may be unreliable, because of the subjective nature of these tests. The method used here, detailed in Petrov et al. (1996), is based on a gas chromatography quantification of volatile compounds contained by the cooking water of 100 g. of grains. By this technique, the presence of 2-acetyl-1-pyrroline at the p.p.b. level (1 p.p.b. equals to 1.10-9 g./g.) can be detected with good reproducibility (Petrov et al., 1996). The technique has recently been improved at CIRAD, France (Nardi, 1997). Only 20 g. of grains are now needed to obtain about five times more AcPy with a better precision. AcPy is known to be the major agent of aroma in rice (Buttery et al., 1983; Buttery et al., 1988).

To compare the results of gas chromatography to those of sensitive tests, the method of scent revelation with KOH (Sood and Siddiq, 1978) using leaves and seeds was applied on a replication of the DH lines population grown in the glasshouse at ORSTOM, France. Each line was evaluated by a minimum of four persons chosen for their capacity to easily distinguish between the two parents. The entire population (135 lines) was evaluated for both leaves and seeds tests.

Results

Sensitive tests using leaves and seeds lead to the same conclusions: 40 lines and Azucena parent were found aromatic, and 90 lines plus IR 64 parent were found to be non aromatic. Five lines were difficult to evaluate and thus were considered as missing data.

AcPy was distributed in the progeny as follows: all lines unambiguously found as aromatic by sensitive tests contained from 3 to 40 p.p.b. of AcPy, and the non scented lines never contained AcPy (Fig. 1). IR 64 and Azucena contained 0.0 ± 0.0 and 24.2 ± 3.9 p.p.b. of AcPy respectively (mean of 12 evaluations). AcPy evaluated by gas chromatography was therefore perfectly correlated with scent evaluation, but it was more accurate since unambiguous and quantitative data for all tested lines were obtained (see Petrov et al. (1996) for detailed information on volatile compound evaluation).

The first QTL analysis performed on the core map of the whole genome revealed only one locus on chromosome 8 (Fig. 2A) with a maximum LOD score of 14.5 at 6.4 cM from marker RG 28. As it explained about 69 % of the variance of the character, it may be considered as a major gene. Two other QTLs for AcPy were found on chromosome 4 and 12 after analysis on scented lines only (Fig. 2B). The associated probabilities to the LODs of these two QTLs were 0.008 and 0.004, respectively.

As the major gene was located on chromosome 8, the mapping effort was concentrated on this linkage group. Thus, sixteen markers were mapped. Considering that (1) AcPy was perfectly correlated with aroma, (2) AcPy has exhibited a roughly bimodal distribution (Fig. 1), and (3) the QTL on chromosome 8 was a major gene regarding the percentage of explained variance, we encoded AcPy as a monogenic trait, i.e., in presence/absence. Segregation analysis allowed us to locate AcPy on chromosome 8 unambiguously between RG 28/Y5 and RG 1 (at 6.4 ± 2.6 and 5.3 ± 2.7 cM respectively; Fig. 3).

The use of the two-point map distance estimate corrected for segregation distortion, gave a total length of the group of 117.5 cM, leading to a reduction of map distances of about 27 %, compared with those obtained with the classical estimate. This corrected length is in good accordance with that found in the intraspecific saturated map (124.8 cM; Kurata et al., 1994), indicating that the proposed estimate of recombination fractions was appropriate for this linkage group.

Discussion

This study permitted us to tag a major gene for aroma between close flanking markers. Moreover, two possible QTLs were identified and localised, which may affect the strength of the aroma in DH lines. This is the first time that the AcPy major gene has been proven to totally cosegregate with the Aroma trait measured by sensitive tests. This result also confirms

that 2-acetyl-1-pyrroline (AcPy) is the major component of aroma in rice.

Some lines were difficult to evaluate for aroma by the sensitive tests. This may be due to different parameters influencing the quantity of AcPy in leaves or seeds (temperature in the glasshouse, age of the plants). Moreover, some known volatile compounds may develop other aromas which may interfere with AcPy and make the sensitive analysis more difficult (Petrov et al., 1996). The difficulties in evaluating aroma of some lines were probably due to an unfavourable combination of these factors.

The question may be asked if there is a common (and/or unique) major locus controlling the presence/absence of AcPy (but not its concentration) in rice varieties. Pinson (1994) observed segregations possibly corresponding to one or two independent recessive genes in crosses between different aromatic/non aromatic varieties. To our knowledge, all recent linkage studies using molecular marker data have lead to the conclusion that aroma is governed by a single recessive gene located on chromosome 8. In addition to the results of Ahn et al. (1992) obtained from Aromatic Lemont , a near-isogenic line of Lemont, aroma was mapped using RFLPs at the same locus by Yano et al. (1992) using an F2 population (cross Surjamkhi x FL-209). Moreover, in a cross involving Basmati 370, aroma was found to be linked at 7 cM to a RAPD marker which mapped close to Aroma in our DH progeny (N. Huang, pers. comm.). Two other recent studies (without molecular markers) tend to confirm these data. Pinson (1994) found that all scented varieties, including Basmati, Jasmine 85 and a mutant of Della share the same recessive gene (which can easily be identified as that of chromosome 8). Kato and Itani (1996) found a single recessive gene segregation in an SSD (Single Seed Descent) lines population derived from the cross BG 1 (scented) x Koshihikari (non scented). According to several authors, the contradictory conclusions founded in the literature are due to problems in handling for the endospermic nature of aroma. For instance, in F2 progenies, this confusion may lead to conclude that the gene is dominant instead of recessive. Segregation distortion can also strongly modify the segregation pattern of a gene.

In this study, two chromosomal regions were identified as possible QTLs controlling the level of aroma. These QTLs would explain why some DH lines are less scented than Azucena, the aromatic parent. We may think that our results could help to understand why a gradient is observed in strength of aroma among scented cultivars. All scented cultivars would bear the same major recessive Aroma/AcPy gene, located on chromosome 8, but would possess different QTLs affecting the level of their aroma. For example, the variety Jasmine 85 is derived from the Thaï rice, Khao Dawk Mali 105, but is less scented. It is possible that QTLs analogous to those we identified were lost by recombination during the creation of Jasmine 85. This model could be a good alternative to that of Pinson (1994), who proposed that differences between varieties are due to mutations of the same gene on chromosome 8.

Numerous additional studies have to be done in order to elucidate the exact function of the major gene and QTLs. AcPy may be experimentally obtained by different reactions (from pyruvaldehyde and proline, from pyruvaldehyde and ornithine, or from fructose and ornithine; Schieberle, 1990). The observation that aroma is a recessive character may lead to several hypotheses. One possible could be that the absence of a protein modifies the biosynthesis chain, leading to synthesis of AcPy which normally would not be present.

An immediate application of our results is the possibility to introduce the major gene for aroma with the aid of molecular markers into any high yielding European or tropical variety faster than with conventional backcross introgression. The advantages of a such approach are: (i) the division of the number of necessary generations by about two by choosing in the BC1 progeny the individual with the higher percentage of recurrent alleles, (ii) the complete elimination of linkage drag (Ragot et al., 1994) and (iii) the direct following of the allele for aroma in successive generations by markers, without the need of self-pollination steps which are necessary in classical breeding schemes involving recessive characters. We are currently experimenting the marker-assisted introgression of Aroma into IR 64. Another promising application is marker-assisted selection (MAS), which can integrate major gene and QTL information in selection indexes. It is not excluded that other QTLs for aroma can be evidenced with larger progeny. To this aim, more IR 64 x Azucena DH lines will be re-evaluated for AcPy content by January 1998 in order to improve the QTL detection. A fine mapping of the chromosome segment around Aroma could be initiated as a first step to isolation and cloning of the major gene. Sequence comparisons for this gene between scented varieties would be very informative to confirm that all scented varieties share exactly the same aromatic allele. Transformation of any variety could then also be envisaged. Nevertheless, some important points remain to be clarified concerning the selection of European high-yielding aromatic cultivars. As indicated above, aromatic cultivars often show undesirable agronomic characters, such as low yield, reduced number of panicles and spikelets, poor filled grain percentage and strong shedding. However, a recent study suggests that the problem of selecting high-yielding aromatic varieties is not impossible to overcome (Kato and Itani, 1996). Moreover, the problem of grain quality cannot be limited to that of aroma. Indeed, several other traits such as long grain, amylose content, etc. contribute importantly to the quality of a cultivar. The question is also complicated by the subjective nature of the notion of quality. So it will be necessary to envisage several methods of selection:

Utilisation of Basmati-type varieties

In Camargue, France, some Basmati varieties coming from Pakistan can produce up to 2 t/ha. These varieties could be grown directly or could be used as good donors for aroma and other quality traits such as grain hardness. Indeed, we observed that they give better recombinant progenies in cross with japonica than other Basmati cultivars. It would be very interesting to obtain high-yielding long-grain japonica cultivars with a Basmati-like aroma. Another way could be to try to increase the yield potential of these Basmati varieties in breaking the linkage between aroma and unfavourable panicle traits. Note that all experiments carried to develop DH lines from F1 hybrids between Basmati and japonica were unsuccessful. A solution could be to perform anther culture on BC1 plants or advanced recombinant generations. The

backcross approach is powerful but time-consuming and cumbersome for the breeder, as BC1F2 families have to be analysed. Thus, a combination of BC1 strategy and molecular marker technology could give new ways to introduce interesting genes coming from Basmati but without unfavourable linked alleles.

Utilisation of other scented varieties

Another way is to use indica or japonica accessions as donors for aroma. For example, we developed a long-grain aromatic variety using A301 (a japonica scented cultivar of which aroma comes from Della and therefore from Azucena) as donor. An indica variety such as IR 841 also gives good recombinants in cross with japonica and could therefore be used as donor. Also, the use of DH lines can be easily controlled and represents a good tool for choosing directly interesting aromatic recombinants in the progeny. The main question is that we do not know how consumers will appreciate these new varieties. Some studies remain to be carried in order to compare their quality parameters with those of standard scented cultivars.

Abreviations :

CIRAD : Centre de Coopération Internationale en Recherche Agronomique pour le Développement (Centre for International Cooperation in Agronomic Research for Development)
GC : Gas Chromatography
ENSIAA : Ecole Nationale Superieure des Industries Agricoles et Alimentaires
(National Senior School of Agricultural and Food Industries)
IRRI : International Rice Research Institute
ORSTOM : L'Institut Français de Recherche Scientifique pour le Développement en Coopératio(The French Institute for Scientific Research for Development in Cooperation)
RAPD : Random Amplified Polymorphic DNA
RFLP : Restriction Fragment Length Polymorphism
STS : Sequence-Tagged Site

Figure 1

Distribution of 2-acetyl-1-pyrroline concentration in the DH line population coming from the F1 hybrid IR 64 x Azucena. The deviation in favour of non scented lines (AcPy concentration = 0 p.p.b.) is due to strong segregation distortion factor close to Aroma on chromosome 8. Among the scented lines (AcPy concentration > 0 p.p.b.), some lines are intermediate between IR 64 and Azucena, some contain as much AcPy as Azucena and others contain more AcPy than Azucena.

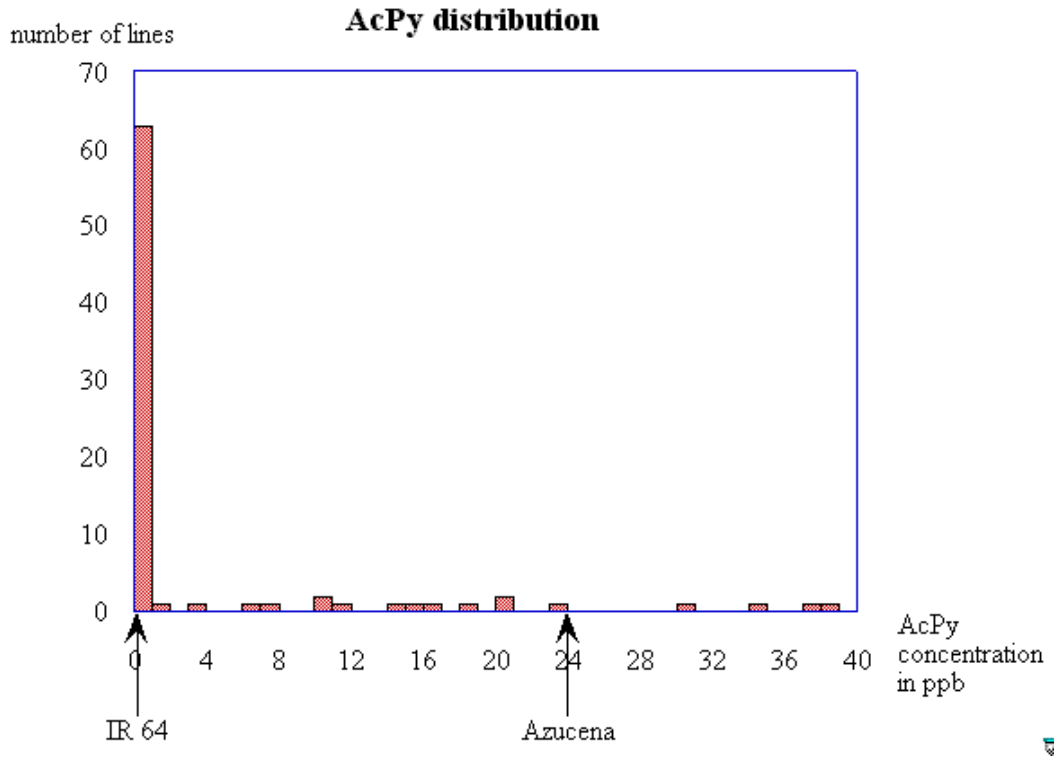


Figure 2

A. Major gene for AcPy presence/absence in rice located on chromosome 8 using the interval mapping (Lander and Botstein, 1989) QTL detection method. B. QTLs on chromosomes 4 and 12 detected using interval mapping on scented

lines only. The LOD score statistic is calculated at each centimorgan (cM) on the linkage group. It is defined as log10 (L1/L0) with L1 = likelihood of observing the data if a QTL is present and L0 = likelihood of observing the data if there is no QTL. For example, LOD = 3 means that L1 = 103 x L0, meaning that the presence of a QTL is highly probable.

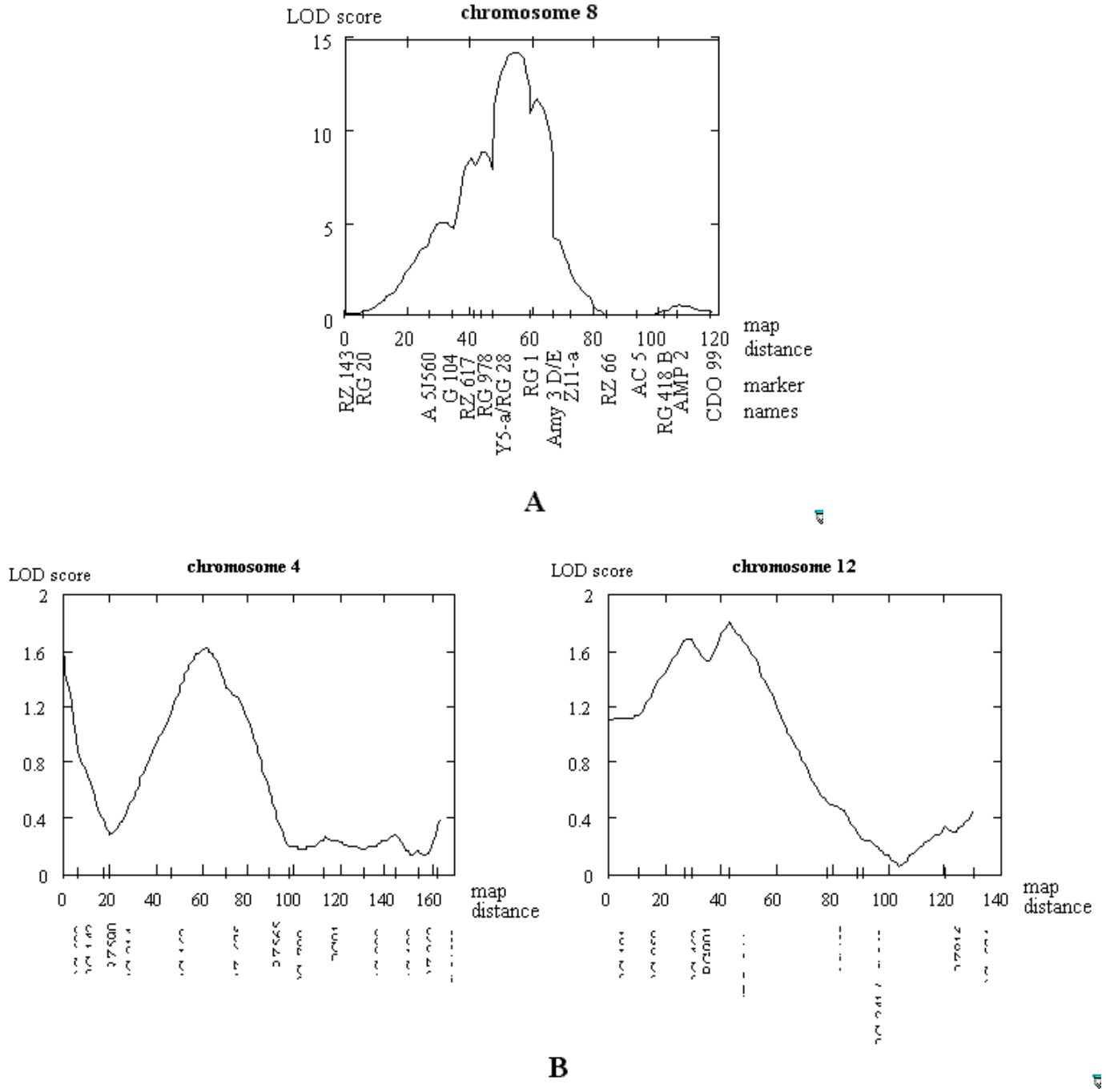
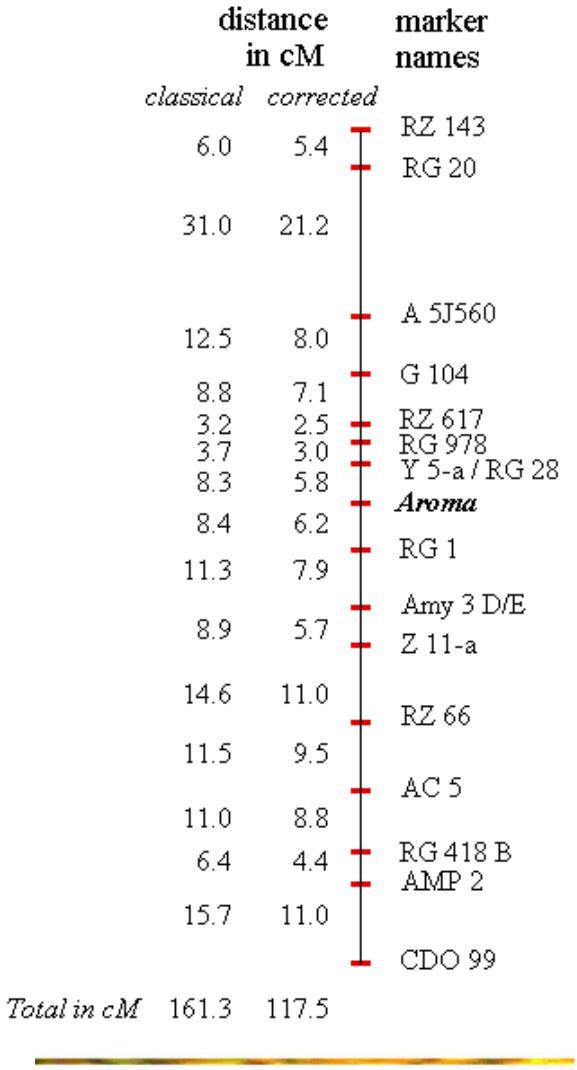


Figure 3.

Location of the rice Aroma/AcPy major gene on the genetic map of chromosome 8. Classical distances and distances corrected for segregation distortion are calculated using the Kosambi's mapping function (Kosambi, 1944). Correction leads to an overall reduction of the chromosome length of about 27 %.



References

Ahn S.N., C.N. Bollich & S.D. Tanksley. 1992. RFLP tagging of a gene for aroma in rice. Theoretical and Applied Genetics 84: 825-828.

Ali S.S., S.J.H. Jafri, M.G. Khan & M.A. Butt. 1993. Inheritance studies for aroma in two aromatic varieties of Pakistan. International Rice Research Notes 18: 6.

Berner D.K. & B.J. Hoff. 1986. Inheritance of scent in american long grain rice. Crop Science 26: 876-878.

Buttery R.G., L.C. Ling, O.B. Juliano & J.G. Turnbaugh. 1983. Cooked rice aroma and 2-acetyl-1-pyrroline. J Agric Food Chem 31: 823-826.

Buttery R.G., J.G. Turnbaugh & L.C. Ling. 1988. Contribution of volatiles to rice aroma. J Agric Food Chem 36: 1006-1009.

Causse M.A., T.M. Fulton, Y.G. Cho, S.N. Ahn, J. Chunwongse, K. Wu, J. Xiao, Z. Yu, P.C. Ronald, S.E. Harrington, G. Second, S.R. McCouch & S.D. Tanksley. 1994. Saturated molecular map of the rice genome based on an interspecific backcross population. Genetics 138: 1251-1274.

Guiderdoni E., E. Galinato, J. Luistro & G. Vergara. 1992. Anther culture of tropical japonica x indica hybrids of rice (Oryza sativa L.). Euphytica 62: 219-224.

Huang N., S.R. McCouch, T. Mew, A. Parco & E. Guiderdoni. 1994. Development of an RFLP map from a doubled haploid population in rice. Rice Genetics Newsletter 11: 134-137.

Inoue T., H.S. Zhong, A. Miyao, I. Ashikawa, L. Monna, S. Fukuoka, N. Miyadera, Y. Nagamura, N. Kurata, T. Sasaki & Y. Minobe. 1994. Sequence-tagged sites (STSs) as standard landmarkers in the rice genome. Theoretical and Applied Genetics 89: 728-734.

Kato T. & T. Itani. 1996. Effects of the gene for scented grain in a rice cultivar BG 1 on agronomic performance. SABRAO Journal 28: 1-9.

Kurata N., Y. Nagamura, K. Yamamoto, Y. Harushima, N. Sue, J. Wu, B.A. Antonio, A. Shomura, T. Shimizu, S.-Y. Lin, T. Inoue, A. Fukuda, T. Shimano, Y. Kuboki, T. Toyama, Y. Miyamoto, T. Kirihara, K. Hayasaka, A. Miyao, L. Monna, H.S. Zhong, Y. Tamura, Z.-X. Wang, T. Momma, Y. Umehara, M. Yano, T. Sasaki & Y. Minobe. 1994. A 300 kilobase interval genetic map of rice including 883 expressed sequences. Nature Genetics 8: 365-372.

Kosambi D.D. 1944. The estimation of map distance from recombination values. Annals of Eugenics 12: 172-175.

Lander E.S. & D. Botstein. 1989. Mapping mendelian factors underlying quantitative traits using RFLP linkage maps. Genetics 121: 185-199.
Lander E.S., P. Green, J. Abrahamson, A. Barlow, M.J. Daly, S.E. Lincoln & L. Newburg. 1987. Mapmaker: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics 1: 174-181.
Lin S.-C. 1990. Rice aroma: methods of evaluation and genetics. Poster présenté à : Second International Rice Genetics Symposium, IRRI, Philippines, 14-18/5/90 783-784.
Lorieux M., B. Goffinet, X. Perrier, D. González de León & C. Lanaud. 1995. Maximum-likelihood models for mapping genetic markers showing segregation distortion. 1. Backcross populations. Theoretical and Applied Genetics 90: 73-80.
Lorieux M., M. Petrov, N. Huang, E. Guiderdoni & A. Ghesquière. 1996. Aroma in rice: genetic analysis of a quantitative trait. Theoretical and Applied Genetics 93: 1145-1151.
Michelmore R.W., I. Paran & R.V. Kesseli. 1991. Identification of markers linked to disease-resistance genes by bulked segregant analysis : a rapid method to detect markers in specific genomic regions by using segregating populations. Proceedings of the National Academy of Sciences of the USA 88: 9828-9832.
Murray M.G. & W.F. Thompson. 1980. Rapid isolation of high molecular weight plant DNA. Nucleic Acids Research 8: 4321-4325.
Nagaraju M., D. Chaudhary & M.J. Balakrishna Rao. 1975. A simple technique to identify scent in rice and inheritance pattern of scent. Current Science 44: 599.
Nardi S. 1997. Caractérisation de l'arôme du riz : optimisation de protocoles d'extraction et d'analyses. Mémoire de fin d'études pour l'obention du Diplôme d'Ingénieur. Ecole Supérieure d'griculture de Purpan (ESAP), Toulouse.
Petrov M., M. Danzart, P. Giampaoli, J. Faure & H. Richard. 1996. Rice aroma analysis.
Pinson S.R.M. 1994. Inheritance of aroma in six rice cultivars. Crop Science 34: 1151-1157.
Raghuram Reddy P. & K. Sathyanarayanaiah. 1980. Inheritance of aroma in rice. Indian Journal of Genetics and Plant Breeding 40: 327-329.
Ragot M., M. Biasiolli, M.F. Delbut, A. Dell'Orco, L. Malgarini, P. Thevenin, J. Vernoy, J. Vivant, R. Zimmermann & G. Gay. 1994. Marker-assisted backcrossing: a practical example. In: "Techniques et utilisations des marqueurs moléculaires". Montpellier, France, 29-31 mars 1994. Ed. INRA, Paris, 1994 (Les Colloques n° 72) p. 45-56.
Schieberle P. 1990. The role of free amino acids present in yeast as precursors of the odorants 2-acetyl-1-pyrroline and 2-acetyltetrahydropyridine in wheat bread crust. Z Lebens Unters Forsch 191: 206-209.
Sood B.C. & E.A. Siddiq. 1978. A rapid technique for scent determination in rice. Indian Journal of Genetics and Plant Breeding 38: 268-271.
Tripathi R.S. & M.J.B.K. Rao. 1979. Inheritance and linkage relationship of scent in rice. Euphytica 28: 319-323.
Yano M., E. Shimosaka, A. Saito & M. Nakagahra. 1992. Linkage analysis of a gene for scent in indica rice variety, Surjamkhi, using restriction fragment length polymorphism markers. Japanese Journal of Breeding 41 (suppl. 1): 338-339.

Figures and tables summary

- Figure 1
- Figure 2, 2b
- Figure 3

Précédente Accueil Remonter Suivante

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Home

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