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Genetic analysis of root traits in maize

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Abstract – In many areas around the world, maize (*Zea Mays* L.) crops are affected by root lodging. Several authors have previously shown that associations of root and shoot traits enabled the prediction of the resistance of genotypes to root lodging. In this preliminary attempt to understand the genetics of these traits, a set of 100 recombinant inbred lines from a cross between élite lines 'F2' (early, susceptible to root lodging) and 'Io' (late, lodging resistant) was considered. This population was characterised for 152 RFLP loci and root system traits in one location and for 2 years. QTLs were mapped using the average over years. Genetic and environmental correlations, together with co-localisation of QTLs for several traits, revealed genetic linkages, and some probable pleiotropic effects, which could be interpreted in terms of within-plant growth competition phenomena. The identification, on chromosome 5, of groups of loci involved in the control of the growth of the root system could help select against root lodging. (© Inra/Elsevier, Paris.)

***Zea mays* L. / root lodging / pleitropic effect / linkage effect / QTL**

Résumé – Analyse génétique des caractères racinaires du maïs. Dans de nombreuses régions du monde, la verse en végétation peut porter préjudice à la rentabilité de la culture de maïs. Plusieurs auteurs ont mis en évidence que des caractéristiques aériennes et racinaires, considérées ensemble, sont déterminantes dans la variation de la résistance. Dans une première approche, les caractères impliqués dans la résistance à la verse sont analysés génétiquement dans un lieu sur deux années, à partir de 100 lignées recombinantes issues du croisement de 'F2' et 'Io'. À l'aide de 152 marqueurs RFLP, les QTL sont recherchés sur la moyenne des deux années. À partir des corrélations génétiques et environnementales ou à partir de la co-localisation des QTL, des linkages et des effets pléiotropiques entre les caractères sont révélés. La mise en évidence, sur le chromosome 5, de groupes de locus impliqués dans la croissance du système racinaire pourrait faciliter la sélection de génotypes résistants à la verse en végétation. (© Inra/Elsevier, Paris.)

***Zea mays* L. / verse en végétation / pléiotropie / linkage / QTL**

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1. INTRODUCTION

Selection for increased root lodging resistance is an important objective of maize (*Zea mays* L.) breeding programmes, since lodging susceptibility can strongly reduce grain or dry matter yield, and the quality of whole-plant harvest. This damage is important in northern temperate regions as well as in the Tropics [24]. The most commonly used criterion for comparing maize genotypes for root lodging resistance is the percentage of lodged plants in field trials. But root lodging occurs very irregularly as it is greatly influenced by wind and rainfall. A large number of environments are therefore necessary to collect discriminant observations.

Many authors have investigated the relationships between root lodging and plant morphological characters, in order to provide prediction tools that would facilitate root lodging resistance evaluation. They demonstrated that root lodging behaviour is linked with several characteristics of the underground part of the stem base of the plant: the visual aspect of the root clump [27, 31], its weight after pulling out [17, 27], the volume of roots [31], the number of roots on the upper internodes [7, 15], the angle of root growth from the stem [5, 11, 15, 26], the diameter of the roots [15, 25], the number of internodes with emerged roots [21], the stalk diameter [20], the length of the base internodes of the plant [15]. It has been observed that the total number of roots is not strongly correlated with the lodging resistance [16]. Guingo and Hébert [14] reported that the strength of the plant anchorage could be explained by the combination of three types of morphological traits of root on upper internodes of the root clump: the average angular root spread, the number of roots and the diameter of roots and, to a lesser extent, the length of the internodes at the base of the plant. The expected lodging behaviour can therefore be predicted by such traits, with consequences on the reduction of the number of observation sites, since no lodging event would be required. Even if it would be desirable to study the correlations with actual lodging field observations, the major role, now clearly demonstrated, that the architecture of the roots plays in lodging resistance makes it quite relevant to study the genetic determinism of the root traits themselves. It would greatly help to derive lodging resistant varieties, combining several optimum characteristics for the standability of the plant, whatever the climatic conditions.

The variations in earliness and biomass production must be taken into account because the length of growth cycle and the aerial development have determining effects on the potential of root development. In temperate regions, it is usually considered that late material has a higher root growth potential, compared with early material [15, 29]. It is not always the case, particularly in tropical areas where some materials exhibit poor root anchorage [11] and are prone to severe lodging when crop density is increased.

The objective of this study is to describe the genetic relationships between the main factors involved in root lodging, and to evaluate the amount of genetic variability in the root traits that depends on earliness and biomass yield. The genetic determinism and relationships are analysed through genetic and environmental correlations and a preliminary attempt to identify quantitative trait loci (QTLs) involved in the variation of those traits.

2. MATERIALS AND METHODS

2.1. Genetic materials

Recombinant inbred lines (RILs) were derived from the cross between élite lines 'F2' and 'Io' up to the F6 generation, following a single seed descent (SSD) procedure at Inra-Le Moulon. These lines have been described by Causse et al. [3]. Considerable differences in earliness and root lodging susceptibility were observed between the parent lines, thus suggesting that genetic variation in root traits and earliness were likely to occur in the offspring.

Because of the extensive number of potential root observations, only 100 lines were chosen at random from this population, and crossed with 'F252', an early dent line considered as a tester, in order to fit the hybrid genetic structure of maize varieties. For simplification, the hybrids between the tester and the RILs and the par-

ents are further referred to as RILs and parents, respectively.

A linkage map was created by using 152 RFLP markers at Inra Le Moulon (France) as described by Causse et al. [3].

2.2. Field experiments

Field experiments were conducted in 1995 and 1996, at Lusignan (France, 46° 26'N, O°7'E, 145 m elevation). Each year, the 100 RILs together with both parents were arranged in a 13 × 8 alpha-lattice design with three replicates. The parents were observed twice each year. Each elementary plot was a single row, 5.2 m long. Plots were 0.80 m apart. Crop density was 90 000 plants per hectare.

2.3. Observations

The plants were studied after the silking of all the genotypes in order to describe the root system when completely developed [30]. Five plants per plot were uprooted with a spade after irrigation to limitate root breakage. Adherent soil was washed away in running water to allow root counting and measuring.

The root system-related traits studied were:

- the number of roots on internodes 6, 7, 8 (RI6, RI7, RI8), according to the description principles from Girardin et al. [13];
- the average angle of root growth direction at internode 7 (Angle7) with reference to vertical. The scores ranged from 0 (vertical roots) to 90° (horizontal roots) by step of 5°;
- the mean of the diameters of five roots on internode 7 (Droot7), measured at 5 mm from the stem (in millimetres);
- the length and maximum diameter (in the median part) of internode 8 in millimetres (LI8 and DI8, respectively).

In order to describe the genetic relationships between root lodging-associated traits on the one hand, and earliness and biomass production on the other, the date of mid-silking and the biomass production were estimated. The mid-silking date was recorded by counting the number of days after July 1st, and the biomass production was estimated by harvesting the plots at silage stage, measuring the whole-plant dry matter (DM) content, and computing the equivalent DM production per hectare.

2.4. Data analyses

Preliminary analyses of variance were performed in order to check the consistency of agronomic data and to estimate the magnitude of genotype by year interactions. Pooled data from the two experiments (1995 and 1996) were used for the quantitative analysis. A mixed model with random genetic effect was used; all other effects (years, replicates and blocks) were considered fixed, since their variances could not be correctly estimated, due to insufficient numbers of levels. The genetic variances σ^2_g of the traits, the covariances σ_{gg}, between two traits as well as the error variance σ^2_e were estimated with a restricted maximum likelihood procedure, using Select software package [12]. Broad sense plot heritabilities were estimated as $\hat{h}^2 = \hat{\sigma}^2_g / \hat{\sigma}^2_p$ where $\hat{\sigma}^2_p = \hat{\sigma}^2_g + \hat{\sigma}^2_e$, the sum of the estimated values of σ^2_g and σ^2_e. Genetic and environmental correlations were computed from the variances and covariances parameters.

2.5. Marker–trait associations

Analyses were performed on the entry means of the RILs over the two experiments, adjusted for sub-block effects. QTL mapping was performed according to the method of simple interval mapping described by Lander and Botstein [19], using PLABQTL computer package [28]. A LOD threshold of 2 was considered, yielding an individual type I risk of 0.35 % and an experiment-wise risk of 10 %, suitable for the biological interpretation of QTLs and linkage patterns. These risks were considered as a correct compromise between type I risk and power, for this preliminary attempt to identify QTLs for root traits.

The percentage of phenotypic variation R^2_p ascribed to an individual QTL was estimated at its most likely position (peak of the LOD statistics in the corresponding region). The QTLs detected and their positions were used for a simultaneous multiple regression to obtain final estimates of additive effects. The amount of total phenotypic variance (R^2_{pt}) explained by all QTLs detected for a given trait was then estimated. The percentage of genetic variation R^2_{gt} explained by all putative QTLs was estimated as R^2_{pt} / h^2.

The additive effects of the QTLs were estimated as half the differences between the genotypic values of the two homozygotes. They were computed using the convention that 'Io' carries the allele increasing the value of the trait studied. It enables us to know how each parent line contributes to the effect of the QTL observed.

3. RESULTS

3.1. Variations in traits among RILs

Broad-sense heritabilities at the plot level were relatively high for most of the traits *(table I)*. In the case of Angle7, the heritability was low because of the high error variance.

The mean values of both parents are presented in *table II*. 'Io' had more roots on internode 8, a lower root diameter, and a shorter internode 8 than 'F2'. In addition, 'Io' was later and yielded more than 'F2'. Transgressive segregation in both directions was observed for some traits (LI8, RI7 and Angle7), since the highest and lowest values among RILs fall outside the parent range *(table II)*. The transgressive segregation was only negative for DI8 and BMYield, and only positive for RI6. For mid-silking date, RI8 and Droot7, the segregation was not transgressive.

For all traits, the means values of the RILs did not appear significantly different from parent mean values as shown by the T-tests of the contrasts between parent means and RIL means.

3.2. Correlations among traits

High (in absolute value) genetic and high environmental correlations were simultaneously observed between some of the traits of the root clump: LI8, RI6 and RI7 were positively correlated to one another, DI8 was positively correlated with Droot7, and RI8 was negatively correlated with LI8 and RI7 *(table III)*.

Table I. Variances and heritability of agronomic characters among F2 × Io RILs.

Traits	$\hat{h}^2$ [a]	var $(\hat{h}^2)$ [b]	$\hat{\sigma}^2_g$ [c]	var $(\hat{\sigma}^2_g)$ [d]	$\hat{\sigma}^2_e$ [e]	var $(\hat{\sigma}^2_e)$ [f]
Number of root on internode 6 (RI6)	0.56	0.0019	0.45	0.0055	0.36	0.0001
Number of root on internode 7 (RI7)	0.56	0.0019	0.76	0.0154	0.61	0.0016
Number of root on internode 8 (RI8)	0.62	0.0016	8.22	1.6981	5.14	0.1168
Direction of roots at internode 7 (Angle7)	0.32	0.0020	4.51	0.7958	9.69	0.4124
Root diameter of internode 7 (Droot7)	0.60	0.0017	0.14	0.0005	0.09	0.0001
Length of internode 8 (LI8)	0.67	0.0014	170.90	70.0487	83.96	31.128
Diameter of internode 8 (DI8)	0.52	0.0020	0.72	0.0142	0.66	0.0019
Days to mid-silking (Flo)	0.59	0.0017	1.81	0.0844	1.24	0.0068
Biomass Yield (BMYield)	0.43	0.0021	1.16	0.0330	1.53	0.0104

[a] Estimated broad-sense plot heritability; [b] variance of the estimated heritability; [c] estimated genetic variance; [d] estimated variance of genetic variance; [e] environmental variance; [f] variance of environmental variance.

On the contrary, some traits exhibited high genetic correlations and low environmental associations: Angle7 was positively correlated with DI8, LI8, RI7 and Droot7; RI8 was negatively correlated with Angle7, RI6 and Droot7.

The correlations between the root clump traits and the mid-silking date were in general low. In absolute value, they were lower than 0.30. The genetic correlations between the root traits and the biomass production were low for the root counts, but moderate and positive for the other traits. The environmental correlations were null.

3.3. Identification of QTLs

Significant effects of chromosomal regions were found for the variation in all traits *(table IV)*. The

Table II. Performances of parents, and minimum, maximum and mean performances of recombinant inbreds for traits implicated in root lodging, mid-silking date (days after July 1st) and biomass yield at silage stage.

Traits	Parents			Recombinant inbreds				Par - RIL[b]	Transg. segreg.[c]
	F2	Io	CI[a]	Min	Mean	Max	CIa		
RI6	4.10	4.94	± 0.42	3.24	4.39	6.84	± 0.49	0.130 ns	+
RI7	8.41	8.12	± 0.54	6.27	8.29	10.94	± 0.62	–0.025 ns	+/–
RI8	3.39	11.99	± 1.58	0.01	7.51	11.85	± 1.87	0.180 ns	/
Angle7	40.68	42.74	± 2.23	35.80	42.36	48.23	± 2.57	–0.650 ns	+/–
Droot7	6.78	5.77	± 0.21	5.38	6.11	7.04	± 0.24	0.165 ns	/
LI8	70.77	48.52	± 5.97	27.34	55.70	107.93	± 6.84	3.945 ns	+/–
DI8	20.02	20.19	± 0.58	17.76	19.86	22.25	± 0.67	0.245 ns	–
Flo	15.41	21.32	± 0.73	15.58	18.67	22.62	± 0.84	0.305 ns	/
BMYield	12.37	15.57	± 0.89	8.20	12.94	15.30	± 1.08	1.028 ns	–

[a] Confidence intervals indicated at the 0.05 probability level.
[b] T-tests of contrasts between parent means and RIL means indicated at the 0.05 probability level.
[c] Transgressions marked as positive (+), negative (–) or not detected (/).

Table III. Environmental and genetic correlations between mid-silking date and morphological traits. The genetic correlations are below diagonal.

	RI6	RI7	RI8	Angle7	Droot7	LI8	DI8	Flo	BMYield
RI6	—	0.46	–0.28	0.07	0.14	0.59	0.35	–0.02	–0.01
RI7	0.74	—	–0.43	0.16	0.11	0.77	0.27	–0.17	0.06
RI8	–0.58	–0.65	—	–0.10	–0.01	–0.80	–0.31	0.30	–0.07
Angle7	0.29	0.46	–0.58	—	0.18	0.58	0.50	0.09	–0.02
Droot7	0.03	0.01	–0.39	0.53	—	0.33	0.45	0.04	0.06
LI8	0.38	0.41	–0.44	0.09	0.22	—	0.18	–0.25	0.04
DI8	0.25	0.27	0.05	0.12	0.42	0.37	—	0.12	–0.02
Flo	–0.01	0.00	0.13	–0.07	–0.10	–0.07	–0.05	—	0.01
BMYield	0.01	0.01	0.13	0.41	0.47	0.25	0.40	0.39	—

QTL map obtained is presented in *figure 1*. The number of QTLs detected for a given trait varied from 1 to 5. Except for Droot7, only one QTL displayed a significant effect for each of the root traits (RI6, RI7, RI8 and Angle7), whereas more than one was detected each for flowering date and the stem traits (LI8 and DI8).

The phenotypic determination coefficients of single QTL (R^2_p) ranged from 8.2 to 21.6 % *(table IV)*. The highest and lowest genotypic determination coefficients (R^2_{gt}) associated with all the detected QTLs for a trait were observed for DI8 (87.6 %) and RI7 (20.8 %) respectively *(table IV)*.

At least one QTL was detected on chromosome 5 for all of the root clump traits, except RI6. Even though the lengths of the support intervals of these QTLs were rather large, their most likely positions were near 114 cM *(table IV)*. Additional QTLs were detected for these traits on chromosome 2 (Droot7 and LI8), chromosome 4 (DI8, LI8 and Droot7), and chromosome 7 (DI8). Their effects were of various magnitudes, and in some cases, as large as those of QTLs on chromosome 5 *(table IV)*.

Three chromosomal regions were found associated with the date of mid-silking, two on chromosome 1 and one on chromosome 10 *(figure 1)*. Two QTLs of the biomass yield were found on chromosomes 4 and 8, accounting for almost 52 % of the genetic variation of this trait.

The regression analysis identified positive and negative effects of the alleles of a given parent in the majority of the traits, including BMYield. For the date of mid-silking, however, all alleles with a negative effect on silking time came from the early parent. On chromosome 5, 'Io' alleles were associated with increased values of Angle7, RI7, LI8, Droot7 and DI8, and a decreased value for RI8.

Table IV. Locations of QTLs implicated in root morphological traits, mid-silking date and biomass yield in recombinant inbred lines. It is assumed that 'Io' carried the favourable allele for the trait under study. Confidence intervals of are presented at the 0.05 probability levels.

Traits	Chr.[a]	Maximum lod-score	Position[b]	Support interval (cM)	Estimated effect	R^2_p	R^2_{gt}
RI6	3	3.10	112	102–120	0.344	14.4	26.1 ± 11.8
RI7	5	2.75	114	102–124	0.394	11.5	20.8 ± 10.9
RI8	5	3.62	108	74–122	–1.398	17.6	28.9 ± 11.3
Angle7	5	2.95	114	102–132	1.068	14.0	43.6 ± 20.1
Droot7	2	3.75	6	4–12	–0.164	16.2	
	4	2.01	66	42–92	–0.145	8.6	54.5 ± 12.8
	5	3.19	160	150–178	0.176	13.0	
DI8	4	3.12	56	34–78	–0.360	12.9	
	4	3.33	210	152–234	–0.728	20.3	
	5	2.30	54	46–64	0.304	9.7	87.6 ± 14.1
	5	3.98	132	112–140	0.482	15.8	
	7	2.78	24	14–42	–0.385	13.2	
LI8	2	2.08	86	80–108	–4.277	9.0	
	4	2.31	84	76–98	–4.647	9.8	48.6 ± 11.5
	5	5.81	114	102–120	7.976	21.6	
Days to	1	5.48	80	66–84	0.690	20.5	
mid-silking	1	2.36	152	140–164	0.536	10.0	51.3 ± 12.8
	10	2.41	86	86–94	0.540	10.3	
Biomass	4	3.88	132	120–152	–0.479	12.9	51.9 ± 17.1
Yield	8	2.68	158	136–178	0.591	8.2	

[a] Chromosome; [b] position of maximum lod-score (cM).

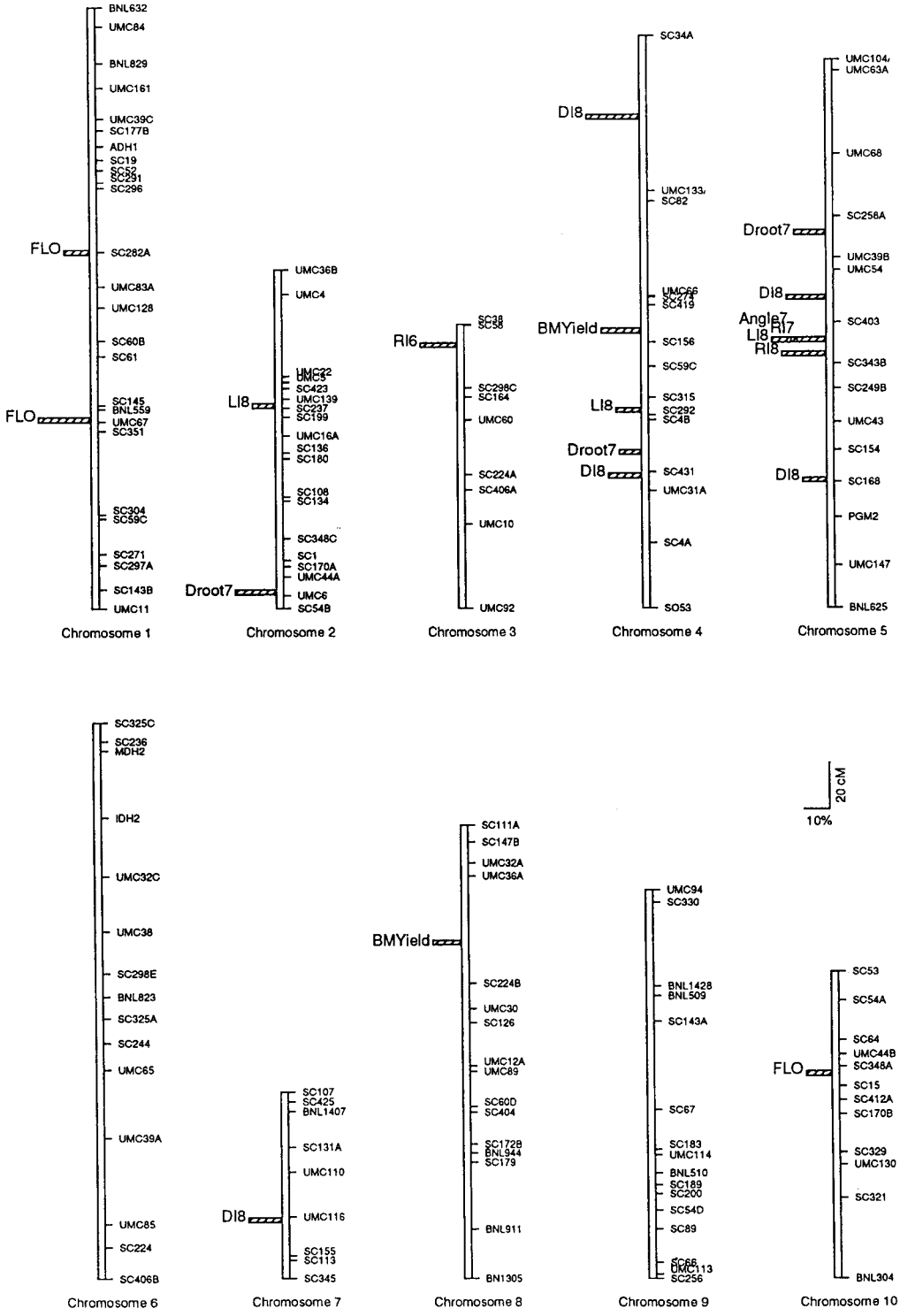

Figure 1. Chromosomal location of QTLs for agronomic traits in the recombinant inbred population. The bars are drawn at the most likely location of the QTLs, where the lod-score is maximum; their sizes represent the amount of phenotypic variation accounted for by a single locus.

4. DISCUSSION

4.1. Relationships between traits

The genetic correlations among traits revealed that numerous roots on internode 8 tend to be associated with a short and large internode, a low number of roots on internodes 6 and 7, thin roots and a narrow root spread. Genetic linkage between RI8, Angle7 and Droot7 could be suspected from the high genetic correlations and the low environmental correlations observed.

These results seem to contradict previous studies [11, 14, 15, 20] which have reported a high number of thick, elongated and branched roots on the upper internodes, together with wide root angles, in lodging-resistant materials. Obviously, the material we used here may be far from the above-mentioned morphological type of plant, and various correlation structures are likely to arise from different genetic materials.

The genetic and environmental correlations observed suggest the presence of groups of linked genes, and/or pleiotropic effects affecting the variation of the root clump. Even if no precise information is available on the actual regulations taking place among these traits, it can be hypothesised that these relationships are the result of a general development and growth process, governed by the quantity of available nutrients or hormones linking roots to the shoot. Growth regulations and competition for available nutrients and photosynthesis products could take place, and thus make possible different resource allocation patterns between the root and stem. Given that roots emerge on one internode after the previous one is completed [22], high associations of the potential of root emergence on the last two internodes could be expected, as the expression of the growth potential permitted by environmental factors.

4.2. QTL detection and genetic determinism

The number of detected QTLs varied among the traits, and, in some cases, the residual part of the variation can consequently remain rather important. That number cannot be related to differences in heritabilities, since these are very similar (except for Angle7). Different numbers of QTLs are likely to arise from the low power of detection of small-effect loci (see for instance [4]. This is particularly the case in our experiments since we used a relatively low number of entries. When the number of lines studied is not very large, sampling variations can also significantly affect QTL detection. In addition, the simple interval mapping method could also account for such a low number of detected loci. It must also be considered that the environments and the unique population studied are responsible for the QTLs detected, because the genotype $\times$ environment interaction could not be partitioned from the genotypic variation.

Nevertheless, our results could indicate that root numbers on internodes 6, 7 and 8 have a more complex determinism than other traits (i.e., numerous loci with small effects or epistatic relationships between loci).

Although QTLs were identified at several positions, several high-effect loci involved in the variation of different root traits were found on chromosomes 4 and 5. In addition, their assumed locations were often found to be very close to one another. Estimated effects at this position were consistent with correlations among traits. The directions of the correlations are corroborated by the effects of the alleles of the QTLs. Opposite effects from the same parent were found for QTLs of negatively correlated traits on chromosome 5 (e.g., RI8 and other traits). Simultaneously favourable effects were found in the case of positive correlations (e.g., RI7 and Angle7). This region may be involved in the control of the development and growth effects described previously. It apparently affects the differentiation of internode 8 and resources allocation between this internode and the previous one. In this context, the Io allele appears favourable to a long and thick internode with few roots.

The transgressive segregations reported for RI6, RI7, Angle7, LI8 and DI8 can be interpreted as both parents contributing positive and negative alleles for those traits. Nevertheless, such conclu-

sions were not always corroborated by the estimates of additive values for the QTL detected, except for LI8 *(table IV)*. The low number of QTLs generally detected in our experiments could explain this apparent contradiction. Concerning RI8 and its QTL on chromosome 5, an allele with positive effect came from F2, the parent that had the fewer roots on internode 8. Thus, this QTL is likely to potentially contribute to the observed transgressive segregation in this population.

The QTLs found for silking date and biomass yield corroborate the correlations observed. The very low correlations between flowering dates and root measurements are attested by the absence of co-localisations of the QTLs found *(figure 1)*. On the contrary, the genetic correlations observed between biomass yield and roots are coherent with the presence of a QTL of biomass on chromosome 4. The directions of the additive effects of the alleles at the QTLs on this chromosome account for the positive correlations observed.

The regions implicated in silking date have similar locations to those found by other authors on different genetic materials: the most consistent QTL of sowing–silking interval found by Koester et al. [18] was on chromosome 1 in the vicinity of marker BNL5.59; Austin and Lee [2] have also identified a QTL of silk emergence of chromosomes 1 and 10; Ribaut et al. [23] have found two QTLs of anthesis–silking interval on chromosome 1, and one QTL on chromosome 10, in locations very similar to ours. In addition, our findings seem to be quite consistent with the more detailed investigation of earliness made by [5] et al. (submitted). As far as yield is concerned, the other works, mainly concerning grain yield, show a wide diversity of results according to the genetic material used and the environmental conditions [1, 9, 23]. In some of these publications, QTLs have already been found on chromosomes 4 and 8.

4.3. Consequences in breeding

Although further investigations will be required to verify the consistency of these results, this work has several consequences from a practical point of view. The identification of a small number of sufficiently strong QTLs for the characteristics of maize root system will allow more efficient breeding, especially when screening well-rooted genitors in early genetic backgrounds where the variability of the root system is narrow. Actually, the strong-effect QTLs we have detected, even though not very precisely located, could be a very powerful tool to predict the morphology of the root system of progenies, without lodging scoring, which strongly depends on uncertain climatic events. Chromosome 5 appears very interesting due to its grouping of several major loci. Marker-assisted selection would allow us to gather positive alleles of traits such as root numbers on upper internodes. This point is particularly important since several studies have confirmed the characteristics that the root system of strongly lodging-resistant maize genotypes should have [8, 14, 15, 21]. Nevertheless, the high magnitude of residual genetic effects (undetectable loci) will make it necessary either to investigate further into the field of low-effect QTLs, or to associate classical techniques in the evaluation of advanced breeding generations.

No significant correlations were found between root traits and silking dates. It was confirmed by QTL localisation, attesting that no strong genetic association existed between root system morphology and earliness in our material. This is an advantage for selection against root lodging. On the contrary, limited, but significant, correlations have been observed between biomass yield and root size and shape characteristics. One QTL on chromosome 4 corroborated these genetic associations. The general meaning of this finding is that any attempt to increase root development will have something to do with the whole plant growth: a significant part of the genetic progress in root number and size partly lies in the use of genetic material with greater growth capabilities. It tends to confirm the early-variety breeders' general feeling. But the relationship is not that close, and the genetic variability of the root system can be used to improve the material through the selection of stronger root architectures, without reducing the harvestable biomass production potential.

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