GENETIC DISSECTION OF MATURITY USING RFLPs

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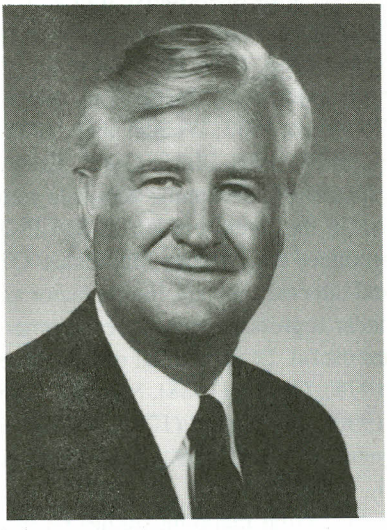
Introduction

Maturity is one of the major adaptability traits in maize. This is true if the objective is to adapt elite genotypes to different latitudes as well as when breeders attempt to incorporate exotic germplasm into their programs. Since the heritability of maturity is relatively high, the trait per se can be easily manipulated. However, it is much more difficult to select genotypes with high yield and early maturity because of the negative correlation between the traits due to linkage or pleiotropy (Troyer and Larkins, 1985; Troyer and Openhsaw, 1987).

Maturity in maize can be measured as days from planting to anthesis, days from planting to silk emergence, days from planting to physiological maturity of the kernel, and percent grain moisture at harvest. All of these traits have agronomic implications and are usually correlated with other traits such as grain yield. Understanding the molecular and genetic basis of maturity in maize would facilitate our efforts to adapt genotypes to diverse environments while maximizing yield potential.



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Estimates of heritability for maturity vary (Giesbrecht, 1960a; Bonaparte et al., 1976), but the best estimates range from 0.50 to 0.75. Parental crosses and different environments and statistical methods employed were probably factors leading to divergent heritability estimates. In general, selection is effective for flowering date in maize (Hallauer, 1965) also indi-

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cating a relatively high heritability for maturity. The high heritability should make the genetic dissection of this quantitative trait more feasible than for many other traits of low heritability.

Using classical gene number estimation methods, two to nineteen genetic factors have been reported as influencing flowering date (Yang, 1949; Abgle, 1954; Zoebisch, 1950; Hallauer, 1965). However, most commonly 4 to 6 genes are reported differentiating two parents relative to maturity (Mohamed, 1959; Bonaparte, 1977; Giesbrecht, 1960a, Agble, 1954; Chase and Nanda, 1967). Genes with major effects for earlier maturity have been reported (Brawn, 1968). Estimates of level of dominance for earliness range from partial dominance (Giesbrecht, 1960b) to overdominance (Rood and Major, 1981).

Earliness is correlated with lower leaf number and shorter plant height (Brown, 1968; Chase and Nanda, 1967; Bonaparte, 1977). Genetic correlations of early flowering with shorter plant height and lower ear height were $r = 0.62$ and $r = 0.59$, respectively (Stuber et al., 1966).

Mapped molecular markers such as for isozyme loci, RAPDs (Random Amplified Polymorphic DNAs), and RFLPs (Restriction Fragment Length Polymorphisms) now provide the geneticist/breeder with a powerful approach for investigating the inheritance of multigenically inherited traits and for locating and manipulating quantitative trait loci (QTLs) associated with these traits (Soller and Beckmann, 1983; Tanskley, 1983; Helentjaris et al., 1985; Edwards et al., 1987; Stuber 1988, 1989; Paterson et al., 1988, 1990, 1991). Molecular marker loci have been extensively mapped in maize (Goodman and Stuber, 1983; Stuber and Goodman, 1983; Wendel et al., 1988; Helentjaris et al., 1985, 1986, 1987; Burr et al., 1988; 1991 Maize Genet. Coop. News Lett.). Considerable effort has been expended to determine adequate statistical analyses and experimental designs to use in the interpretation of RFLP-QTL data. Lander and Botstein (1989) have produced the program Mapmaker-QTL which uses maximum likelihood methods and interval analysis. Single factor analysis of variance (Edwards et al., 1987) and linear regression techniques (Romero-Severson et al., 1989; Cowen, 1989) also are useful. Experimental design issues have been addressed by Soller and Genizi (1978), Cowen (1988), Simpson (1989), Knapp and Bridges (1990), Knapp et al. (1990), and Knapp (1991). QTLs with siginificant expression for more than 80 quantitative traits have been identified in maize (Bateman et al., 1986; Edwards et al., 1987; Stuber et al., 1987).

Molecular mapping studies on maturity in maize are limited. Several isozyme loci are linked to a number of QTLs associated with silking date in the cross of Co159 × Tx303 (Edwards et al., 1987). Factors contributed by Gaspe flint which control plant height and maturity have been localized to chromosomes 3, 8 and 10 (Koester et al., 1991). Using principal component regression analysis of adjusted means vs. RFLP variant frequencies, Godshalk et al. (1990) found 16 variants associated with genes controlling grain moisture. Localization of genes using molecular markers provides information about their map position but implies

nothing about their function, biochemical nature, or tissue of expression. Our ultimate goal is to clone genes controlling maturity in order to better understand flowering in maize as well as to learn more about the nature of quantitative inheritance.

The studies reported herein attempt to genetically dissect the trait early maturity by identifying genomic regions with major effects on maturity and maturity-correlated plant height traits.

Approach and Discussion

We have utilized F_2 and F_3 populations (Lander and Botstein, 1989; Edwards et al., 1987) as well as backcross-derived lines (BDLs) at the University of Minnesota (Kaeppler, Kim and Phillips, in preparation) to map loci controlling maturity in maize (Kim et al., 1990, 1991). Analysis of backcross derived lines allows screening of many different genotypes using a relatively small number of samples. RFLP genotyping of as few as three genotypes—donor parent, recurrent parent, and backcross derived line—allows the detection of linkage between the marker locus and the trait. This method takes advantage of the low probability of donor parent DNA being present in derived lines, especially those produced by high numbers of backcrosses. We have outlined the statistical method for utilizing backcross derived line data to map quantitative trait loci (Phillips et al., 1991). The idea of crossing an early maturing inbred with a late elite line followed by multiple backcrosses to the late parent while selecting only for earliness was proposed by Shaver (1976) as a means to recover lines with major genes for early flowering.

Table 1 lists the genotypes examined to date. The lines listed were screened with 164 Pstl genomic probes from the University of Missouri-Columbia, Brookhaven National Laboratory, and Native Plants Inc. using the restriction enzymes Hind III, EcoRI, and EcoRV. The number of informative (polymorphic) probes depended upon the individual genotypic combination.

Table 2 provides a summary of the markers we have identified to date as putatively linked to maturity loci using mostly the BDL method. Quantitative loci (QTLs) for maturity were found on seven of the ten chromosomes. Chromosomes five and eight have regions important across a number of genetic backgrounds. We have a substantial amount of information about the UMC12 region on the long arm of chromosome 8.

The UMC12 region of chromosome 8 is interesting for two reason: 1) this region is associated with maturity in a number of diverse genetic backgrounds; 2) we have identified a QTL in this region that has a large effect on maturity, using several types of analysis on several populations. When comparing chromosomes from a number of backcross-derived lines we find the UMC12 region on chromosome 8 inherited from the early donor parent to be common in a number of early maturity derivatives (Figure 1). Analysis of 164 F_2 plants from A662 $\times$ B73 also showed this region to be highly significant; see analysis using Mapmaker QTL

TABLE 1—Genotypes Used in Mapping Studies.

Genotype	Pedigree	DTP
A662	Minn. Synthetic-AS-A	74
B73	BSSS C_5	92
A679	(A662 × B73) $B73^3$	84
A680	(A662 × B73) $B73^3$	86
A681	(A662 × B73) $B73^3$	85
Gaspe	Canadian flint	51
N28	Nebraska SSS	98
N28E	(Gaspe × N28) $N28^{20}$	87
Oh43	Oh40 × W8	88
Oh43E	(Gaspe × Oh43) $Oh43^{10}$	79
Mo17	Cl187-2 × C103	91
Mo17E	(Gaspe × Mo17) $Mo17^8$	86
A632	(Mt42 × B14) $B14^3$	86
A632E	(Wf9E × A632) $A632^{10}$	80
CM105	(CMV3 × B14) B14	82
CM105E	(A632E × CM105) $CM105^6$	78
A634	(Mt42 × B14) $B14^3$	87
A634E	(A632E × A634) $A634^6$	79
A619	(A171 × Oh43) Oh43	86
A619E	(A632E × A619) $A619^8$	83
C123	C103 derivative	87
C123E	(A632E × C123) $C123^{11}$	85

Superscript indicates number of backcrosses
DTP = days from planting to 50% pollen shed
E = early maturity

(Figure 2). Finally, in the analysis of N28 × N28E and A679 × B73 F_2, UMC12 has been found to be associated with a large proportion of the phenotypic variation (Table 3). The difference between the means of the homozygous UMC12 genotypes was 7.5 and 4.4 days in the two populations, respectively. This is considered a substantial difference in maturity. Having identified genetic materials where 50% of the variation is associated with a specific molecular marker offers exciting opportunities for the cloning of a QTL.

The N28, N28E combination of lines is very useful because of the large number of backcrosses (20), followed by selfing, used in deriving N28E. In unlinked regions, these lines should differ only by $(1/2)^{21}$ or about 1 in a million. The region around the selected maturity factor is theoretically estimated to be about 9 cM after 20 backcrosses (Hanson, 1959; Naveira and Barbadilla, 1992). Only two of 82 informative probes (ie. ones detecting a polymorphism between the original parents, N28 and Gaspe Flint) detected the donor parent (Gaspe) allele in N28E. One of these, UMC 84, on chromosome one, showed no association with maturity in an analysis of N28 × N28E F_2s. We also did not detect linkage between UMC84 and days to pollen shed or silking in the (A662 × B73) F_3 per se evaluation (Table 4). However, our A662 × B73 testcross data (Table 5) indicated an association of UMC84 and days to pollen shed and silking. UMC12,

TABLE 2—Markers Putatively Linked to Loci Controlling Maturity Measured as Days from Planting to 50% Pollen Shed.

Chromosome	Marker (Position)	Early Parent	Late Parent	Method of Analysis
1	UMC11 (41)	A632E	A619	BDL*
	NPI234 (57)	Gaspe	Mo17	BDL
2	UMC139 (117)	A662	B73	BDL
3	UMC16 (134)	A662	B73	A662 × B73 (F_2)
5	BNL6.25 (1)	Gaspe	C123	BDL
	UMC90 (39)	A632E	A634	BDL
	UMC27 (49)	Gaspe	Oh43	BDL
		A632E	CM105	BDL
		Gaspe	B73	Gaspe × B73 (F_3)
	BNL6.22 (68)	Gaspe	C123	BDL
	UMC40 (76)	Gaspe	Mo17	BDL
	BNL5.71 (92)	A632E	A634	BDL
		A632E	H100	BDL
	BNL5.40 (115)	Gaspe	C123	BDL
	UMC54 (119)	A632E	CM105	BDL
		A662	B73	A662 × B73 (F_2, F_3)
	UMC51 (123)	A632E	A634	BDL
7	BNL15.21 (46)	Gaspe	Oh43	BDL, Oh43 × Oh43E (F_2, F_3)
	UMC35 (128)	Gaspe	C123	BDL
8	UMC124 (53)	Gaspe	C123	BDL
	UMC12 (94)	A662	B73	BDL, A662 × B73 (F_2, F_3), A679 × B73 (F_2)
		Gaspe	N28	BDL, N28 × N28E (F_2, F_3)
9	UMC113 (14)	A632E	H100	BDL
	UMC114 (50)	A632E	A634	BDL

Information from analysis of backcross-derived lines
F_2, F_3—Information from analysis of F_2 or F_3 populations derived from given parents.

the other marker having a donor parent allele in N28E, has a clear association with maturity. The effect of the region was completely additive (Table 3), i.e. the mean maturity of heterozygous marker genotypes was almost exactly midway between the two homozygous marker genotypes. However, perhaps the most important result is that F_3 families, produced from N28 × N28E F_2s, were found in a 1:2:1 ratio of homogeneous early, segregating, or homogeneous late. In essence, we have isolated a region controlling a trait with definite quantitative inheritance into a uniform background, N28. In doing so, one region now shows a nearly Mendelian type of inheritance and is marked by UMC12.

N28 and N28E should differ genetically by only one-millionth except in the selected region(s). The RFLP probing done thus far supports the similarity of these lines. Deviations in morphological development might give some indication of the latest time at which the chromosome 8 QTL acts. Previous measurements we have made show that N28E is 35 cm shorter than N28 (120 vs 155 cm) and that N28E has 2 fewer leaves than N28 (12 vs 14); plant height and leaf number are commonly correlated with maturity in maize. Aside from the differences in

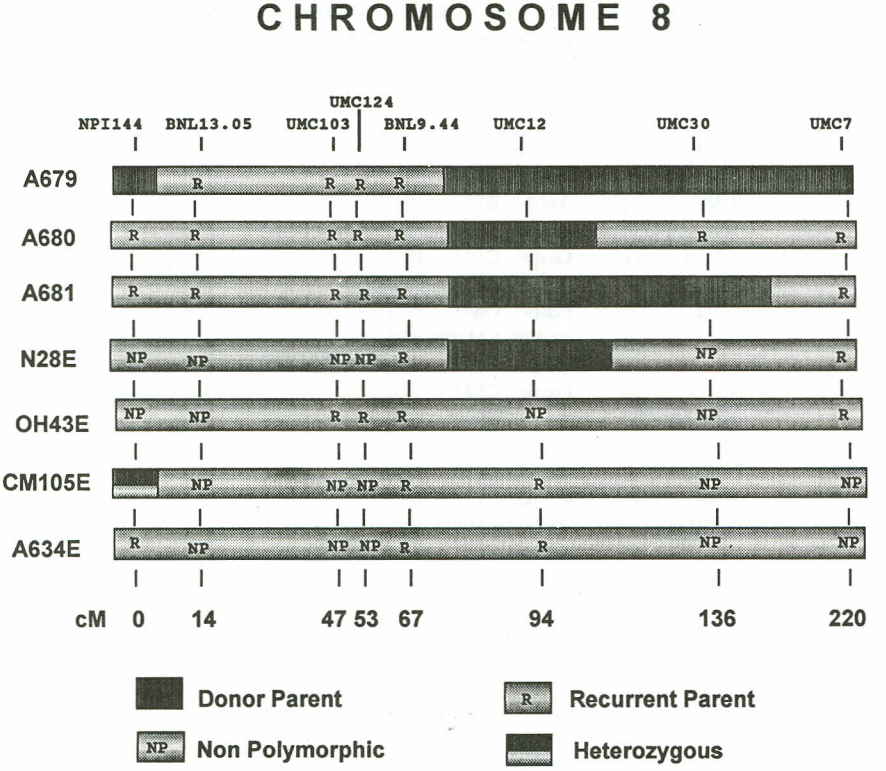

Figure 1. Chromosome 8 markers significantly associated with days to pollen shed from several BDL's.

maturity, plant height, and leaf number, these two lines look identical upon visual inspection. We know that by 40 days after planting, N28E is well into tassel formation whereas N28 has no visible immature tassel. We also know that Gaspe Flint has visibly initiated the tassel primordium by the fifth day of germination (Brawn, 1968). Although Gaspe and N28 would have allelic differences for several maturity QTLs, the chromosome 8 QTL could well be involved in the early tassel initiation of Gaspe because of its major effect on maturity.

In a follow-up marker-trait association study (Parentoni et al., 1992), we produced an F_3 population from the 151 F_2 plants of the cross A662 $\times$ B73 previously genotyped using 63 RFLP markers. A662 has been successfully used as a source of earliness in the University of Minnesota corn breeding program. The one hundred and fifty-one F_3 lines obtained by selfing individual F_2 plants were evaluated per se (Table 4) and in testcrosses (Table 5) in three Minnesota environments (2 replications of a double row plot/location). Maturity was measured as days to 50% pollen shed and days to 50% silking. The traits plant height, node number and internode length were measured in all environments (4 plants

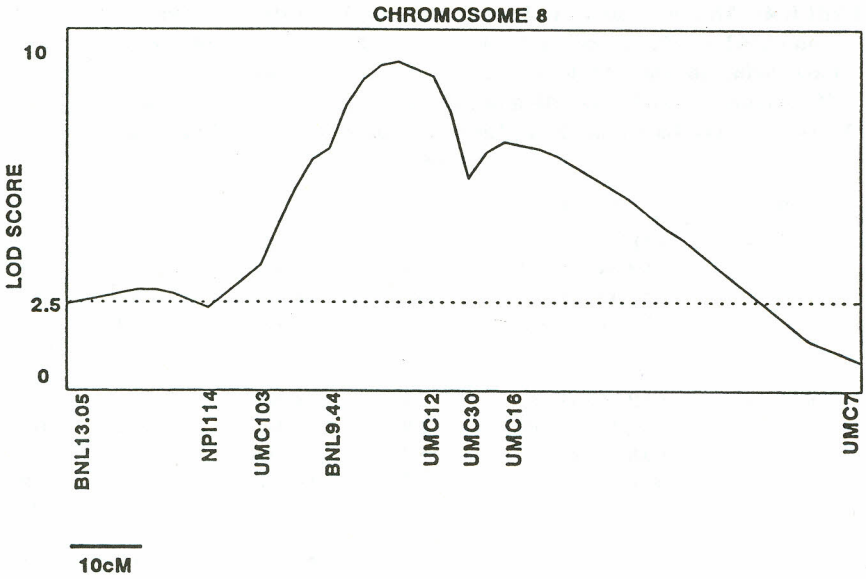

Figure 2. Mapmaker-QTL analysis of marker-trait (days to pollen shed) linkages for chromosome 8 from A662 × B73 F_2 plants.

scored/entry/location). MAPMAKER-QTL was used for analyzing the F_3 data. Single factor ANOVA was used for analyzing the testcross data, considering only the two parental marker classes. A major maturity factor was again identified close to the marker UMC12 (chromosome 8). This marker also is strongly linked to a region controlling node number suggesting that the two traits are governed by closely linked genes or by a single gene with a pleiotropic effect. A mixed model ANOVA was used for testing the significance of marker × location interactions using the F_3 data. Marker classes were considered fixed and location and progenies were considered random. SAS (OS/2 version 6) was used for analyzing the data. The location effect was significant ($p < 0.001$) for all five traits. Only two

TABLE 3—Means of Genotypic Classes for Days from Planting to Anthesis Using Probe UMC12. Data from (Recurrent Parent × Backcross-Derived Line) F_2 Analysis.

Marker Genotype	B73 × A679 (DP = A662)	N28 × N28E (DP = Gaspe)
	DTP	DTP
Homozygous DP	85.4	91.4
Heterozygous	87.4	94.9
Homozygous RP	89.8	98.9
r^2	0.30	0.52

DF = Donor Parent
RP = Recurrent Parent
DTP = Days from planting to 50% pollen shed

TABLE 4—Markers Linked to Loci Controlling Maturity and Plant Height Based on (A662 × B73) F_3 per se Evaluation. LOD Scores, Phenotypic Effect of Exchanging an A662 Allele for a B73 Allele at This Locus (U Value), Level of Dominance (a), and Proportion of the Phenotypic Variance Explained by the Marker (r^2) are Based on 151 F_3 Lines Evaluated in Three Minnesota Locations in 1992.

Trait	Marker[a]	LOD	U	a	$(r^2)^b$
Days to pollen shed	UMC154 (3-57)	2.4	0.9 days	1.0	0.04
	UMC54 (5-119)	3.1	1.1 days	0.7	0.06
	UMC12 (8-94)	20.6	2.8 days	0.0	0.45
	BNL8.17 (9-86)	2.7	0.9 days	0.9	0.05
					0.56[c]
Days to silking	UMC154 (3-57)	2.4	0.8 days	0.8	0.04
	UMC54 (5-119)	2.8	1.0 days	0.8	0.05
	UMC12 (8-94)	15.7	2.5 days	0.0	0.37
	BNL8.17 (9-86)	2.7	0.9 days	0.9	0.08
					0.50[c]
Plant height	UMC15 (4-120)	6.5	−8.4 cm	0.4	0.16
	BNL5.71 (5-92)	5.2	9.6 cm	0.2	0.13
	UMC12 (8-94)	8.7	10.8 cm	0.2	0.22
					0.40[c]
Node number	UMC12 (8-94)	21.4	0.9 node	0.3	0.46
	BNL8.17 (9-86)	3.1	0.4 node	0.6	0.07
					0.51[c]
Internode length	UMC15 (4-120)	6.8	−0.5 cm/node	0.5	0.17
	BNL5.71 (5-92)	9.3	0.6 cm/node	0.1	0.24
					0.36[c]

[a] Closest marker linked to the trait. ( ) = chromosome-map position.
[b] r^2 from linear regression for each marker-trait combination.
[c] R^2 from multilocus model for each trait.

marker × location interactions were significant out of the 315 marker-trait combinations tested, indicating that the marker-trait associations were consistent across environments. The mean of the three locations was therefore used for reanalyzing the data (Tables 4 and 5). Plant height is a function of node number and internode length, and in this study they appear to be determined by different chromosome regions (Tables 4 and 5). A region was found in chromosome 4 (UMC15) where the B73 (taller inbred) allele reduces plant height by reducing internode length (Table 4). The individual effects identified by each marker in each trait × location combination were additive (Table 4) when a multilocus model was used for the F_3 analysis (R^2 of the multilocus model for each trait was close to the sum of the individual coefficients of determination).

Information on markers linked to factors controlling maturity measured as GDUs (Growing Degree Units) to pollen shed (Fig. 3) and silking (Fig. 4) has

TABLE 5—Markers Linked to Loci Controlling Maturity and Plant Height in (A662 × B73) F_3 Testcrosses. P Values, Differences Between the Two Homozygous Parental Marker Classes (D) and Coefficients of Determination (r^2) From a Single Factor ANOVA Using the Two Parental Homozygous Marker Classes for the Traits Days to Pollen Shed, Days to Silking, Plant Height, Node Number, and Internode Length From 151 Testcross Progenies ((A662 × B73 F_3's) × A682)) Evaluated at Three Minnesota Locations in 1992.

Trait	Marker[a]	p Value	D	$(r^2)^b$
Days to pollen shed	UMC84 (1-201)	0.008	1.3 days	0.08
	UMC121 (3-18)	0.039	0.8 days	0.04
	UMC54 (5-119)	0.004	1.4 days	0.10
	UMC12 (8-94)	<0.001	3.6 days	0.47
	BNL8.17 (9-86)	0.048	1.0 days	0.05
Days to silking	UMC84 (1-201)	0.001	1.4 days	0.12
	UMC154 (3-57)	0.001	1.4 days	0.10
	UMC54 (5-119)	0.009	1.3 days	0.08
	UMC12 (8-94)	<0.001	4.0 days	0.45
	BNL8.17 (9-86)	0.014	1.3 days	0.08
Plant height	UMC15 (4-120)	<0.001	−12.1 cm	0.16
	UMC5.71 (5-92)	<0.001	12.4 cm	0.16
	UMC12 (8-94)	<0.001	25.2 cm	0.48
	BNL8.17 (9-86)	0.010	8.9 cm	0.09
Node number	UMC12 (8-94)	<0.001	2.0 nodes	0.50
	BNL8.17 (9-86)	0.001	0.7 nodes	0.14
Internode length	UMC15 (4-120)	<0.001	−0.5 cm/node	0.26
	BNL5.71 (5-92)	<0.001	0.7 cm/node	0.25

[a] Marker lined to the trait. ( ) = chromosome-map position.
[b] r^2 from linear regression for each marker-trait combination.

been provided by Drs. D. Grant, B. Beavis, and R. Fincher of Pioneer Hi-Bred International Inc. The data are from 144 F_4 progenies derived from an inbred cross evaluated in 1988 using 1 replication at eight locations. MAPMAKER-QTL was used for analyzing the data. Proprietary concerns preclude the release of parentage and much of the specific probe information, but clearly the results are similar to ours in several respects. The inbreds used as parents in the Minnesota study were B73 (1540 GDU to 50% pollen shed) and A662 (1110 GDU). The parents in the Pioneer study required 1570 GDU versus 1150 GDU to reach 50% pollen shed. Thus, the maturity range of the two crosses was similar. As in our studies the chromosomes important in determining time to pollen shed are the same as those for time to silking. In addition, chromosomes 5 and 8 are shown to be especially important in controlling the expression of these traits. Our F_3 analysis (Table 4) implicated chromosomes 5, 8, and 9 and the testcross analysis (Table 5) documented significant effects for chromosomes 1, 3, 5, 8, and 9. The

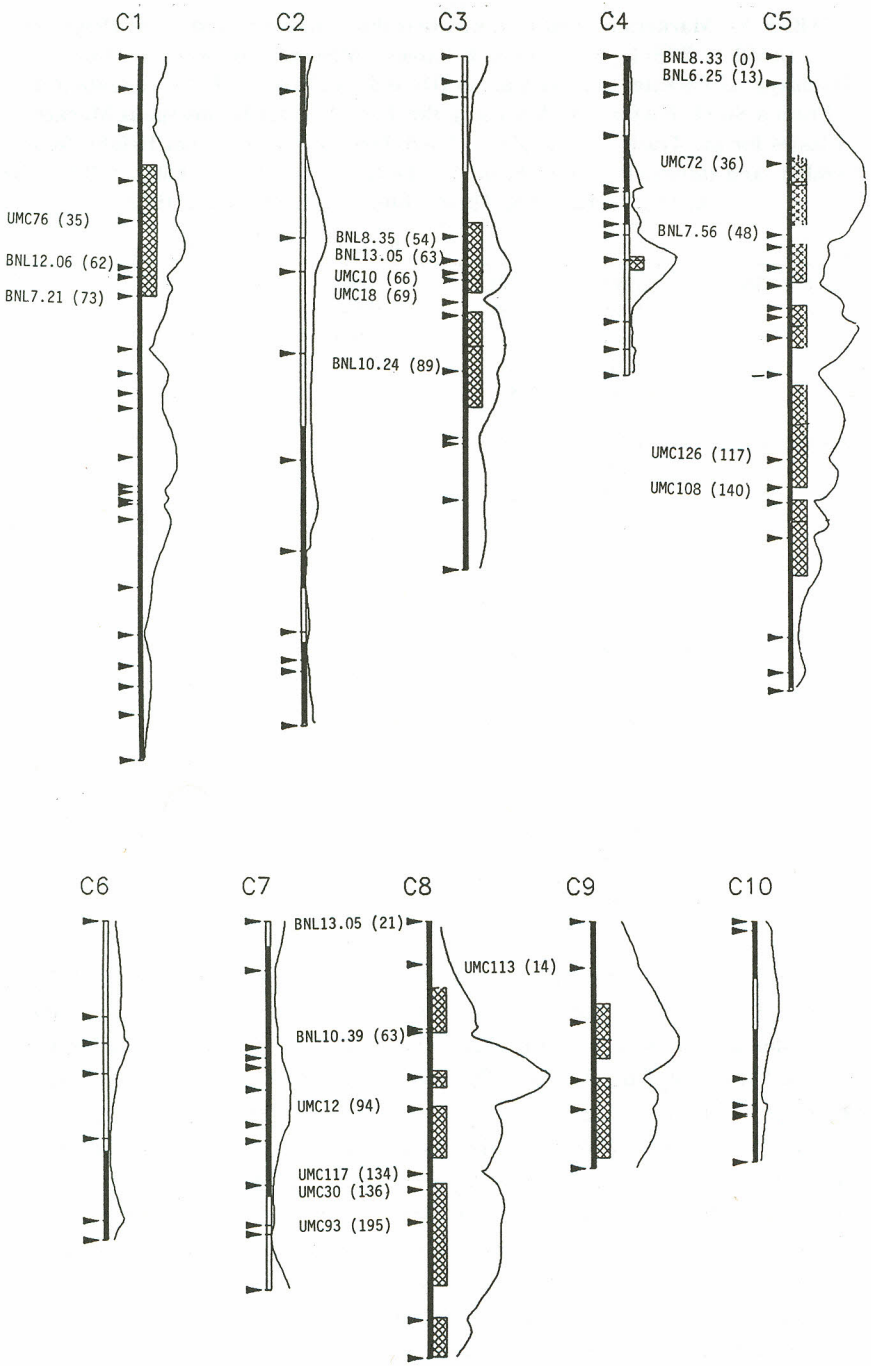

Figure 3. LOD score distributions for GDU's to pollen shed. Boxes indicate significance at the LOD >2.0 threshold; data are from 144 F_4 progenies from an inbred cross. Arrows represent position of markers tested. Results courtesy of Pioneer Hi-Bred International, Inc.

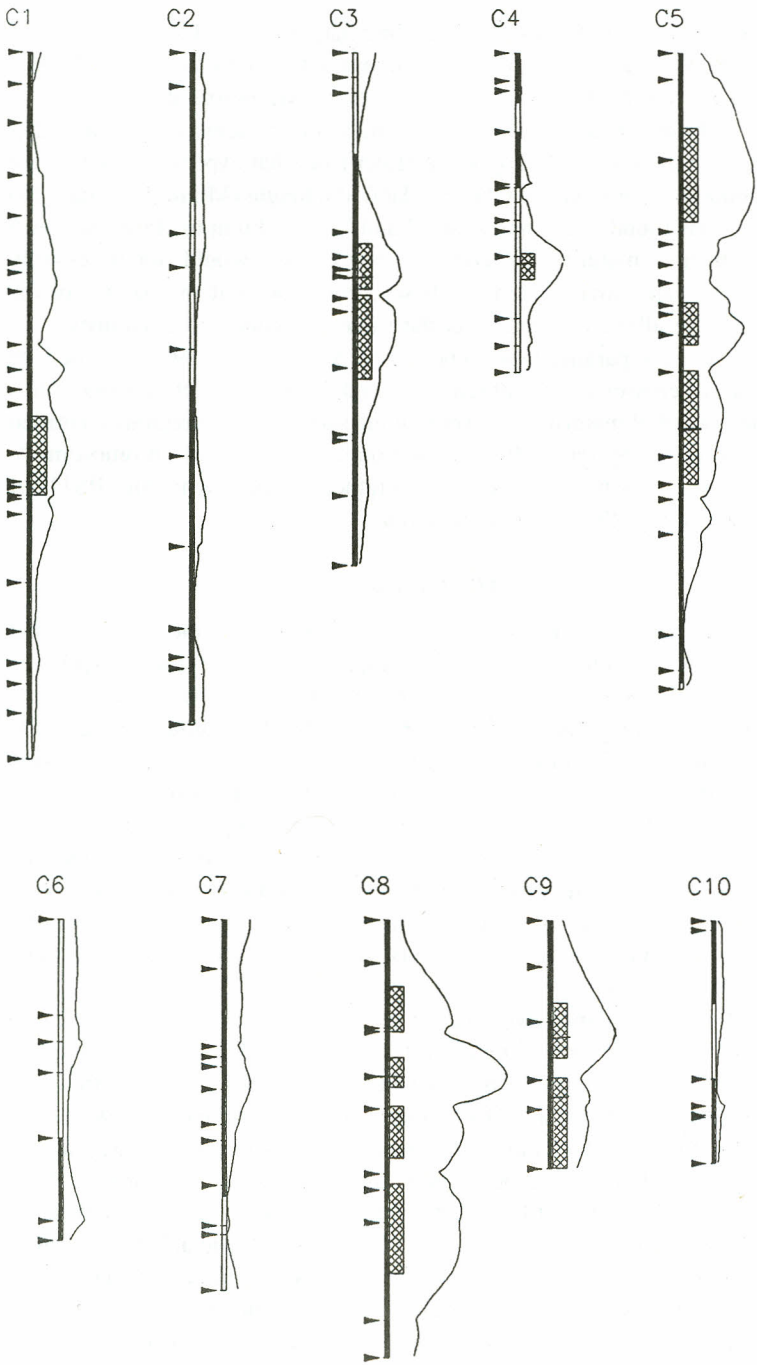

Figure 4. LOD score distributions for GDUs to silking. Boxes indicate significance at the LOD >2.0 threshold; data are from 144 F_4 progenies from an inbred cross. Arrows represent positions of markers tested. Results courtesy of Pioneer Hi-Bred International, Inc.

results reported here from Pioneer Hi-Bred International, Inc. (Figs. 3 and 4) also show 1, 3, 5, 8, and 9 to be the most important chromosomes. Additional similarities between the Pioneer and University of Minnesota data include: 1) detection of a chromosome 8 region with the highest LOD score and U value; 2) a chromosome 4 region having an opposite effect from that expected based on the parental phenotypes for maturity (Pioneer data) and height (Minnesota data); and 3) similar regions found in chromosomes 3 and 9 (in addition to chromosomes 5 and 8) to influence maturity. Of course, other crosses would not necessarily demonstrate the same involvement of these chromosomes if the parents of the cross do not have allelic differences at the same loci controlling maturity.

Our results closely parallel those reported by Stuber et al. (1992) for the trait days to tassel in crosses of the inbreds B73 and Mo17. Zehr et al. (1992) also reported the control of maturity by several of the same genomic regions identified in our studies, including the UMC12 region on the long arm of chromosome 8. Their genetic materials were derived from a rather complex synthetic (BS11) of corn belt lines and southern prolific material.

The Future

Cloning and characterization of quantitative trait loci are the important and logical next steps after molecular marker mapping of these regions. Map-based cloning of a quantitative trait locus has not yet been accomplished in agronomically important crop species. The N28 versus N28E material is unique and undoubtedly will be useful for the cloning of a quantitative trait locus. Evaluation of F_3 families derived in a way that isolates essentially a Mendelizing factor in a uniform background should allow high resolution mapping of the region. The highly uniform background also will allow morphological comparisons between N28 and N28E. These comparisons will be a start toward predicting the likely tissue and time of expression of the gene(s) in the UMC12 region of chromosome 8, information which may be useful as we try to identify the DNA of interest in a several megabase region.

Cloning of genes with unknown function is a science still in its infancy. This is even more true for genes controlling quantitative traits in plants. Recent advances in DNA separation technology (Schwartz and Cantor, 1984; Anand, 1986; Carle et al., 1986; Chu et al., 1986) and DNA cloning vectors (Burke et al., 1987) have made possible map-based cloning. The main concepts of this strategy are 1) identification of flanking molecular markers that map within 1 cM or less of the region of interest, 2) cloning of DNA between the flanking molecular markers by chromosome walking using cosmid or YAC (Yeast Artificial Chromosome) clones, and 3) identification of the gene of interest within the cloned DNA. An example of success using a similar strategy is the genetic characterization and cloning of the locus responsible for cystic fibrosis in humans (Rommens et al., 1989; Riordan et al., 1989; Kerem et al., 1989).

At this point in our understanding, no accurate prediction can be made of the

nature of the DNA composing a quantitative trait locus. Often a QTL is viewed as a single gene, but it may well be a series of genes perhaps with extensive upstream control regions. Deletions more than 20 kb upstream of hemoglobin genes in mammals can have a dramatic effect on globin gene expression (Orkin, 1990). These distant regulatory regions are known as LCRs (Locus Control Regions). It also appears that the gene closest to the LCR may be expressed first during development. The LCR is proposed to affect chromatin structure permitting regulatory factors access to the individual genes. Thus, a QTL may include complex regions controlling level of expression in a temporal or spatial manner. Isolation and analysis of extensive DNA regions containing a QTL should provide important insights. The nature of quantitative trait expression is consistent with the idea of a complex regulatory mechanism.

Maturity is usually the first trait that needs to be considered when incorporating exotic germplasm into a breeding program. The ultimate cloning of a major maturity loss has the potential to be important in speeding up the adaptation of genotypes to different environments. This would impact not only U.S. breeders and geneticists, but also international breeding programs which deal with an extreme range of environments. Our ongoing mapping of maturity loci will help in understanding the inheritance of this trait, identifying loci important in many backgrounds, and characterizing the effect of environment. Markers linked to maturity will be useful as indirect selection tools to pyramid maturity QTLs. Furthermore, this research may help us to learn how to use molecular markers to avoid negative correlations between traits when doing routine selection and genetic improvement.

Summary

Several genetic regions having major effects on maturity have been identified using RFLP analysis. One such region on chromosome 8 is important across several diverse genotypes and accounts for up to 50% of the variation for maturity in a cross involving an inbred line (N28) and a 20-backcross generation derivative (N28E).

In addition to the chromsome 8 QTL for maturity, we have evidence using the backcross-derived line approach for regions controlling maturity on chromosomes 1, 2, 3, 5, 7, and 9. Chromosome 5 appears to be especially important in both magnitude of effect and across several genetic backgrounds. Maturity as measured by days to pollen shed or silking may be controlled by additive or nearly dominant gene action depending on the chromosome region.

The marker-trait linkages were consistent across environments based on A662 $\times$ B73 F_3 per se and testcross evaluations from three locations in one year. UMC12 (chromosome 8) and UMC54 (chromosome 5) also marked important regions for maturity in these materials.

Acknowledgments

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