Genetic Relationship of Stalk Strength and Ear Height in Maize

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ABSTRACT

The rind penetrometer is an effective tool for measuring stalk strength in an effort to improve maize (*Zea mays* L.) germplasm for stalk lodging resistance. However, previous studies have indicated a significant negative correlation between rind penetrometer resistance (RPR) and ear height (EH). The correlation between RPR and EH is of interest in understanding response to selection for RPR. Has selection for high RPR resulted primarily in increased stalk strength per se and coincidentally lower ear heights, or has selection for high RPR resulted in lower ear heights and subsequently higher stalk strength? The objective of this study was to determine the genetic relationship between RPR and the correlated trait EH. To accomplish this goal, three $F_{2:3}$ populations were used to characterize and compare quantitative trait loci (QTL) for RPR, EH, and RPR adjusted for EH (RadjE). The original QTL analysis of RPR detected a total of 26 QTL across populations. Adjusting RPR for EH caused 11 of the original RPR QTL to lose their significance. However, the majority, 15 of 26, of the original RPR QTL remained significant as QTL for RadjE. Because EH clearly had an effect on RPR, adjusting RPR for EH likely resulted in more accurate descriptions of QTL for stalk strength per se. We have demonstrated that QTL analysis can be used to separate the effects of correlated traits from the genetic effects of the trait of interest, and recommend determining which correlated traits may influence measurement of the main trait before initiating a QTL experiment.

STALK LODGING resistance is an important aspect of plant standability in maize. Stalk lodging is breakage at or below the ear, which may result in loss of the ear at harvest. Several methods have been devised to measure stalk strength as a means of improving stalk lodging resistance. Sibale et al. (1992) described use of a modified electronic rind penetrometer to measure stalk strength. Rind penetrometer resistance (RPR) was negatively correlated with stalk lodging (Chesang-Chumo, 1993; McDevitt 1999; Spiess, 1995; Jampatong, 1999). Recurrent S_0 plant selection for RPR has been effective in separating the synthetic population MoSCSSS into two distinct subpopulations (Alsirt, 1993). The rind penetrometer, therefore, is a valuable tool for measuring stalk strength.

Thompson (1964) found that lower internodes had greater stalk strength than higher internodes. Chesang-Chumo (1993) reported that ear height (EH) was decreased by 22.5% over five cycles of selection for high RPR in MoSCSSS. The correlation between RPR and EH is of interest in terms of direct vs. indirect selection for stalk strength. That is, to what extent does selection for high RPR increase stalk strength per se, or does decreasing EH result in increased stalk strength?

Little research has been conducted to investigate the nature of QTL for correlated traits. Paterson et al. (1991) found a chromosomal region affecting both mass per fruit and soluble solids in tomato (*Lycopersicon esculentum* Mill). This region contained the Self-pruning Protein (*sp*) locus which was shown to affect both traits. Schön et al. (1993) adjusted tunnel length (TL), a measure of European corn borer (ECB, *Ostrinia nubilalis* Hübner) damage, for plant height (PH). They found that four of the seven original TL QTL remained significant. One of the three QTL that lost significance after adjusting for PH overlapped a PH QTL. The authors determined that that particular QTL was not responsible for a physiological mechanism for resistance to ECB, but rather, was limiting TL since PH determines the total length of tunnels possible.

Several statistical programs have been developed to map QTL for multiple traits. In the multiple trait analysis method proposed by Jiang and Zeng (1995), multiple traits are mapped simultaneously, taking advantage of the correlation between traits by considering the correlated trait data as repeated measurements of a single trait. In doing this, parameter estimation is improved and statistical power is increased. Because it was our goal to reduce correlated trait effects on QTL detection to obtain a truer genetic description of the trait of interest, RPR, we decided analyze correlated traits in a way nearly opposite of the method of Jiang and Zeng. We adjusted RPR means for differences in EH by using analysis of covariance procedures (Steele and Torrie, 1960, p. 305).

The objective of this study was to determine the genetic relationship between RPR and the correlated trait EH. This was accomplished by utilizing QTL analysis to characterize and compare QTL for RPR, EH, and RPR after adjusting for EH.

MATERIALS AND METHODS

Population Development

Recurrent S_0 plant selection for increased and decreased RPR within the synthetic MoSCSSS (USDA-ARS and Mo.

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Abbreviations: ECB, European corn borer; EH, ear height; LOD, log-odds ratio; MoSCSSS-High, MoSCSSS(H24-HRP)C10; MoSCSSS-Low, MoSCSSS(H25-LRP)C11; MoSQB-Low, MoSQB(S10)C6; PH, plant height; QTL, quantitative trait locus; R^2, percent of phenotypic variation explained; RadjE, rind penetrometer resistance adjusted for ear height; RPR, rind penetrometer resistance; SSR, simple sequence repeat; TL, tunnel length.

Agric. Exp. Stn., 1986) yielded MoSCSSS(H24-high rind penetrometer [HRP])C10 and MoSCSSS(H25-low rind penetrometer [LRP])C11, respectively. Recurrent S_0 plant selection for low stalk crushing strength (another method of measuring stalk strength) within MoSQB (Gerdes et al., 1993) yielded MoSQB(S10)C6. To initiate population development without delay, samples of each of MoSCSSS(H24-HRP)C10 and MoSQB(S10)C6 were grown in a greenhouse ground bed and evaluated for RPR. We selected the plant with the highest RPR in the MoSCSSS(H24-HRP)C10 sample and the plant with the lowest RPR in the MoSQB(S10)C6 sample. These plants were self pollinated, and the resulting progeny are hereafter referred to as MoSCSSS-High1 and MoSQB-Low, respectively. Because there was no overlap between the two original populations [MoSCSSS(H24-HRP)C10 and MoSQB (S10)C6], we believe that adequate parental materials were selected. MoSCSSS-High1 was self pollinated and the derived progeny are referred to as MoSCSSS-High2 and MoSCSSS-High3.

Population 1 was formed by crossing an individual MoSQB-Low plant (female) with an individual MoSCSSS-High1 plant. Population 2 was formed by crossing an individual MoSCSSS-High2 plant (female) with an individual plant from MoSCSSS(H25-LRP) (hereafter referred to as MoSCSSS-Low). Population 3 was formed by crossing Mo47 (female) with an individual MoSCSSS-High3 plant. Population 4 was formed by crossing B73 (female) with Mo47. For all populations, F_1 plants were self pollinated yielding F_2 individuals, which were self pollinated to produce $F_{2:3}$ families. Populations 1, 2, 3, and 4 included 282, 291, 291,and 244 $F_{2:3}$ families, respectively. The $F_{2:3}$ families were sib pollinated to increase seed for phenotypic data collection.

Populations 1 and 2 were designed specifically to map stalk rind strength QTL since both parents were selected for high and low stalk strength phenotypes. Population 3 was designed to map QTL for RPR and resistance to second-generation ECB with Mo47 as the source of resistance.

Phenotypic and Genotypic Data Collection

Phenotypic data used in this study were collected as described in Flint-Garcia et al. (2003, this issue). Locations used for evaluation trials in this study included Agronomy Research Center near Columbia, MO, on Mexico silt loam; a site near Tipton, MO, in Cooper County on Clafork and Crestmeade silt loam; and a site managed by the Illinois Crop Improvement Association near Juana Diaz, Puerto Rico, on San Antón sandy clay loam. Briefly, Population 1 was planted as three 10×10 triple lattices at each of three locations: Agronomy Research Center in 1999, and Tipton and Agronomy Research Center in 2000. Populations 2 and 3 were planted as three 10×10 triple lattices per population at each of four locations: two locations in Puerto Rico in 1999, and Tipton and Agronomy Research Center in 2000. Data collected included RPR, PH, and EH. Rind penetrometer resistance was determined for 10 competitive plants plot^{-1} with a modified electronic rind penetrometer (Sibale et al., 1992). About two weeks after flowering, plants were probed in the middle of the flat side of the internode below the primary ear node. Ear and plant heights were obtained by measuring the distance from the ground to the primary ear node and the collar of the flag leaf, respectively, for 10 competitive plants plot^{-1}.

Populations 1, 2, and 3 were genotyped with 89, 77, and 86 SSR markers, respectively, according to the procedures described in Flint-Garcia et al. (2003, this issue]).

Data Analysis

Year–location combinations were treated as independent environments. Rind penetrometer resistance was adjusted for EH at each environment generating a new trait, RadjE, as follows: $\text{RadjE}_i = \text{RPR}_i - b_l(\text{EH}_i - \overline{\text{EH}})$ where b_l is the linear regression coefficient between RPR and EH. Environment means and broad-sense heritability estimates were calculated (Flint-Garcia et al., 2003, this issue). Family means across environments were used to compute phenotypic correlation coefficients with SAS PROC CORR (SAS Institute, Inc., 1998).

MAPMAKER/EXP version 3.0b was used to construct linkage maps (Lander et al., 1987; Lincoln et al., 1992). QTL Cartographer version 1.14d (Basten et al., 1994; Basten et al., 2000) was employed for QTL analysis of family means across environments as described in Flint-Garcia et al. (2003, this issue). For each trait-population combination, experiment-wise log-odds ratio (LOD) thresholds at $P = 0.05$ were determined by analyzing 1000 permutations of the data (Churchill and Doerge, 1994). A one-LOD drop from the peak position was used as a confidence interval for QTL location. Overlapping confidence intervals were used to determine QTL in common among traits.

The statistical program EPISTACY was used to test for the presence of epistatic interactions between marker pairs at $P < 0.001$ (Holland, 1998). To build multilocus models, markers nearest to single-effect QTL and those involved in epistatic interactions were subjected to stepwise regression at $P < 0.05$ by SAS PROC REG (SAS Institute, Inc., 1998). Markers were added to the model in order of increasing significance (forward regression in), and were removed if their significance while in the model exceeded 0.05 (backward regression out).

RESULTS AND DISCUSSION

The correlation between EH and RPR, ranging from −0.21 to −0.53 (Table 1), is consistent with the observation by Thompson (1964) that lower internodes had increased stalk strength compared with higher internodes. Chesang-Chumo (1993) reported that EH decreased by 22.5% over five cycles of selection for high RPR in MoSCSSS, and that EH and RPR were highly correlated. However, selection for high stalk crushing strength, an alternative measurement of stalk strength, increased EH by 27.4% over 12 cycles in MoSQB (Lyimo, 1988). The correlation between RPR and PH was only significant in Population 3, indicating that selection for stalk strength had a stronger influence on EH than PH. The highly significant positive correlation between PH and EH found in all populations was expected as this relationship has occurred in many studies. Because of the lack of consistent correlation between RPR and

Table 1. Selected phenotypic correlation coefficients among rind penetrometer resistance (RPR), plant height (PH), ear height (EH), and rind penetrometer resistance adjusted for ear height (RadjE) in all populations: Population 1, (MoSCSSS-High1 × MoSQB-Low)$F_{2:3}$; Population 2, (MoSCSSS-High2 × MoSCSSS-Low)$F_{2:3}$; Population 3, (MoSCSSS-High3 × Mo47)$F_{2:3}$.

Population	RPR & EH	RadjE & EH	RPR & PH	EH & PH
Population 1	−0.21**	0.08	0.04	0.70**
Population 2	−0.53**	−0.31**	−0.07	0.70**
Population 3	−0.40**	−0.21**	−0.14*	0.74**

* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.

Table 2. Summary of QTL results for original rind penetrometer resistance (RPR) data, RPR adjusted for ear height (RadjE), and ear height (EH). For each population, significant single-effect QTL are reported, followed by significant epistatic interactions and percent phenotypic variation explained by multi-locus models.

Chrom./ Interaction	Position	RPR†		RadjE		Ear height	
		LOD‡	R^2§	LOD	R^2	LOD	R^2
Population 1							
2	0–10¶					24.9	4.7
2	18–34	5.8	5.6				
3	62–79					11.3	12.1
3	83–109	6.2	6.3	4.7	5.7		
4	154–172	8.2	7.1	5.6	5.1		
5	18–47	4.1	3.6	7.8	8.5		
6	2–23					7.5	7.6
6	96–114					7.0	9.1
6	121–135	3.7	3.8				
7	4–18			5.4	4.8		
7	47–59					10.1	11.6
8	61–80					11.2	12.0
8	90–120			6.3	8.2		
9	58–70	6.2	7.2	13.9	16.7		
9	74–100	8.8	12.9				
9	121–130	5.1	4.3				
10	25–54					5.7	8.1
bnlg1270×bnlg1496#			6.3		7.4		
bnlg1375×bnlg345			7.4				
umc1066×umc1649			7.3				
umc1685×umc1856			7.9		8.3		
bnlg1046×phi029					7.0		
bnlg2132×umc1649					6.2		
bnlg1306×umc1015							6.1
bnlg1360×phi021							7.0
Total R^2††:		**33.4%**		**32.0%**		**45.1%**	
Population 2							
1	85–104	6.5	7.5				
1	104–114	6.7	9.3	4.6	21.5		
2	39–49			6.5	7.3		
2	74–98	4.4	5.3				
2	100–124	6.2	6.8	6.5	7.2		
3	71–103	3.7	4.9			11.4	10.8
4	33–59					5.0	5.1
4	75–110	4.7	5.8	6.8	8.1		
5	2–22					4.1	4.7
5	93–123					6.5	9.0
6	95–117	5.3	6.1	4.9	5.1		
7	28–53	6.0	7.1	7.2	7.8		
8	88–104					3.9	3.6
9	37–59	4.3	4.6			19.7	21.0
10	38–59	5.7	6.3	9.3	12.4		
bnlg1225×umc1260			6.8				
umc1331×umc1033			6.8		6.9		
bnlg1671×bnlg292							6.5
phi054×umc1033							5.7
Total R^2:		**44.8%**		**41.7%**		**45.6%**	
Population 3							
1	0–22					4.8	5.7
2	6–40	4.9	4.4				
2	43–63	6.9	4.6	19.2	17.7		
2	100–104	8.0	5.5	5.6	4.2	5.2	4.7
3	76–91	6.7	4.7	3.6	2.5	19.9	22.0
3	122–144			3.7	2.8		
4	147–161			4.0	3.9		
5	83–121			3.8	3.1	6.9	7.0
6	49–64					5.2	4.4
6	71–100	6.1	4.9	8.4	7.7		
7	30–52	8.5	5.6	6.0	4.1		
8	8–26					3.6	3.0
8	77–96					9.3	8.2
9	1–26			3.7	4.4		
9	51–61			3.6	2.5		
10	2–16	5.5	5.2				
10	37–60	3.8	2.4				
bnlg1046×umc1733					7.1		
bnlg1045×umc1979							6.2
bnlg1046×bnlg1144							6.7
bnlg1451×phi029							7.6
bnlg2132×mmc151							6.8
Total R^2:		**48.4%**		**49.6%**		**41.2%**	

PH, emphasis was placed on EH as the more important correlated trait for our study of RPR.

The correlation between RPR and EH is of interest in understanding response to selection for RPR. Has selection for high RPR resulted in increased stalk strength per se and coincidentally lower ear heights, or has selection for high RPR resulted in lower ear heights and subsequently higher stalk strength? Is one able to manipulate RPR and EH independently, or does the ear's placement on the plant primarily determine its stalk strength?

There are three main causes for correlation between traits: pleiotropy, linkage, and environmental influence (Aastveit and Aastveit, 1993). If EH had a pleiotropic effect and was responsible for differences in RPR, then one should make selections for high RPR on the basis of low EH since measuring EH is easier and faster than measuring RPR. If RPR and EH are correlated because of linkage, that is, high RPR alleles at a given locus are linked with low EH alleles, then one would expect some proportion of individuals in a population to have high RPR and high EH, and vice versa, because of recombination between loci. It would also be possible to break the correlation between EH and RPR through recombination between RPR and EH loci. Environmental correlation results when two traits are influenced by the same difference in environment; for example, drought usually causes decreased PH and decreased yield. Of course, it is probable that there is simultaneous action of any or all of these causes on correlation.

We decided to analyze the relationship between stalk strength and EH to obtain a more accurate estimate of RPR effects. We adjusted RPR means for differences in EH by using analysis of covariance procedures (Steele and Torrie, 1960, p. 305).

The inheritance of RPR is rather complex (Flint-Garcia et al., 2003, this issue) (summarized in Table 2 and Fig. 1). Many QTL (8, 10, and 8 QTL for Populations 1, 2, and 3) with small effects were detected with an average partial R^2 across populations of 5.5%, and only one QTL in Population 1 with a partial R^2 greater than 10%. Four, two, and zero significant epistatic interactions were detected in Populations 1, 2, and 3. The amount of variation explained by multi-locus models (total R^2) ranged from 33.4 to 48.4%.

The results of QTL analysis for EH (Table 2, Fig. 1) are typical of those reported in other studies (Beavis et al., 1994; Veldboom et al., 1994; Berke and Rocheford,

† Underlined single-effect QTL and epistatic interactions were significant components of the multi-locus model.

‡ For the test of H_3 ($a \neq 0$, $d \neq 0$):H_0 ($a = 0$, $d = 0$). LOD scores can be converted to likelihood ratios by multiplying by 4.6052.

§ Percent phenotypic variation explained by the QTL as reported by QTL Cartographer (Basten et al., 2000) for single-effect QTL and by EPISTACY (Holland, 1998) for epistatic interactions.

¶ Distance measured in centimorgans from the terminal marker on the short arm of the chromosome. The range of distances includes overlapping QTL confidence intervals for comparing QTL among traits.

Epistatic interactions are identified by markers, and have no position per se.

†† Total phenotypic variation accounted for by a multi-locus model including the underlined single-effect QTL and interaction components as determined by forward and backward stepwise regression.

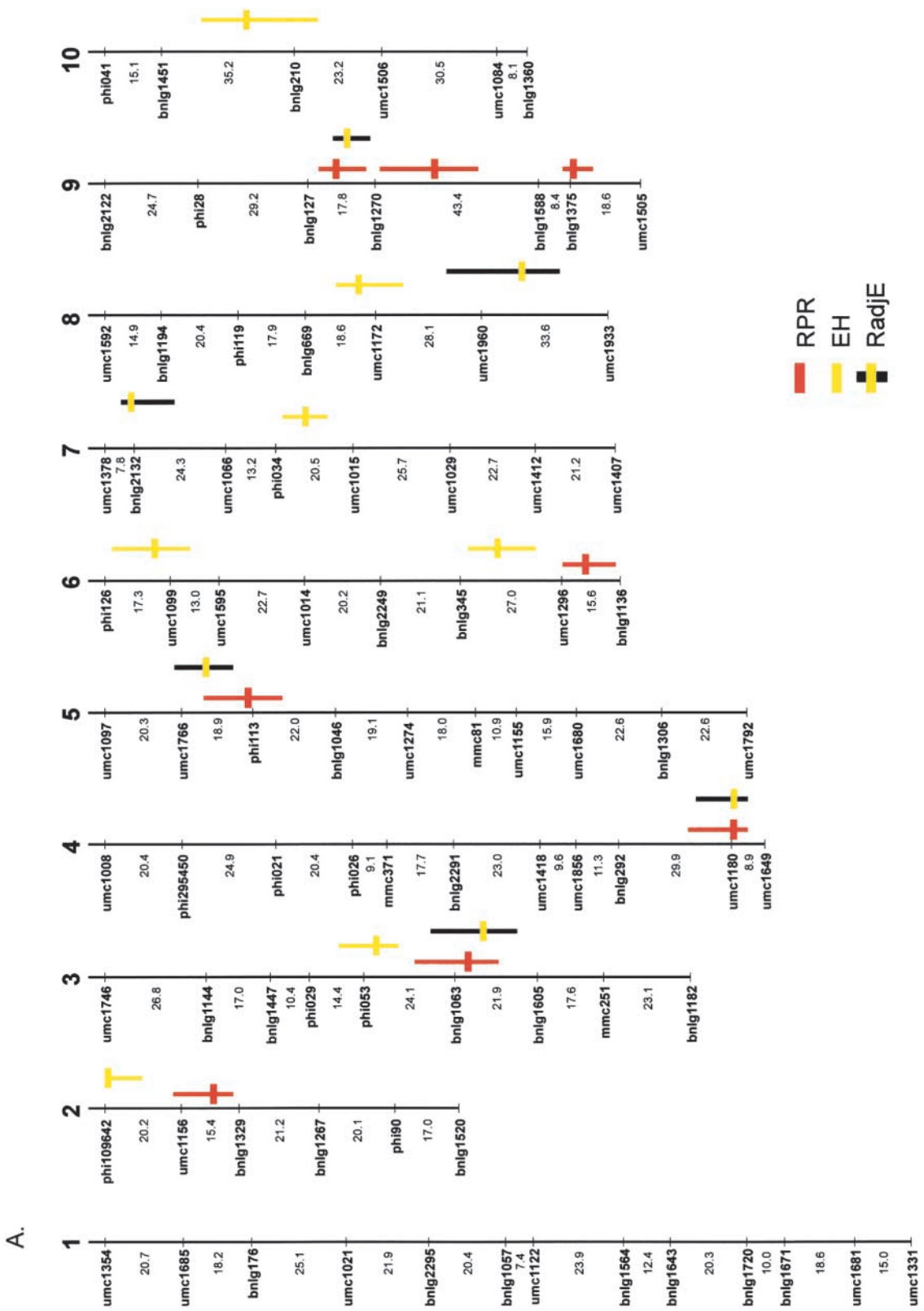

Fig. 1. Relative locations of QTL detected by composite interval mapping for rind penetrometer resistance (RPR), rind penetrometer resistance adjusted for ear height (RadjE), and ear height (EH) for three populations. Horizontal bars represent QTL peak locations and vertical bars represent a one-LOD confidence interval. (A) Population 1 (MoSCSSS-High × MoSQB-Low)$F_{2:3}$, (B) Population 2 (MoSCSSS-High × MoSCSSS-Low)$F_{2:3}$, and (C) Population 3 (MoSCSSS-High × Mo47)$F_{2:3}$.

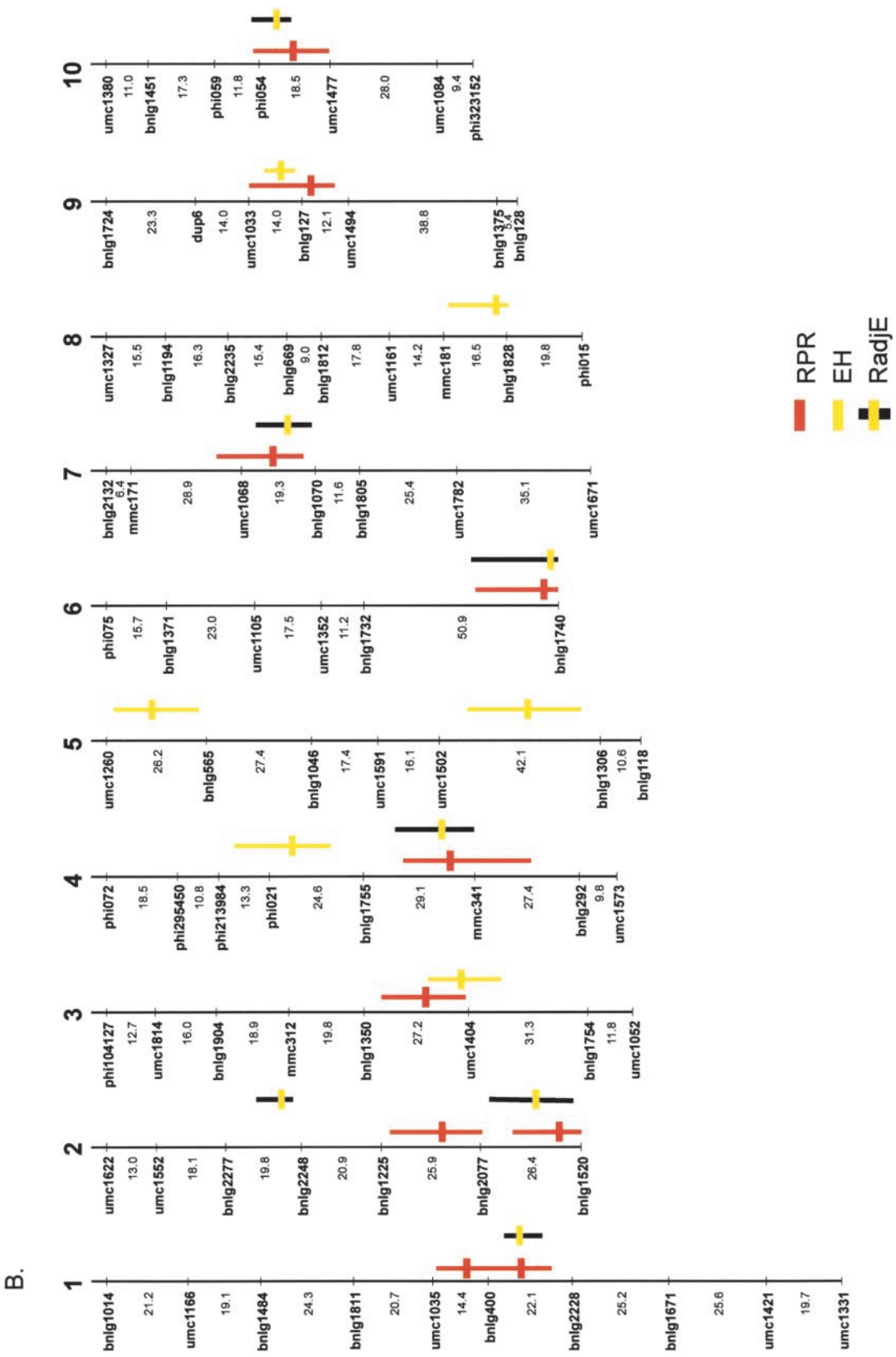

Fig. 1. Continued.

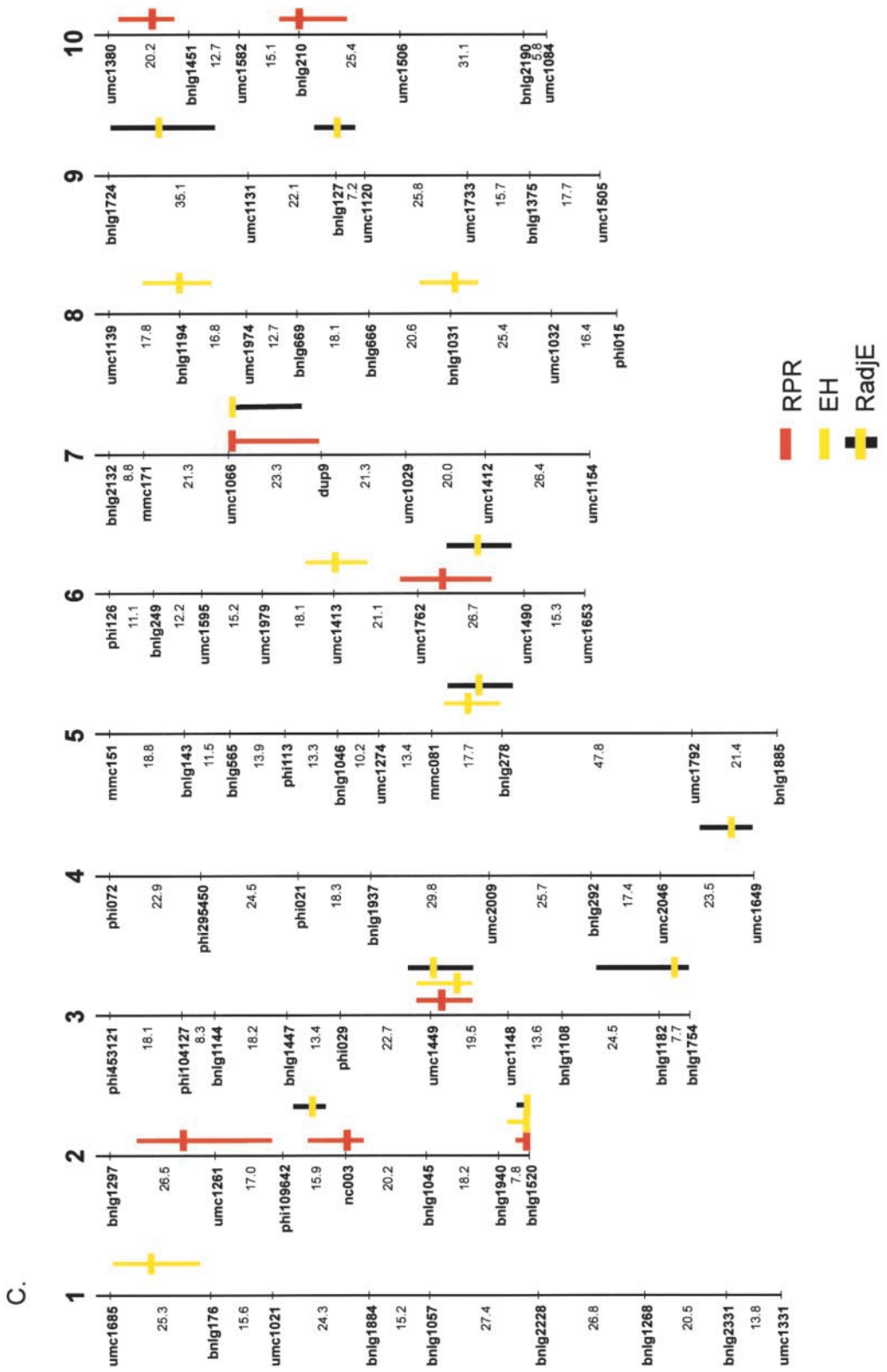

Fig. 1. Continued.

1995; Austin and Lee, 1996; Veldboom and Lee, 1996) in terms of number and locations of QTL detected, and total R^2. Seven, six, and seven QTL with small-to-moderate individual effects, ranging from 3.0 to 22.0% partial R^2s, were detected for EH. The individual QTL had larger partial R^2s compared to RPR QTL, averaging 8.7% over all populations. In Populations 1, 2, and 3, there were three, two, and one QTL with partial R^2s

greater than 10%. Several epistatic interactions were significant in each population (two, two, and four in Populations 1, 2, and 3). Multilocus models explained 45.1, 45.6, and 41.2% total R^2 for EH in Populations 1, 2, and 3, respectively. Of the 20 EH QTL detected in the present study, there were seven novel QTL, i.e., not identified in previous studies, while 13 QTL were identified in at least one previous study.

On the basis of overlapping confidence intervals, there were zero, two, and two QTL in common between RPR and EH in Populations 1, 2, and 3, respectively (Fig. 1). It was surprising that there were so few QTL in common between RPR and EH as the correlation between them was significant in all three populations (Table 1). However, there were three, one, and one EH QTL linked to (within 50 centimorgans) RPR QTL for Populations 1, 2, and 3, respectively. Nevertheless, out of a total of 26 RPR QTL, there were only nine RPR QTL that were either linked to or overlapped EH QTL.

The results for the QTL analysis of RadjE (Table 2, Fig. 1) are similar to those of the original RPR data, that is, there were a large number of QTL (6, 7, and 10) with small-to-moderate effects. The average partial R^2 was 7.5%, and there were four QTL with partial R^2s greater than 10% across populations. Four, one, and two epistatic interactions were significant in the three populations, respectively. After adjustment for EH, multi-locus models for RadjE accounted for 32.0, 41.7, and 49.6% of the phenotypic variation.

Fifteen of the original 26 RPR QTL remained significant as QTL for RadjE across populations: 4 of 8, 6 of 10, and 5 of 8 QTL in Populations 1, 2, and 3, respectively. Two interactions in Population 1 and one interaction in Population 2 remained significant after adjustment for EH. Adjustment for EH caused several changes in LOD score and/or partial R^2 for the QTL in common between RPR and RadjE. Decreases in LOD score ranged from 0.4 to 3.1, and increases ranged from 0.3 to 12.3. Overall, increases in LOD score were more significant than decreases. Associated with these changes in LOD scores were changes in partial R^2s for the individual QTL: decreases ranged from 0.6 to 2.2%, and increases ranged from 0.4 to 13.2% across populations. There were six decreases in R^2 vs. nine increases. Again, increases in R^2 were greater overall than decreases in R^2. The increases in LOD score and R^2 for RadjE vs. RPR can be interpreted such that RadjE QTL represent stalk strength loci per se, and removing the correlated effects of EH enhanced the estimation of genetic effects attributed to stalk strength per se.

Interestingly, after adjusting RPR for EH, more alleles that increased stalk strength originated from MoSCSSS-High for Population 1 (data not shown). The original RPR results for Population 1, that the majority of the positive RPR alleles originated from MoSQB-Low (Flint-Garcia et al., 2003, this issue), were an artifact of the MoSCSSS-High parent being taller and having higher ear heights. This particular relationship between RPR and PH/EH in MoSCSSS-High is opposite of what is usually observed, and, as a result, high RPR alleles originated from MoSQB-Low based on its lower EH. Adjustment of RPR for EH removed the correlated effects of EH such that the remaining QTL were true RPR QTL. These results clearly indicate that correlated loci from EH have an effect on RPR. Populations 2 and 3 remained the same with respect to the source of high RPR alleles as compared to the original RPR data.

There was a loss of 11 RPR QTL across all three populations after adjustment for EH. In Population 1, two of the four QTL lost were linked to EH QTL. A third lost QTL was the largest RPR QTL in Population 1, with a LOD score of 8.8 and a partial R^2 of 12.9%. In Population 2, two of the four QTL lost overlapped the two largest EH QTL. The remaining six original RPR QTL lost from the populations were not linked to EH QTL detected in this study, and had relatively small effects on RPR, with partial R^2s ranging from 2.5 to 7.5% and LOD scores ranging from 3.8 to 6.5. Some of the QTL lost after adjusting for EH likely represent the correlated QTL. However, not all of the QTL lost after adjustment will be correlated QTL because of sampling size for the QTL analyses. In experimental populations with less than 500 families, only a subset of QTL with small effects will be detected because of insufficient statistical power (Beavis, 1998). Several of RPR QTL detected in this study had LOD scores just above the significance threshold. These loci may not be significant after adjusting for EH simply because of the random sample of genotypes obtained.

There was a gain of eight RadjE QTL across populations when compared with the original RPR analysis: two, one, and five in the three populations. Two novel QTL in Populations 1 and 2 were highly significant with LOD scores of 6.3 and 6.5, and partial R^2 values of 8.2 and 7.3%. The remaining novel RadjE QTL had small effects ranging from 2.5 to 4.8% and LOD scores ranging from 3.6 to 5.4. It is likely that these QTL were approaching the level of significance in the original RPR analysis, but were masked by EH. Removal of the confounding effects of EH caused by the correlation between RPR and EH allowed the QTL LOD score to exceed the significance threshold. Again, small population size may have caused only a subset of QTL to be detected (Beavis, 1998). The QTL that were just below the significance threshold in the RPR analysis may become significant simply because of sampling error within the population.

The amount of phenotypic variation explained by multi-locus models did not change substantially from RPR to RadjE for any of the populations (Table 2). This is not surprising when one considers the total amount of change resulting from the adjustment for EH. In Population 1, four QTL were lost, two QTL were gained, and two QTL were significantly increased in their effects, resulting in a slight reduction in total R^2 from 33.4 to 32.0%. In Population 2, four QTL were lost, one was gained, and two were significantly increased in their effects, resulting in slight a decrease in total R^2 from 44.7 to 41.7%. In Population 3, three QTL were lost, five were gained, and one QTL was significantly increased in its effect, resulting in a change in total R^2

from 48.4 to 49.6%. A balance in changes caused the total R^2 to remain the same; lost QTL caused a decrease in total R^2, while the novel QTL increased total R^2. While the RPR QTL represent a directly measured field trait, the RadjE QTL should be a better genetic estimate of the physiological trait of stalk strength independent of position of the ear on the stalk.

Interestingly, though, there was still a significant negative correlation between RadjE and EH in Populations 2 and 3, $r = -0.31$ ($P < 0.01$) and $r = -0.15$ ($P < 0.05$), respectively. The adjustment made to RPR did not remove all EH effects. This was surprising because of the lack of QTL in common between RadjE and EH for these populations. In Population 2, where the absolute value of the correlation was higher, there were no QTL in common between RadjE and EH, while in Population 3, where the correlation was lower, there were three QTL in common between RadjE and EH.

These results demonstrate that EH has a significant effect on RPR as reflected in the negative correlation. When the effects of EH were reduced, 11 of the 26 original RPR QTL lost their significance and eight gained significance. On the other hand, RPR is not merely determined by the ear's position on the plant. The majority of RPR QTL, 15 of 26, remained significant after adjustment for EH, and 11 EH QTL were detected that weren't linked to or overlapped RPR QTL. Moreover, the original RPR variable was still highly correlated with the adjusted variable, RadjE (Table 1).

There are many examples of phenotypic correlation between agronomic traits in maize, i.e., EH and flowering date (Beavis et al., 1994; Veldboom and Lee, 1996), etc. Photoperiod sensitivity may be used to explain partially the correlation between these two traits; however, EH and flowering date likely have distinct developmental and physiological pathways. Ultimately, dissecting the genetic basis of complex traits to their underlying physiological and biochemical bases is essential to enhance predictive modifications of crop plants (McMullen et al., 1998; Beavis et al., 1991). Knowledge of the proper physiological and biochemical pathways underlying the trait is also necessary to isolate the correct candidate genes for QTL when candidate genes for a correlated trait are located nearby.

The results of our study confirm the importance of examining correlated traits when conducting QTL experiments. Before initiating a QTL experiment, correlated traits which might influence measurement of the trait of interest should be determined. Then, one must ask if it is necessary to adjust for the correlated trait to improve measurements. To determine whether the correlated trait needs to be further studied, the variability of the correlated trait needs to be examined. A sample situation where analysis of correlated traits might be especially relevant is the stage of plant development during infestation–inoculation in entomology–pathology studies, particularly when a mixture of adapted and unadapted varieties is studied.

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