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ORIGINAL PAPER

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QTL analysis of lodging resistance and related traits in Italian ryegrass (*Lolium multiflorum* Lam.)

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Abstract Italian ryegrass (*Lolium multiflorum* Lam.) is the most widely cultivated annual forage grass in Japan. Lodging damage reduces both harvested yield and forage quality. To identify the chromosomal regions controlling lodging resistance in Italian ryegrass, we analyzed seven quantitative characters—heading date, plant height, culm weight, culm diameter, culm strength, tiller number, and culm pushing resistance—and evaluated lodging scores in the field in a two-way pseudo-testcross F_1 population. Significant correlations between most combinations of the traits examined were found. Seventeen QTLs for all traits except culm weight were detected on six of seven linkage groups by simple interval mapping using cross-pollination (CP) algorithm, and 33 independent QTLs were also detected by composite interval mapping from both male and female parental linkage maps. In addition, up to 18 QTLs for lodging scores evaluated at nine different times were detected on all linkage groups. The flanking markers of those QTLs will serve as a useful tool for marker-assisted selection of lodging resistance in Italian ryegrass.

Introduction

Italian ryegrass (*Lolium multiflorum* Lam.) is the most widely cultivated annual forage grass in Japan. Lodging damage reduces both yield by machine harvest and forage quality due to the pre-harvest sprouting of lodging culms. Therefore, lodging resistance is one of the most important goals in Italian ryegrass breeding. However, lodging is difficult to evaluate in the field, because not only is it a complex trait related to several factors, it is also caused by a combination of wind and rain and can be enhanced by pathogens and pests, affecting culms or roots. Other factors such as high nitrogen fertilization, high sowing density, and drought can also affect lodging (Brady 1934; Pinthus 1973; Easson et al. 1993; Crook and Ennos 1995; Milczarski and Masojc 2002; Sanchez et al. 2002).

Scoring for lodging resistance in the field can be inconsistent, as incidents causing lodging can occur at any stage of plant development or not at all (Atkins 1938). Therefore, it has always been a major aim of research to establish methods to assess lodging resistance independent of weather conditions (Heyland 1960). Most of the studies conducted so far have tried to find morphological traits that are correlated with lodging and could be used as indirect selection parameters. However, no single trait, or group of traits, has proven to be generally reliable as an index of lodging resistance. Therefore, marker-assisted selection could be an important tool to improve lodging resistance in cereals. Studies of QTLs for lodging resistance have been conducted on soybean (Mansur et al. 1993; Lee et al. 1996), barley (Backes et al. 1995; Hayes et al. 1995; Tinker et al. 1996), rice (Champoux et al. 1995), wheat (Keller et al. 1999; Börner et al. 2002), maize (Flint-Garcia et al. 2003), and field pea (Tar'an et al. 2003). Most studies have found that QTLs for lodging and plant height are linked or located in the same chromosomal region or regions.

In this paper, we describe the chromosomal positions and the contribution of putative QTLs affecting lodging resistance and related traits in Italian ryegrass, an outbreeding forage grass, and compare our results with the results obtained from QTL analysis of lodging resistance in other crop plant species.

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Materials and methods

Plant materials

A two-way pseudo-testcross F_1 population derived from a pair cross between single individuals selected from the Italian ryegrass cultivars Nioudachi (ND, resistant, as female parent) and Nigatawase (NW, susceptible, as male parent), consisting of 220 individuals, was used for linkage map construction and QTL analysis. The seeds of ND and NW were provided by Dr. T. Sasaki (Japan Grassland Farming and Forage Seed Association, Forage Crop Research Institute, Tochigi, Japan).

Phenotypic data collection

The F_1 mapping population and 32 individuals (not the individuals used for making F_1 population) of each parental cultivar were cultivated and evaluated at the Forage Crop Research Institute in April and May 2000. In the F_1 mapping population, however, only one individual

Table 1 The traits related to lodging resistance evaluated in the F_1 mapping population. *CD* Culm diameter, *CPR* culm pushing resistance, *CS* culm strength, *CW* culm weight, *HD* heading date, *LS* lodging scores, *PH* plant height, *TN* tiller number

Trait	Evaluation method
CD (mm)	Basal diameter of a culm measured two times at cross direction, the average of five culms per plant
CPR (g)	Degree of the culm strength for a whole plant, the value was the average of 100 culms (see text)
CS (gf)	Degree of the individual culm strength, the average of ten culms per plant (see text)
CW (g)	The average weight of five culms per plant
HD (days)	No of days to panicle emergence from April 1
LS (score)	1 (erect) – 9 (lodging), observed at nine different growing stages
PH (cm)	Distance from the ground to the top of the flag leaf
TN	Number of tillers per plant

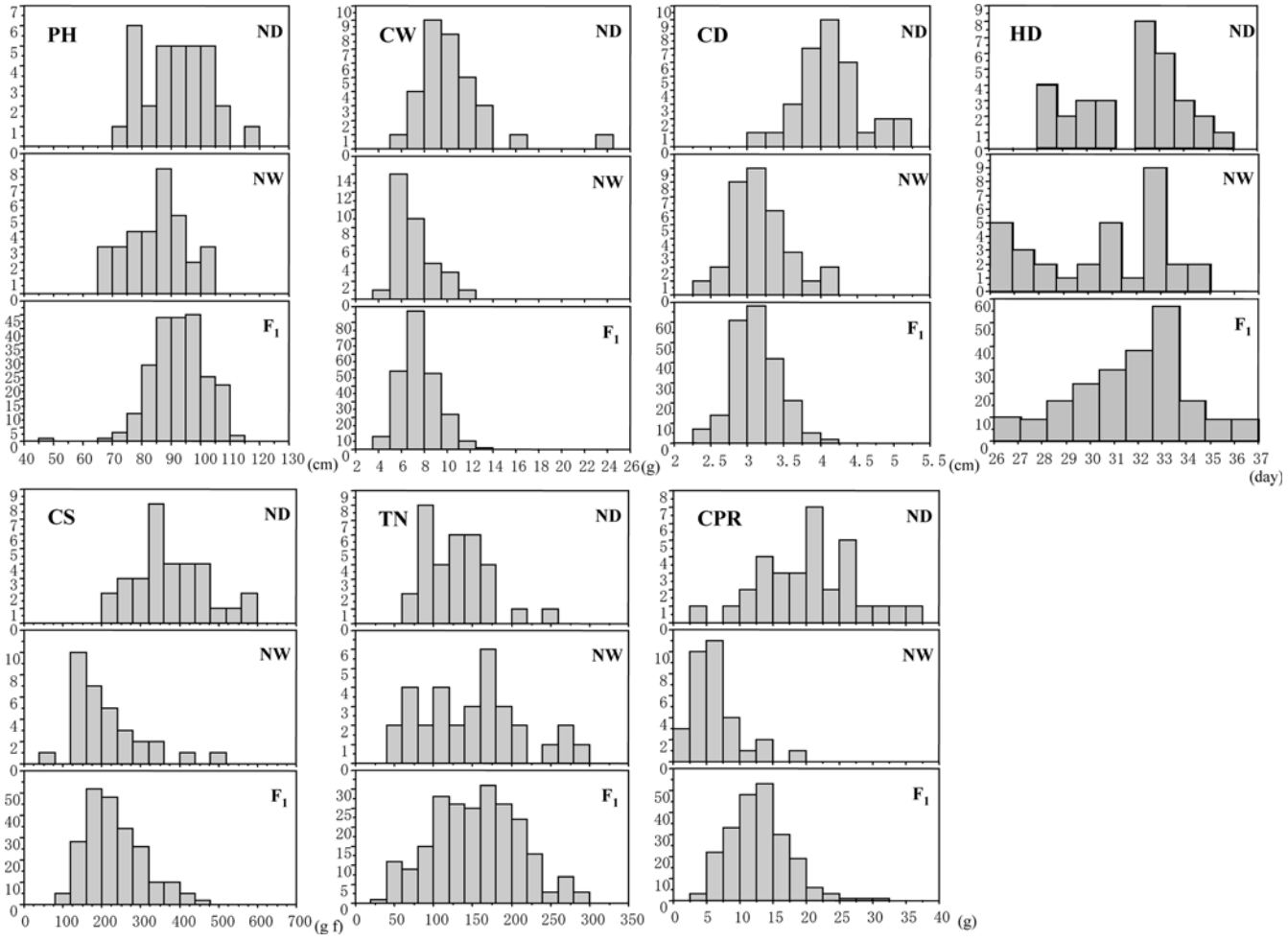

Fig. 1 Frequency distribution of six traits: plant height (*PH*); culm weight (*CW*); culm diameter (*CD*); culm strength (*CS*); tiller number (*TN*); and culm pushing resistance (CPR) and heading date of F_1 mapping population and two parent cultivars Nioudachi (ND) and Nigatawase (NW). *Bars* show number of individuals

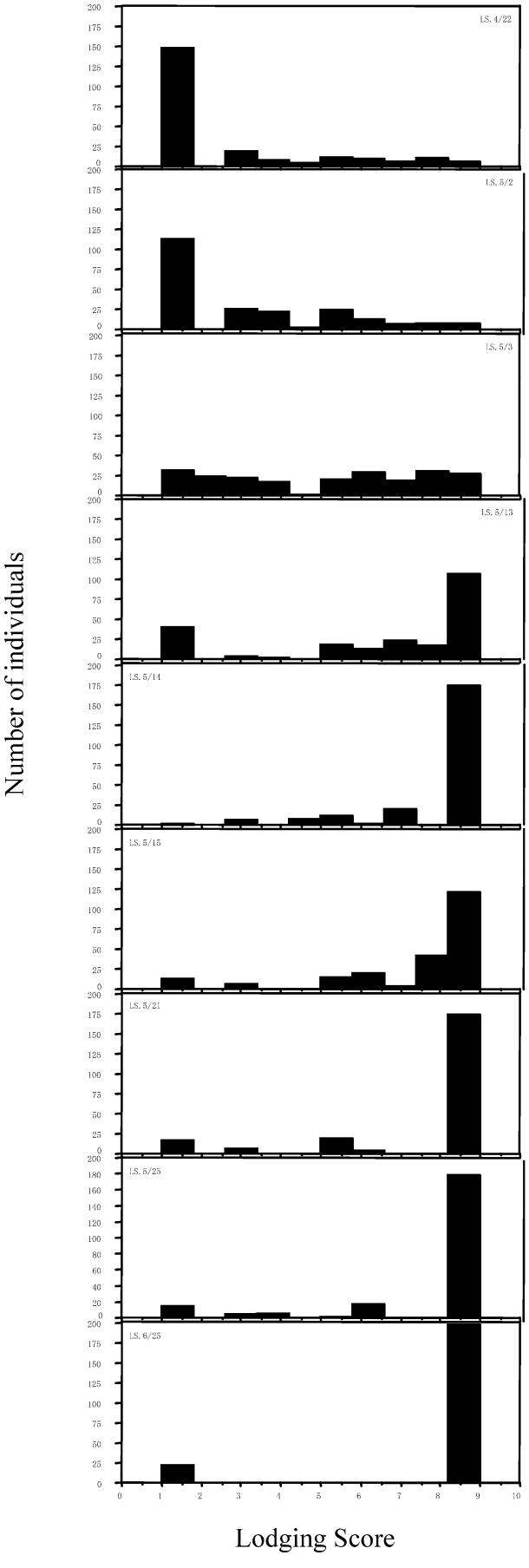

Fig. 2 Frequency distribution of lodging score of F_1 mapping population on nine dates. Lodging score (LS): 1 = resistant to 9 = susceptible

was evaluated for each genotype, because Italian ryegrass is a self-incompatible annual species, and no genotypic replications were available. All materials were sown on 15 September 1999 in paper pots in a greenhouse and transplanted into the field on 15 October 1999 at a density of 80×60 cm. A total of 1 kg each of nitrogen, phosphorus, and potassium per 100 m^2 was supplied.

On the basis of the results of previous published studies (Ohyama and Ishiguro 1986; Suginobu et al. 1989a, b) and our preliminary study (Z. Gao et al., in preparation), we selected the following traits that showed significant correlation with lodging resistance at the cultivar level for evaluation of lodging resistance: plant height (PH); culm weight (CW); culm diameter (CD); culm strength (CS); tiller number (TN); and culm pushing resistance (CPR). All these traits except for CPR were evaluated after heading. In addition, heading date (HD) was recorded. Lodging scores [(LS) 1 = erect to 9 = lodged] were evaluated nine times, immediately after rainy or windy days after the stage of internode elongation on 22 April, 2, 3, 13–15, 21, and 25 May, and 25 June.

Evaluation methods are briefly given in Table 1. The CS value was shown by the force required to break the basal part of a culm measured using a digital force gauge (FGX-0.5, Shimpo, Kuzetonosiro, Kyoto, Japan). CPR value was measured before heading with a Prostrate Tester (DIK-7401, Daiki Soil and Moisture, Nishiogu, Tokyo, Japan) set 20 cm from the ground against an unlodged plant. Reading of the tester when the plant was pushed to an angle of 45° was recorded.

Data analysis

Trait correlations and distribution histograms for each trait were calculated by StatView, version 5.0 (SAS Institute, Cary, N.C., USA).

We previously constructed a consensus linkage map including 385 (mostly RFLPs) markers on seven linkage groups at an LOD threshold value of 9.0 by using 82 individuals of the same mapping population (Inoue et al. 2004). From the map information and trait data in the present study, we determined putative QTL locations by using the simple interval mapping (SIM) method of MapQTL (van Ooijen and Maliepaard 1996) with the cross-pollination (CP) algorithm. We used LOD≥3.0 as a probability threshold for a significant QTL, and the one-LOD support region as a confidence interval for the location of a QTL on the genetic map.

To confirm the presence of putative QTLs, we separated the consensus map into two maps of the parents using only the markers with a segregation ratio of 1:1 and reanalyzed the QTL with the BC_1 algorithm of Windows QTL Cartographer, version 2.0 (Wang et al. 2004), using composite interval mapping (CIM). Both minimal LOD

Table 2 Correlation coefficients between all traits evaluated in the F_1 mapping population

	CD	CPR	CS	CW	HD	PH	TN	LS							
								4/22	5/2	5/3	5/13	5/14	5/15	5/21	5/25
CD															
CPR	0.436**														
CS	0.751**	0.420**													
CW	0.686**	0.214**	0.753**							*n*=220					
HD	0.092NS[a]	−0.015NS	0.136*	0.107NS											
PH	0.357**	0.352**	0.269**	0.383**	−0.250**										
TN	−0.302**	−0.186**	−0.261**	−0.115NS	−0.240**	0.132NS									
LS															
4/22	−0.250**	−0.388**	−0.122NS	0.135*	0.076NS	−0.129NS	0.256**								
5/2	−0.344**	−0.466**	−0.265**	−0.014NS	−0.045NS	−0.135*	0.487**	0.607**							
5/3	−0.294**	−0.393**	−0.265**	0.022NS	−0.194*	−0.054NS	0.590**	0.443**	0.612**						
5/13	−0.293**	−0.257**	−0.287**	−0.121NS	−0.089NS	0.204**	0.359**	0.226**	0.317**	0.467**					
5/14	−0.170*	−0.168*	−0.131NS	−0.018NS	−0.112NS	0.280**	0.326**	0.142**	0.229**	0.342**	0.591**				
5/15	−0.211**	−0.197**	−0.230**	−0.060NS	−0.109NS	0.333**	0.310**	0.204**	0.254**	0.332**	0.668**	0.811**			
5/21	−0.197**	−0.151*	−0.247**	−0.092NS	−0.096NS	0.242**	0.340**	0.163*	0.200**	0.332**	0.617**	0.710**	0.784**		
5/25	−0.245**	−0.226**	−0.324**	−0.141*	−0.132NS	0.203**	0.338**	0.162*	0.245**	0.391**	0.670**	0.724**	0.795**	0.844**	
6/25	−0.093NS	−0.044NS	−0.023NS	0.029NS	−0.100NS	0.177**	0.201**	0.161*	0.174*	0.327**	0.506**	0.416**	0.423**	0.387**	0.358**

Significance levels: *P=0.05, **P=0.01
[a]*NS* Not significant

Table 3 Putative QTLs related to lodging resistance detected by simple interval mapping under cross-pollination (*CP*) algorism of MapQTL and composite interval mapping under backcross algorism of Windows QTL Cartographer in the F_1 mapping population

Traits	QTL	Origin	Flanking markers	Linkage group	LOD score	Explanation (%)	Additive effect
CD	*qCD4*	CP	tp1 k123–IRG252-2	4	3.2	17.0	
	qCD-f1.1	BC, female	tp3d301–IRG318-6	1	3.1	12.7	0.23
	qCD-f1.2	BC, female	AAA-CGG11–CDO78-2	1	2.4	9.0	0.19
	qCD-f5.1	BC, female	IRG5-4–IRG56-5	5	3.1	11.7	0.22
	qCD-f5.2	BC, female	IRG37-5–tp4d303	5	2.5	15.0	−0.30
	qCD-m1	BC, male	tp3d301–tp4d301	1	2.3	6.9	0.17
	qCD-m3	BC, male	tp3d29–CDO460-3	3	2.6	10.7	−0.21
	qCD-m4	BC, male	AGA-TAA211–AAC-CAT8	4	2.4	8.8	−0.19
	qCD-m7	BC, male	IRG26–AGT-AAG12	7	3.0	10.8	0.21
CPR	*qCPR1*	CP	tp4d307–IRG303-2	1	3.1	33.9	
	qCPR4	CP	tp3d303–tp1d302	4	3.4	27.3	
	qCPR5-1	CP	tp4d303–IRG320	5	4.8	23.8	
	qCPR5-2	CP	CDO459–CDO202-2	5	5.6	31.8	
	qCPR5-3	CP	tp3d21–AGG-CGG3	5	6.7	49.9	
	qCPR6	CP	AGA-AAT8–AAT-TAG7	6	3.1	25.8	
	qCPR-f1	BC, female	AAA-CGG11–AGC-CCT7	1	4.4	13.9	3.88
	qCPR-f4	BC, female	tp3d303–tp1d302	4	2.0	6.1	−2.60
	qCPR-f6	BC, female	AAT-CCC9–AAT-TAG31	6	3.6	11.0	−3.63
	qCPR-m4	BC, male	CDO20–tp3d211	4	2.1	8.5	−2.99
	qCPR-m5	BC, male	tp4d217–IRG305	5	6.5	29.4	6.05
	qCPR-m7	BC, male	tp3d27–tp4d224	7	3.9	19.3	−4.95
CS	*qCS4*	CP	IRG252-1–IRG250-2	4	3.6	18.8	
	qCS-f1.1	BC, female	tp3d301–IRG318-6	1	3.7	16.3	67.14
	qCS-f1.2	BC, female	tp3d221–AGT-CAC10	1	2.4	9.6	65.87
	qCS-f1.3	BC, female	tp3d23–tp3d217	1	2.1	8.1	46.98
	qCS-m1	BC, male	IRG150–IRG318-3	1	2.7	11.5	57.76
	qCS-m5	BC, male	AGG-CGG3–IRG115	5	2.3	11.3	−57.12
CW	*qCW-f1*	BC, female	tp3d221–AGT-CAC10	1	2.2	7.8	1.26
	qCW-f3	BC, female	tp4d29–IRG296	3	2.3	8.3	1.03
	qCW-f7.1	BC, female	IRG60-2–AGA-AAT12	7	3.0	15.0	−2.09
	qCW-f7.2	BC, female	AGA-CGG17–IRG286	7	3.1	12.1	−1.61
	qCW-m1	BC, male	tp3d221–AGT-CAC10	1	3.2	14.1	1.67
HD	*qHD6*	CP	CDO516-IRG144-1	6	4.2	28.9	
	qHD7	CP	tp3d27-tp4d224	7	3.2	24.3	
	qHD-f4	BC, female	IRG27–IRG39-1	4	3.0	17.8	1.78
	qHD-f6	BC, female	tp1d307–tp1d22	6	2.2	7.3	1.17
	qHD-f7	BC, female	tp4d220–tp4d224	7	4.1	12.6	1.49
	qHD-m3	BC, male	IRG39-2–IRG226-2	3	2.1	6.7	−1.08
	qHD-m4	BC, male	CDO38–AGT-TAC11	4	3.3	11.1	1.37
	qHD-m6	BC, male	AGT-AAG10–tp1d307	6	5.7	17.7	1.74
	qHD-m7.1	BC, male	IRG91-6–tp1d305	7	3.9	14.3	−1.57
	qHD-m7.2	BC, male	tp3d27–tp4d224	7	3.6	17.2	1.84
PH	*qPH1-1*	CP	IRG303-2–IRG321-3	1	5.8	39.1	
	qPH1-2	CP	tp3d23–AGG-CCA30	1	3.0	17.3	
	qPH4	CP	IRG123–IRG173	4	3.0	15.8	
	qPH5	CP	IRG37-5–IRG37-4	5	5.5	36.4	
	qPH7	CP	IRG4-1–AAT-AAG9	7	3.9	28.0	
	qPH-m1	BC, male	IRG321-4–IRG235-2	1	2.6	16.6	−8.67
	qPH-m4	BC, male	tp3d211–tp1 k121	4	3.7	13.1	21.68
	qPH-m6	BC, male	CDO1380–tp3d306	6	2.6	9.0	5.81

Table 3 (continued)

Traits	QTL	Origin	Flanking markers	Linkage group	LOD score	Explanation (%)	Additive effect
TN	*qTN2*	CP	CDO345–AAG-CCA6	2	3.7	44.3	
	qTN7-1	CP	IRG136-3–IRG94	7	3.4	17.9	
	qTN-f2	BC, female	CDO244-4–tp4d27	2	2.4	8.6	−30.55
	qTN-f3	BC, female	CDO920-4–CDO920-2	3	2.3	12.9	38.61
	qTN-f6	BC, female	tp1d307–tp1d22	6	2.1	9.1	−32.34
	qTN-m7.1	BC, male	AGT-AAG12–IRG94	7	3.1	12.6	−39.18
	qTN-m7.2	BC, male	IRG313-1–IRG91-1	7	3.6	15.4	72.30

threshold of 2.0 and the LOD threshold generated by 300 times permutation tests at a 0.05 significant level (from 3.1 to 4.1 depends on the trait) were used to detect putative QTLs.

The QTL nomenclature followed the rules described by McCouch et al. (1997).

Results and discussion

Distribution and correlation of traits

Figure 1 shows the frequency distribution of the parent cultivars and the F_1 population in the seven traits other than LS. Two parent cultivars, ND and NW, that differ in mean values particularly in CW, CD, CS, and CPR, showed a nearly normal distribution within each cultivar except for HD. This might be due to the high heterozygosity of Italian ryegrass, which is an open-pollinated species. F_1 populations showed also nearly normal distributions in all traits. The mean value of the F_1 population tended to approach to that of one parent, NW, in CD, CS, and CW, but intermediate between the two parents in CPR.

Figure 2 shows the lodging scores in evaluation date order in F_1 population. Most individuals were erect on 22 April and 2 May. About half were lodging on 3 May, and most were lodging on and after 13 May.

As shown in Table 2, the seven traits supposedly related to lodging were mostly correlated with each other, except

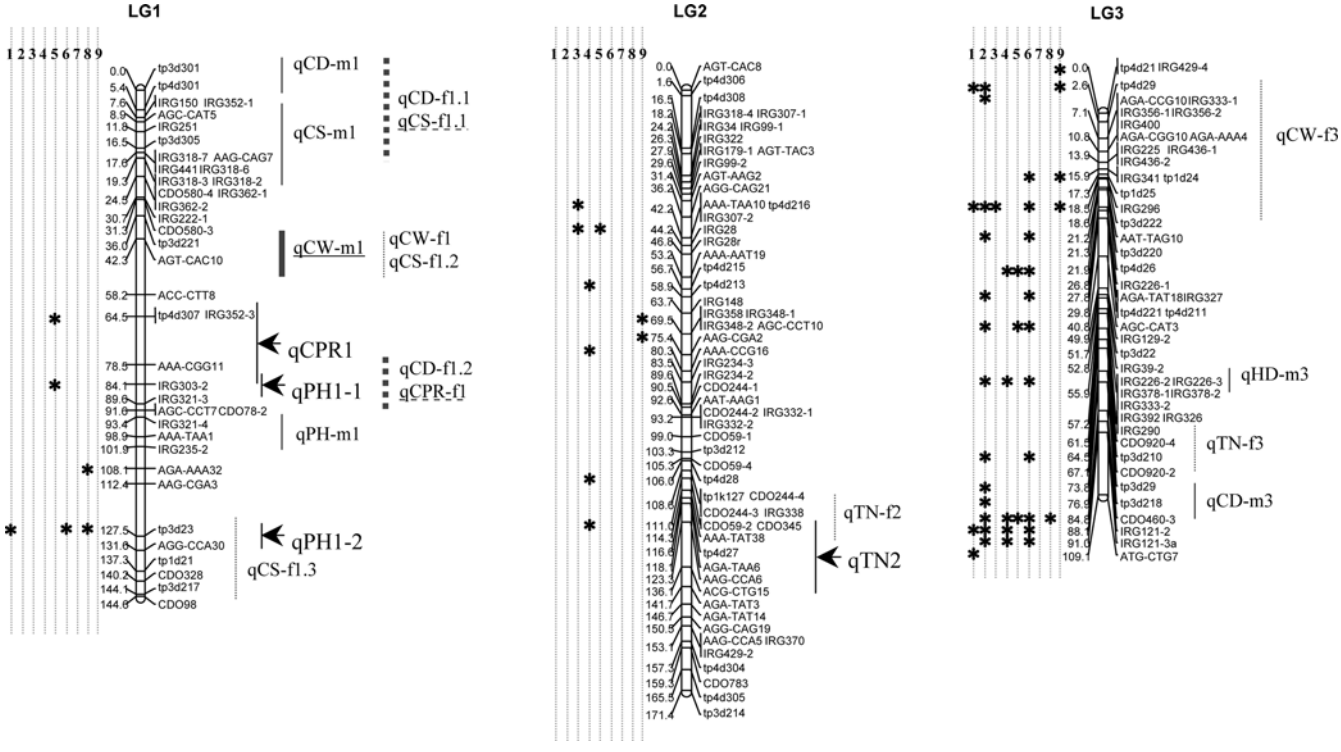

Fig. 3 Genetic linkage map of Italian ryegrass showing QTLs for seven traits and LS distributed over seven linkage groups (*LGs*). The QTLs for the six traits detected by simple interval mapping of MapQTL are given on the *right side* of each LG, indicated by an *arrow*. The composite interval mapping (CIM) QTLs detected from the male parent are indicated by *solid line* with the name *qXX-m*x and the CIM QTLs detected from the female parent are indicated by *dotted line* with a name *qXX-f*x. The QTLs *underlined* were detected also by a permutation test of CIM at a 0.05 significant level. Supported intervals for each QTL are indicated by *vertical bars*. QTLs for LS detected by the Kruskal–Wallis test are marked on the *left side* of each LG. Numbers 1–9 are the evaluation dates: *1* 22 April, *2* 2 May, *3* 3 May, *4* 13 May, *5* 14 May, *6* 15 May, *7* 21 May, *8* 25 May, *9* 25 June

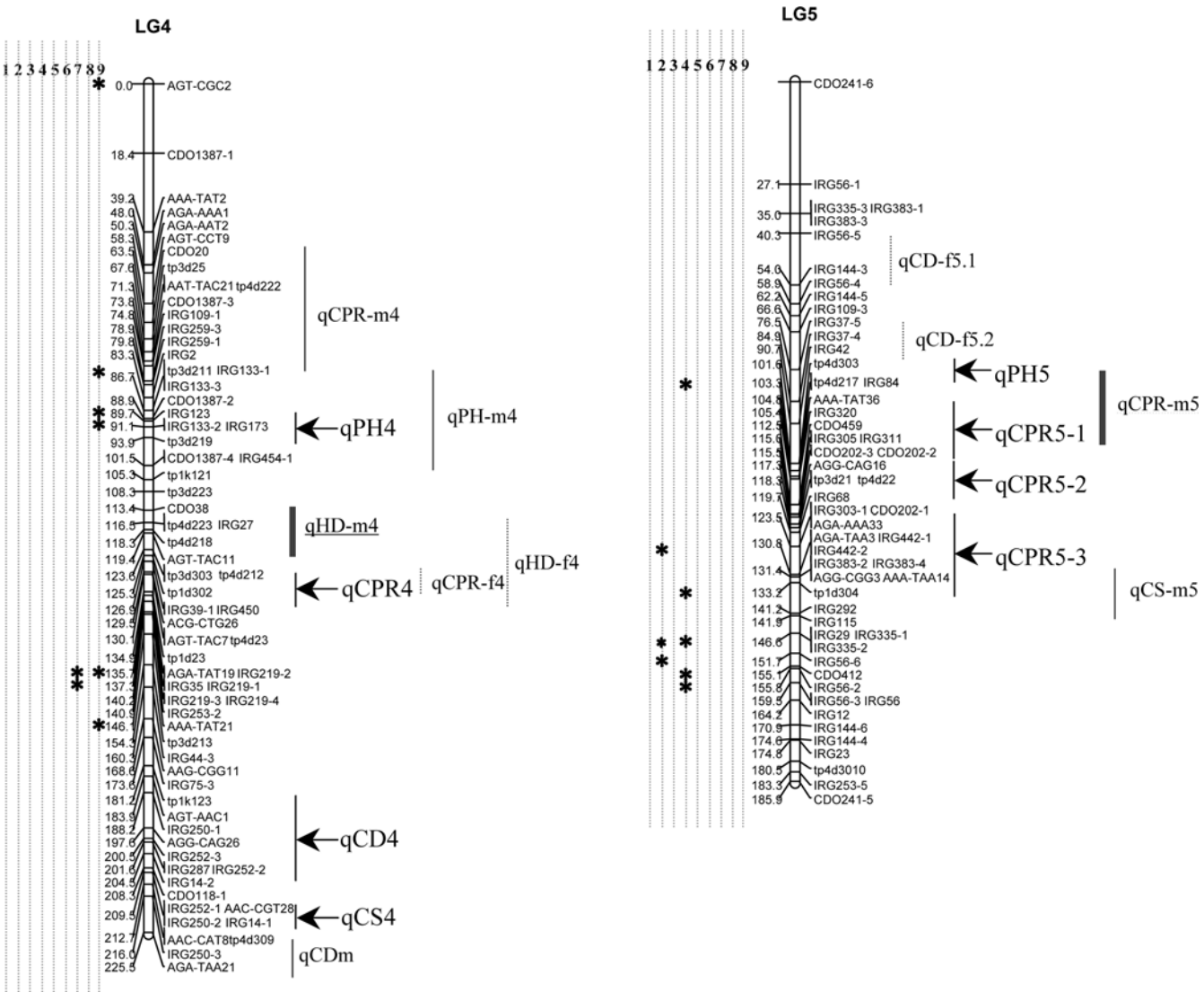

Fig. 3 (continued)

that HD was not always related with others. The correlations of CS/CD, CW/CD, and CW/CS were highest. Correlations between LS recorded at seven different dates were all significant. The correlation coefficients between LS evaluated at later dates were higher than the others. Most correlations between all LS (except 25 June) and the examined traits except CW and HD were significant. This result agrees with the results of Suginobu et al. (1989a). General absence of correlations between HD and lodging resistance observed in the present study differs from the results reported by Keller et al. (1999) in wheat and Suginobu et al. (1989a) in Italian ryegrass, who reported significant correlations between HD and LS.

QTL analysis

Seventeen QTLs for all traits except CW were detected at LOD>3.0, using the SIM method of MapQTL (Table 3; Fig. 3). Of them, six QTLs for CPR were detected on four linkage groups (LGs), LG1, LG4, LG5, and LG6, and explained 23.8–49.9% of total variance, five QTLs for PH were detected on four linkage groups (LG1, LG4, LG5, and LG7) and explained 15.8–39.1% of total variance; two QTLs for TN detected on LG2 and LG7 explained 44.3% and 17.9% of total variance, respectively; two QTLs for HD detected on LG6 and LG7 explained 28.9% and 24.3% of total variance; and one QTL for CD and one for CS detected on LG4 explained 17.0% and 18.8% of total variance. No significant QTLs for CW were detected. The results of SIM by QTL Cartographer were almost same with that detected by MapQTL.

Among the 17 QTLs detected above, flanking markers of three QTLs (*qPH5*, *qPH7*, and *qCPR4*) were not significant by single-point analysis of variance by the CP algorithm of MapQTL (the Kruskal–Wallis test), though data were not shown. To confirm whether those QTLs detected by the CP algorithm were truly present, we separated the consensus linkage map into two parental linkage maps and re-analyzed those QTLs by the BC_1

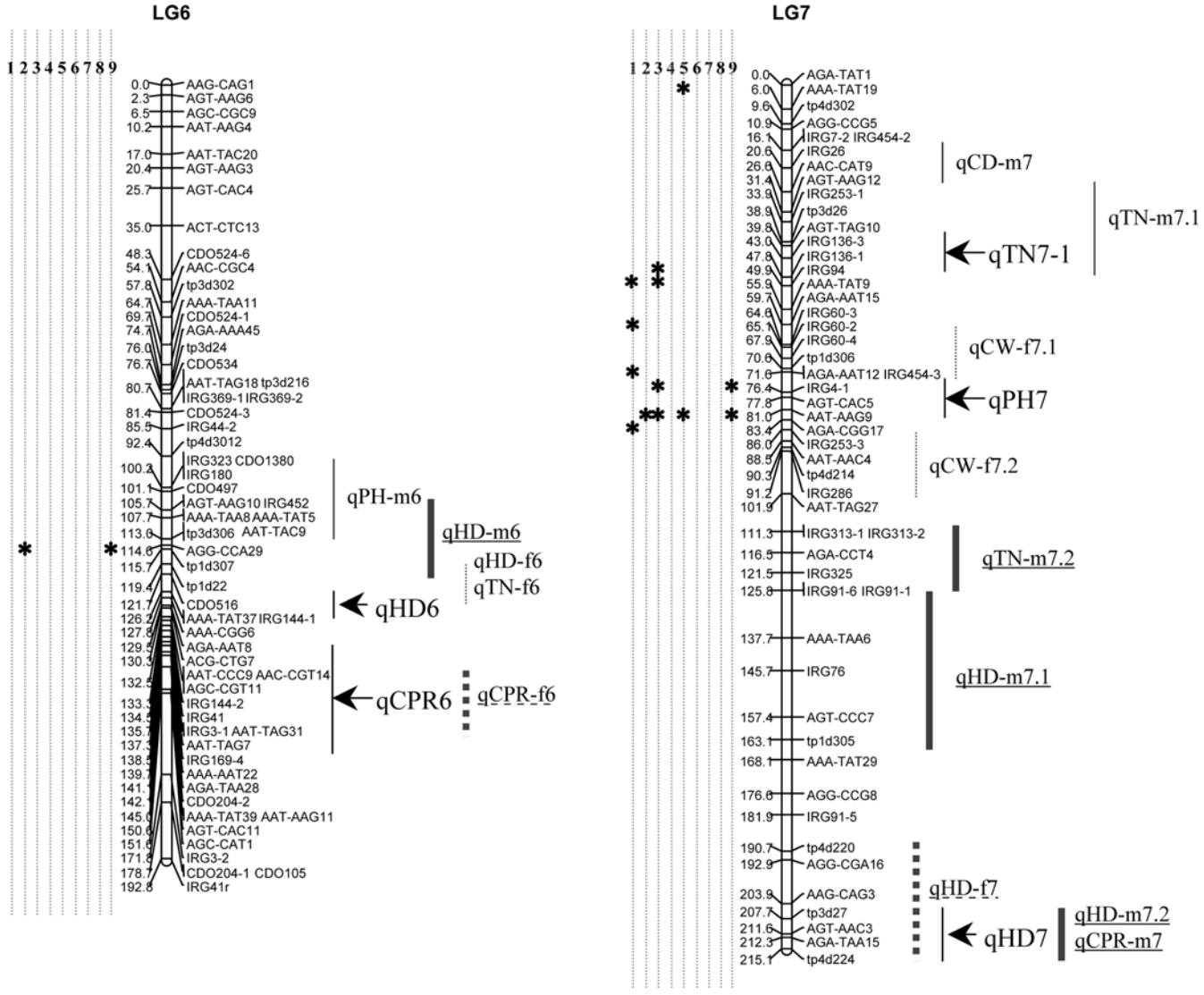

Fig. 3 (continued)

algorithm, using the CIM methods of Windows QTL Cartographer. A total of 33 independent QTLs were detected from both male and female parental maps (20 each) at an LOD=2.0 level for all seven traits explaining 6.7–29.4% of total variance (Table 3; Fig. 3). Nine of them were detected in the same region as detected by the SIM method of MapQTL; some QTLs detected by SIM method could not be detected by CIM, for example, *qPH1-2*, *qCD4*, *qCS4*, *qCPR5-2*, *qCPR5-3*, and *qPH7*. On the other hand, QTLs such as *qCD-f1.1* and some others were detected only by CIM, probably because some QTLs—especially groups with similar magnitude in tight repulsion linkage—are only resolved by CIM. The flanking markers of *qPH5* and *qPH7*, which were not significant by the CP algorithm, were also not significant by QTL Cartographer. In addition, 12 QTLs from two parental maps were detected when the LOD value was set to the values generated by a 300 times permutation test at a 0.05 significance level. Of them, five QTLs were located on the same or very close region of the QTLs for the same trait detected by MapQTL. The interactions between QTLs detected were not found at this analysis.

Because the LS distributions were not normal, we conducted only the nonparametric Kruskal–Wallis test to find the QTLs affecting LS. Regions showing significance at the 1% level are shown in Fig. 3. Eight QTLs were detected in samples collected on 22 April (1), 18 on 2 May (2), 7 on 3 May (3), 14 on 13 May (4), 11 on 14 May (5), 17 on 15 May (6), 2 on 21 May (7), 3 on 25 May (8), and 15 on 25 June (9). Some QTLs for LS were located in the same regions as QTLs for other traits, for example, at *qPH1-2* (LG1) and *qPH7* (LG7). It should be noted that most QTLs for LS were detected on LG3. On LG3, SIM detected no QTLs for other traits, but CIM and single-point analysis (data not shown) identified some significant markers for other traits.

Correlation between lodging resistance and plant height

A number of studies have found that QTLs for lodging resistance and QTLs for plant height are linked or located in the same regions (Mansur et al. 1993; Backes et al. 1995; Hayes et al. 1995; Lee et al. 1996; Tinker et al. 1996; Keller et al. 1999; Börner et al. 2002; Tar'an et al. 2003). Our results also showed QTLs for LS are nearly located to QTLs for plant height on LG1, LG4, LG5, and LG7. In addition, QTLs for CPR and QTLs for plant height were near or overlapped on LG1, LG5, and LG6.

Comparison between our results and QTLs related to lodging resistance in other crops

The genomic studies of Italian rye grass, not only marker development but also QTL analysis, have lagged behind that of other major crops. The synteny among Italian rye grass, wheat, and rice was pointed out by several studies (Jones et al. 2002; Inoue et al. 2004). QTL information published in other major crops such as wheat, maize, and rice will facilitate the progress of Italian rye grass QTL analysis in the future. Börner et al. (2002) detected three QTLs related to lodging in wheat, two on chromosome 2 and one on chromosome 6. In our results, although the heterologous anchor probes used were limited, the QTL region for CPR, *qCPR6*, was mapped to LG6, which shows synteny with chromosome 6 of wheat (Inoue et al. 2004).

Lignin is an important constituent of plant cell walls (Moore and Hatfield 1994). It has long been proposed that lignin synthesis might be related to stem strength. Reduced lignin levels have been observed in *brown-midrib* mutants of maize (Kuc and Nelson 1964; Kuc et al. 1968; Gentinetta et al. 1990) and are associated with reduced stem strength. Cardinal et al. (2003) detected 65 QTLs related to fiber and lignin content in maize. A QTL of acid detergent lignin reported by Cardinal et al. (2003), found near *umc54* on chromosome 5, was near the QTL region of CPR on LG6 in our result. To collect more detailed information of synteny between the QTLs we detected with those in other crops, mapping of more common markers such as RFLP or expressed sequenced-tag markers will be needed.

In this study, we detected a total of 17 QTL for six traits related to lodging resistance and HD by the SIM and 33 independent QTLs from male and female parents by CIM. Among them, the QTLs, *qCPR1*, *qCPR5-1*, *qHD6*, *qCPR6*, and *qHD7* were detected in both SIM and CIM and had higher LOD values. The flanking markers of those QTLs will serve as a useful tool for marker-assisted selection of lodging resistance in Italian ryegrass.

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