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QTL mapping of seedling root traits in Synthetic W7984 × Opata M85 bread wheat (*Triticum aestivum* L.) mapping population

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Abstract: Root system architecture, as a complex trait, has gained attention due to climate change and abiotic stress pressure on crops. The incorporation of root traits in breeding objectives may enable new advances in climate-resilient crops. Here, the genetics of the seedling root system architecture in the Synthetic W7984 × Opata M85 Doubled Haploid mapping population was investigated. Three traits at the seedling stage and mature stage root and shoot biomass traits were mapped for quantitative trait loci (QTL) identification. A total of five different loci on chromosomes 1B, 5A, and 7D with major effects were identified for total root length, primary root length, and seminal root growth angle. Four regions on chromosomes 2A, 5A, and 7D had colocating loci for seedling and mature stage root traits. Chromosome 5A, with a locus affecting most of the seedling root traits, is promising. The correlations between seedling and mature root traits, and newly identified QTL for seedling root traits, maybe promising to unravel the genetic structure of root traits and for the marker-assisted selection.

Keywords: *Aegilops tauschii*, amphiploid, QTL, seminal root growth angle, root length

1. Introduction

Bread wheat (*Triticum aestivum* L.) is the staple crop of more than half of the world population with more than 760 million tonnes of production (FAOSTAT, 2019). Even though there is a continuous effort to increase grain yield, there is still a need for 1.5 to 2 times more production by 2050 (Ray et al., 2013). There are many factors limiting grain yield improvement including but not limited to drought, salinity, toxicity, as well as many other abiotic and biotic factors (Godfray et al., 2010). The global average yield of bread wheat is about 3.5 t/ha, while some countries are achieving much higher or lower yields (Hawkesford et al., 2013).

Bread wheat is an allohexaploid of three wild species with diploid genomes: *Aegilops speltoides* Tausch (SS) the "B" genome, *Triticum urartu* Tum. ex. Gandil (AuAu) the "A" genome and *Aegilops tauschii* Coss. (DD) the "D" genome donors (Kihara, 1944; Dubcovsky and Dvorak, 2007). Thousands of years of evolution, natural and artificial selection and hybridization events gave rise to today's wheat. The twentieth century became the golden era of wheat breeding with new cultivars being released which improved agronomic performance. Resistance/tolerance to dozens of diseases was developed and lodging and day length sensitivity issues were mostly resolved (Salamini et al., 2002). The Green Revolution was a notable milestone with most of the outcomes above mentioned. The introduction of the so-called dwarfing genes (*Rht*) into European and American gene pools as well as *Ppd* (day length insensitivity) genes was a success for wheat breeders (Pingali, 2012; Salvi et al., 2013). However, the loss of genetic diversity is one major setback of modern breeding and the Green Revolution, and farmers quickly adopting modern cultivars over traditional varieties or landraces. Modern cultivars were readily accepted because some landraces were not fit for mechanical farming and were prone to lodging when synthetic fertilizers applied. The *Rht* and *Ppd* genes in addition to irrigation and fertilizer applications were the main reasons for the replacement of old varieties and landraces (Pingali, 2012). There was a significant loss of genetic diversity within the last century due to the replacement of landraces with modern cultivars (Van de Wouw et al., 2010; Jaradat, 2012). The importance and necessity of genetic variation are widely recognized within the last couple of decades and efforts to protect or extend available diversity have gained a lot of attention (Jaradat, 2012; Castaneda-Alvarez et al., 2016).

The need for synthetic hexaploids was born due to the limited diversity available in the modern wheat gene

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pool (Mujeeb-Kazi et al., 1996). Synthetic hexaploids are manmade amphidiploids created by crossing durum wheat and *Ae. tauschii*. The Synthetic W7984 was crossed with cv. Opata M85 and the first International Triticeae Mapping Initiative (ITMI) recombinant inbred (RIL) population was created in the 90s (Mujeeb-Kazi et al., 1996). It was widely used around the world as a resource for breeding programs, genetic marker development, and QTL mapping (Sorrells et al., 2011). Synthetic W7984 × Opata M85 doubled haploid (SynOpDH) and recombinant inbred (SynOpRIL) populations were recreated (Sorrells et al., 2011) and continued to be distributed to wheat researchers.

The original ITMI population has been studied extensively since the 1990s (Mujeeb-Kazi et al., 1996; Sorrells et al., 2011). Mohammadi et al. (2007) reported significant diversity among progeny and lines. According to their results, the synthetic line had a more efficient stress response, higher relative water content, leaf water content, and less wilting compared to Opata M85. Similarly, Landjeva et al. (2008) reported 35 QTLs on chromosomes 1A, 1B, 2A, 2B, 2D, 3D, 5B, 6B, 6D, and 7D associated with the root, coleoptile, and shoot length, and root/shoot ratio in the same population. Significant differences in drought tolerance between the two parents encouraged us to identify genome regions related to seedling root architecture that may be causing these differences.

Previous studies on various mapping populations in bread wheat reported many QTLs for the longest root length (Landjeva et al., 2008; Liu et al., 2013; Zhang et al., 2013a; Botwright Acuña et al., 2014, Kabir et al., 2015, Petrarulo et al., 2015); total root length (TRL) (Sanguineti et al., 2007; Li et al., 2011; Bai et al., 2013, Liu et al., 2013, Canè et al., 2014); deep root ratio (Hamada et al., 2012) and the number of root tips or seminal roots (Liu et al., 2013; Christopher et al., 2013, Zhang et al., 2013a; Canè et al., 2014; Kabir et al., 2015; Petrarulo et al., 2015). Seminal root growth angle (RA) was also studied quite common and QTL for RA were reported on various chromosomes (Oyanagi 1994; Manschadi et al., 2007; Christopher et al., 2013; Liu et al., 2013; Canè et al., 2014). Genotypes with narrow RA tend to have a deeper root system, while a wide RA is advantageous for mineral nutrient uptake (Hamada et al., 2012; Christopher et al., 2013; Canè et al., 2014). Each root ideotype (Lynch, 2013) has advantages and limitations under different stress conditions. There is a need for incorporating root traits in breeding objectives, however, due to excessive labor requirements in root studies, this is still not feasible.

Marker-assisted selection (MAS) of root traits may enable early selection, otherwise, the inclusion of root-related traits in breeding programs would not be realistic in near future. There is a need for finding gene-based single nucleotide polymorphism (SNP) markers for root traits, especially for traits such as root growth angle, deep rooting, root surface area, total root length, and the number of roots. Genomic and phenomics tools still have very limited use in wheat root system studies and breeding. Therefore, this study aims to: 1) identify QTL for seminal root traits under controlled conditions and, 2) coanalyze seedling and mature root traits for possible pleiotropic interactions.

2. Materials and methods

2.1. Experimental design and plant material

Seed samples of the SynOpDH mapping population were provided by Dr. Mark Sorrells, Department of Plant Breeding and Genetics, Cornell University, Ithaca, NY. The population consists of 215 double haploids (DH) lines generated from the F1 hybrid of Synthetic W7984 with cv. Opata M85. Synthetic W7984 is a manmade amphiploid generated by crossing the durum wheat line, 'Altar 84' (*Triticum turgidum* L.), with the accession (219) 'CIGM86.940' of *Aegilops tauschii* Coss. (Mujeeb-Kazi et al., 1996). From the entire set of DH lines in the SynOpDH population 147 lines and parents were selected for the experiments to benefit from the vast pool of SNP data published in Poland et al. (2012).

2.2. Seminal root trait phenotyping

The DH lines of the SynOpDH population were phenotyped for seminal root traits using a modified version of the cigar roll method (Zhu et al., 2006). The system has similarities to the Cyg germination growth pouches (Mega International, West St. Paul, MN, USA). It consisted of two plexiglass plates 20 cm × 30 cm fitted with spacers, germination paper, racks holding the plates upright, and tubs used to hold water. Details of the experimental design were given in Hohn and Bektas (2020). Briefly, seeds of similar size from each line were sterilized with 1% sodium hypochlorite (NaClO) solution and rinsed with distilled water. Seeds were imbibed in distilled water for 24 h to initiate uniform germination. The next day, germination papers were wetted with deionized water and placed on plexiglass plates. Two seeds (with embryos down 5 cm below the top edge of the paper and 8 cm apart) were placed on germination papers and the second layer of germination paper was placed on top of the other one. Experiments were designed according to randomized complete block design with eight replications and two plants per replication. The plexiglass plates were placed in a tub with approximately 45° angle and the water level was kept at approximately 10 cm deep. Seedlings were grown for 7 days at room temperature without supplemental lighting in a head house (20–30 °C and 50%–90% relative humidity) at the University of California, Riverside from November 2014 to February 2015. The plates were

removed from the tubs, disassembled, and seminal roots were imaged using a handheld digital scanner (VuPoint Solutions, Magic Wand PDS-ST415-VPS) set to 300 DPI. First, the top layer of the plexiglass and the germination paper were removed, and images were collected by scanning from seed level to root tips. Seminal root length and growth angles were measured using the angle and measurement tools in ImageJ (Schneider et al., 2012). Data for the number of the seminal root (NOR), the longest root length (LRL), primary root length (PRL), total root length (TRL), and seminal root growth angle (the angle between the first set of seminal roots (RA) were collected from the image analysis. Data used from Bektas et al. (2020) for the comapping of seedling and mature traits were root biomass 2013 (RM2013), shoot biomass 2013 (SM2013), shallow root weight 2013 (SRW2013), days to anthesis 2013 (DTA2013), grain yield 2013 (GY2013), plant height 2013 (PH2013), root length 2013 (RL2013), deep root weight 2013 (DRW2013), and same data for 2014. Details of the experimental design and data collection procedures for mature root traits were given in Bektas et al. (2020).

2.3. Genetic mapping

The genetic linkage map was generated using a total of 1485 SNP markers obtained from Poland et al. (2012). Markers that were polymorphic between parents were assigned to linkage analysis using JoinMap 4.1 (Van Ooijen, 2006) software. Identical individuals and the ones with more than 10% missing data were excluded. Linkage mapping was done on a chromosome-by-chromosome basis including only markers mapped to a given chromosome. Markers with identical locations were removed prior to mapping. Groupings and linkage groups were made using the default settings for independence LOD and maximum likelihood algorithm, respectively. Kosambi function was used to convert recombination frequencies (Θ) to map distances in cM values (Kosambi, 1944).

2.4. Statistical analysis and QTL mapping

Statistical analyses were performed using the Statistix v10 software (Analytical Software; Tallahassee, FL, USA). The normality of data distribution was tested by normal probability plots. Analysis of variance (ANOVA) (Steel et al., 1997) was performed to evaluate the main phenotypic effect of the genotype for all traits. Heritability (H^2) was calculated as $H^2 = VG/VP$, where VG is the genetic variance and VP is the phenotypic variance by using the ANOVA function of the software package ICIMapping v4.1 (Meng et al., 2015). Quantitative trait loci (QTL) analysis was performed with Windows QTL Cartographer v2.5 software (Wang et al., 2012) using the linkage map for the population and the mean phenotypic values. The composite interval mapping (CIM) method (Model 6: Standard model with backward regression method) with a step of 1 cM (walk speed and window size) was used and the threshold for QTL detection was determined using 1000 permutations where $\alpha = 0.05$. The LOD threshold was auto affixed to CIM analysis for identification of major QTLs at $p = 0.05$; the LOD score was reset to the value of 2.5 for minor loci detection. The walk speed of 1.0 cM was chosen for all QTL detection. Genotype mean values of mature root traits from the previously published (Bektas et al., 2020) data for the same population were used to comap seedling and mature root traits.

3. Results

3.1. Genetic variation in seminal root traits

Analysis of variance (ANOVA) was performed to evaluate the diversity of SynOpDH progeny and parental lines for seedling root architectural traits. Phenotypic variation for TRL, PRL, and RA were significant ($p < 0.01$) for the 147 lines in SynOpDH population (Table). Mean, minimum and maximum values for all traits showed wide genetic variation. Minimum and maximum values for PRL, TRL, and RA were between 0.01–36.92 cm, 6.27–125.11 cm, and 25.32–143.02°, respectively (Table). Broad sense heritability was 0.49 for RA, 0.61 for PRL, and 0.83 for TRL.

3.2. QTL identification for seminal root traits

The SynOpDH population is a standard population mapped multiple times. The SNP data created by Poland et al. (2012), using a two-enzyme genotyping-by-sequencing (GBS) approach, was used for linkage and QTL analysis. A

Table. Mean values, standard deviations (SD), variance, standard errors (SE), coefficient of variations (CV), minimum and maximum values, skewness and kurtosis, and broad-sense heritability (H^2) values for the primary root length (PRL), total root length (TRL) and seminal root growth angle (RA) traits of SynOpDH biparental doubled haploid mapping population.

	PRL-(cm)	TRL-(cm)	RA-°(degrees)
N	2371	2371	2305
Mean	22.30	55.40	77.90
SD	6.48	14.79	16.49
Variance	42.04	218.78	272.03
SE mean	0.13	0.30	0.34
C.V.	29.08	26.70	21.17
Minimum	0.01	6.27	25.32
Maximum	36.92	125.11	143.02
Skew	–0.6603	0.20	–0.12
Kurtosis	7.88E-03	1.01	0.24
H^2	0.61	0.83	0.49
p	0.0001	0.0001	0.0001

total of 1485 GBS SNP markers were placed on 21 linkage groups with a total of 3243.53 cM map length. The average distance between the two markers was 2.18 cM. Using the linkage map, a number of marker-trait associations for all traits (Figure 1) were identified. A locus is considered a QTL when the LOD score was equal to or above 3.0. However, in order not to miss any marker-trait associations, the ones within the 2.5 and 3.0 LOD range are also highlighted. A major QTL for primary root length was located on chromosome 1B with a LOD score of 4.45. Three marker-trait associations were identified on chromosome 2A with LOD scores of 2.90 (TRL), and 2.29 (PRL). These loci were not deemed QTL but, due to previously identified QTL on the same arm of chromosome 2A in the same population, these loci are worth further consideration. Chromosome 5A had three different loci related to all traits. Two different loci with LOD scores of 6.17 and 3.78 for TRL and another locus with LOD scores of 3.44 and 9.33 for PRL and RA were located, respectively. Two loci below LOD score 3.0 were located on chromosomes 6A and 7A. Another QTL was identified on chromosome 7D for RA with a LOD score of 3.92. The distribution of QTL and all marker-trait associations, as well as additive effects of each locus on all six chromosomes, are given in Figure 2. Four out of six chromosomes with a minor or major effect loci were from genome A (2A, 5A, 6A, and 7A), while the others were on chromosomes 1B and 7D.

3.3. The interactions between seedling and mature root traits

Any possible interaction between seedling and mature plant traits are helpful for breeding and may accelerate selection. With this aim, previously published mature root traits and seedling root traits of this study were comapped. Colocated loci for three different chromosomes were identified. The first two loci for seedling-mature root trait interaction were on chromosome 2A for PRL, RM2013, and SRW2013 between 45 and 57 cM (Figure 3a). Another colocated locus (LOD below 3.0) was on the same chromosome. Total root length and PRL were identified near the QTL for grain yield (GY2013) between 23 and 57 cM (Figure 3b). Chromosome 5A had colocated loci for PRL, RA, RM2013, and SRW2013 between 110 and 116 cM region (Figure 3c). The last colocated loci for seedling-mature root traits were on chromosome 7D for RA, DRW2014, and SM2014 between 87 and 110 cM region (Figure 3d).

4. Discussion

Root system traits gained attention recently due to the increasing risks of climate change and limited diversity available in modern cultivars. Root system becomes critically important under low input farming and limited mineral and irrigation conditions (Manschadi et al., 2006). Therefore, the identification of novel alleles using QTL studies is a promising field with significant potential for marker-assisted breeding. Evaluation of root traits in part and as a system from seedling to maturity would help to understand root functions through environmental fluctuations (Ehdaie et al., 2012; de Souza Campos et al., 2020) as well as the genetic constitution of the root system traits (Salvi and Tuberosa, 2005; Uga et al., 2013). SynOpDH biparental mapping population with its unique pedigree was a good candidate for the identification of novel allelic diversity.

The root system can be evaluated under controlled conditions such as tubes (Sharma et al., 2009), pots (Waines and Ehdaie, 2007), hydroponics (Gregory et al., 2009), germination papers (Zhu et al., 2005), and various other techniques (Kuijken et al., 2015) and under field conditions such as trenching and shovelomics (Paez-Garcia et al., 2015). Root system evaluation of mapping populations with large sets of accessions with a high throughput technique is still not feasible. Seedling studies for fast and accurate screening are promising (Kabir et al., 2015). Finding colocated QTL for seedling and mature root traits is not common, and in most cases, these two growth stages do not have overlapping QTL. Phenotypic plasticity, the ability to change phenotype in response to environmental fluctuations, may alter root structure significantly throughout the plants' life (Nicotra et al., 2010; Ehdaie et al., 2012). Therefore, identification of any correlation between seedling and mature root as well as shoot traits may be convenient for breeding. This study aimed to identify novel allelic diversity for the root system traits at the seedling stage and detect any possible interaction between seedling and mature root traits.

A set of DH lines from the SynOpDH population were screened under controlled climate conditions for five different seedling root traits. However, only three of the traits (PRL, TRL, and RA) had trustable heritability levels, and two traits with low heritability values (LRL and NOR) were not discussed further. Linkage maps generated with 1485 SNP markers were used for QTL identification. A total of five different loci on chromosomes 1B, 5A, and 7D with major effect QTL (LOD above 3.0) were identified, and three different loci with LOD scores between 2.5 and 3.0 were located on chromosomes 2A, 6A, and 7A (Figure 1). The loci identified on chromosomes 1B, 2A, 5A, and 7D were colocated with previously identified QTL for root and shoot biomass traits (Bektas et al., 2020), on the same set of accessions, at maturity (Figures 3a–3d).

4.1. Seminal root growth angle

Seminal root growth angle (RA) is an easy-to-measure trait and promising for the identification and selection of deep-rooted genotypes (Uga et al., 2013). There was a significant variation (25.32°–143.02°) for RA within the

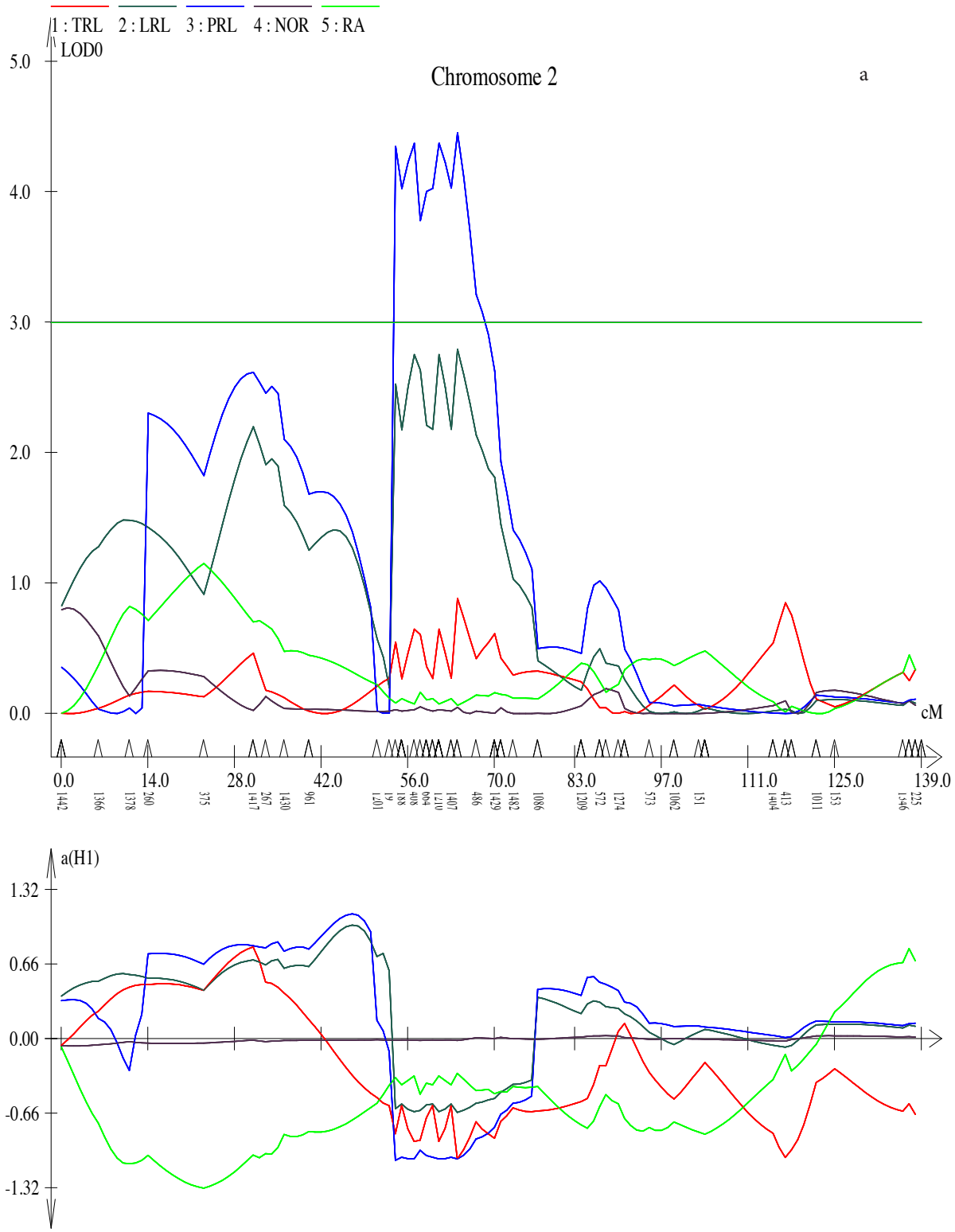
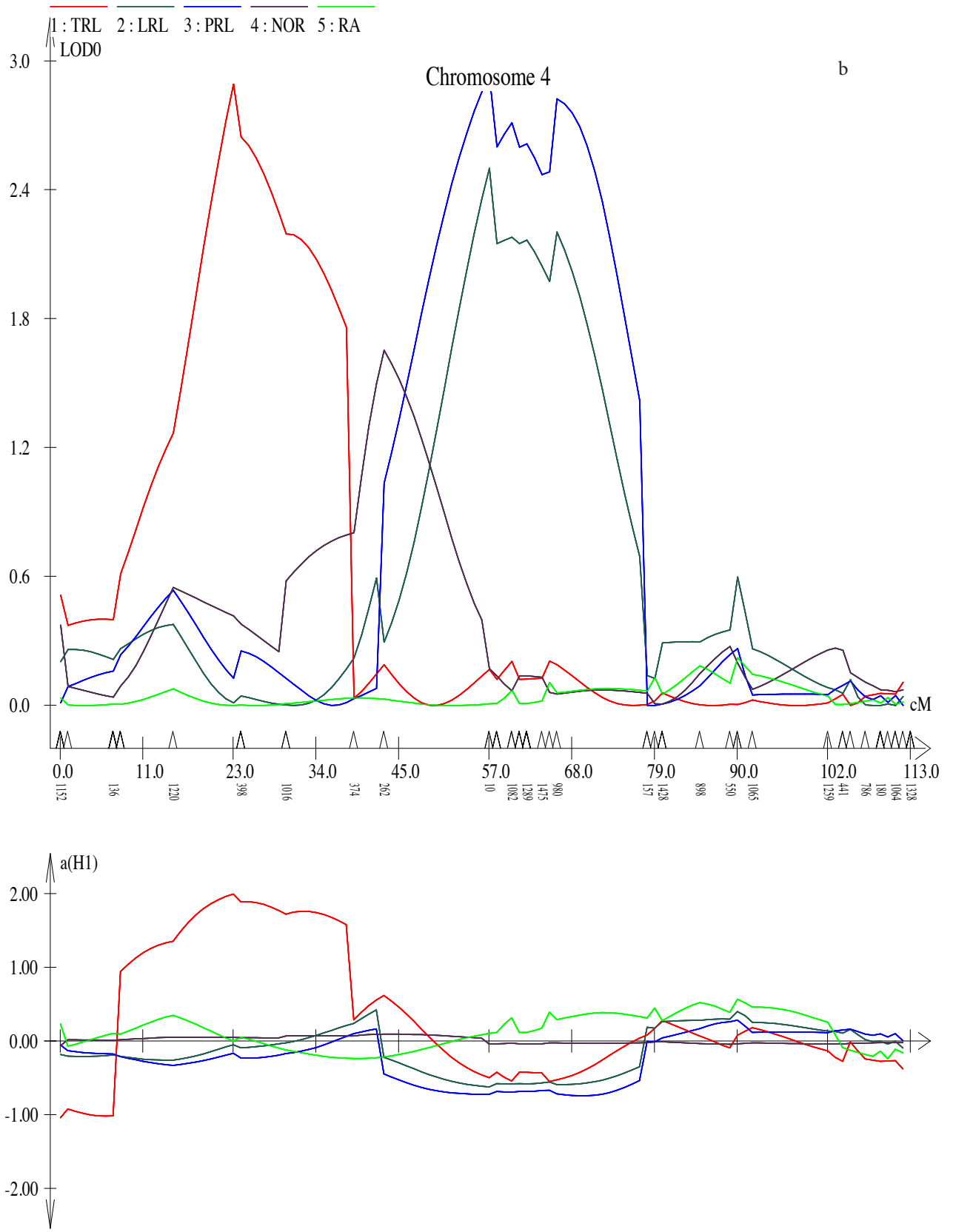


Figure 1. Marker-trait associations for the seedling root architecture traits; total root length (TRL-red), longest root length (LRL-dark green), primary root length (PRL-blue), number of roots (NOR-purple), and seminal root growth angle (RA-green) were detected on chromosomes; a) 1B (PRL), b) 2A (TRL and PRL), c) 5A (TRL, PRL, and RA), d) 6A (RA), e) 7A (RA), and f) 7D (RA). A LOD significance threshold of 3.0 is accepted to call a QTL. Heritability levels for LRL and NOR were too low to consider these traits in QTL analysis.



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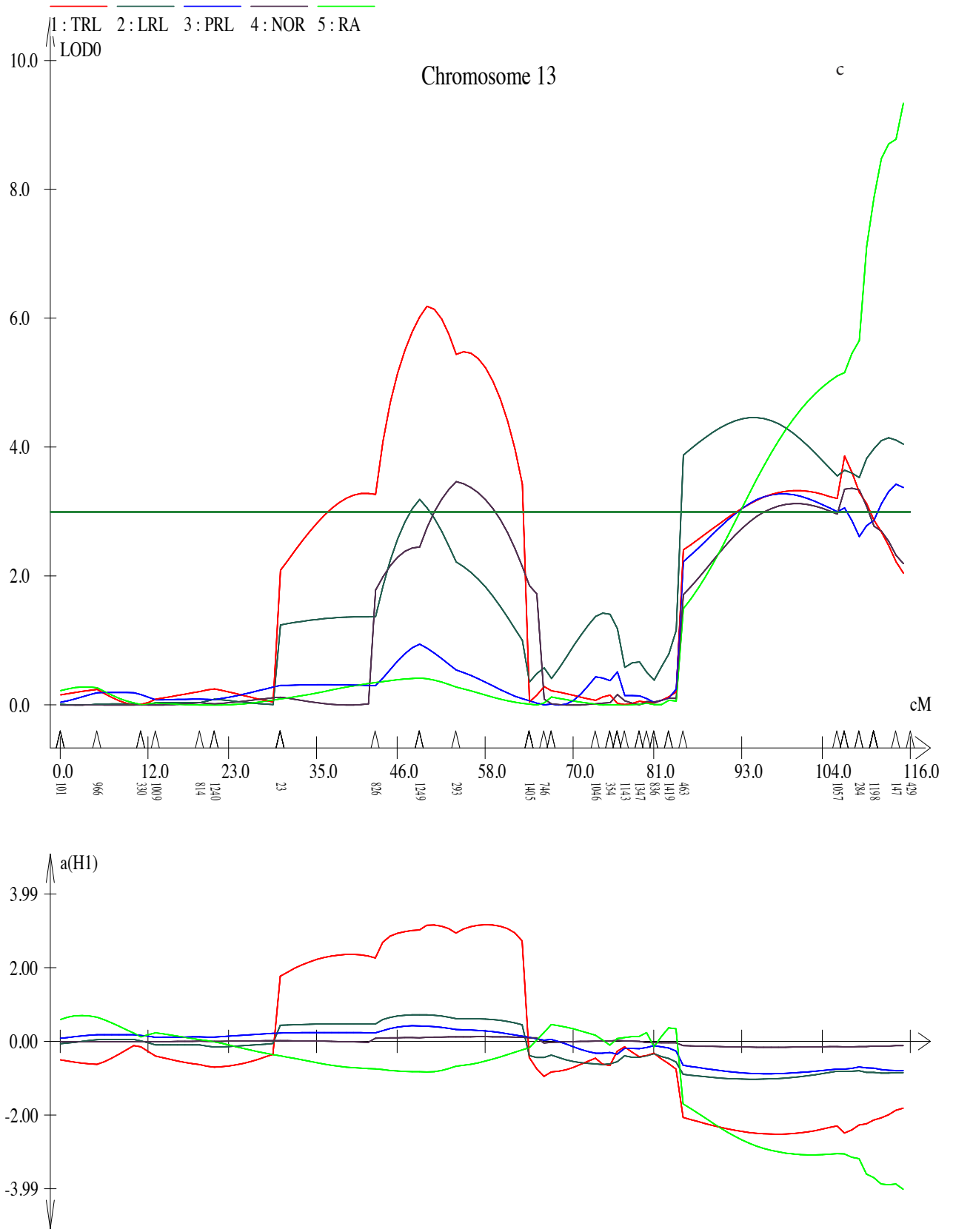

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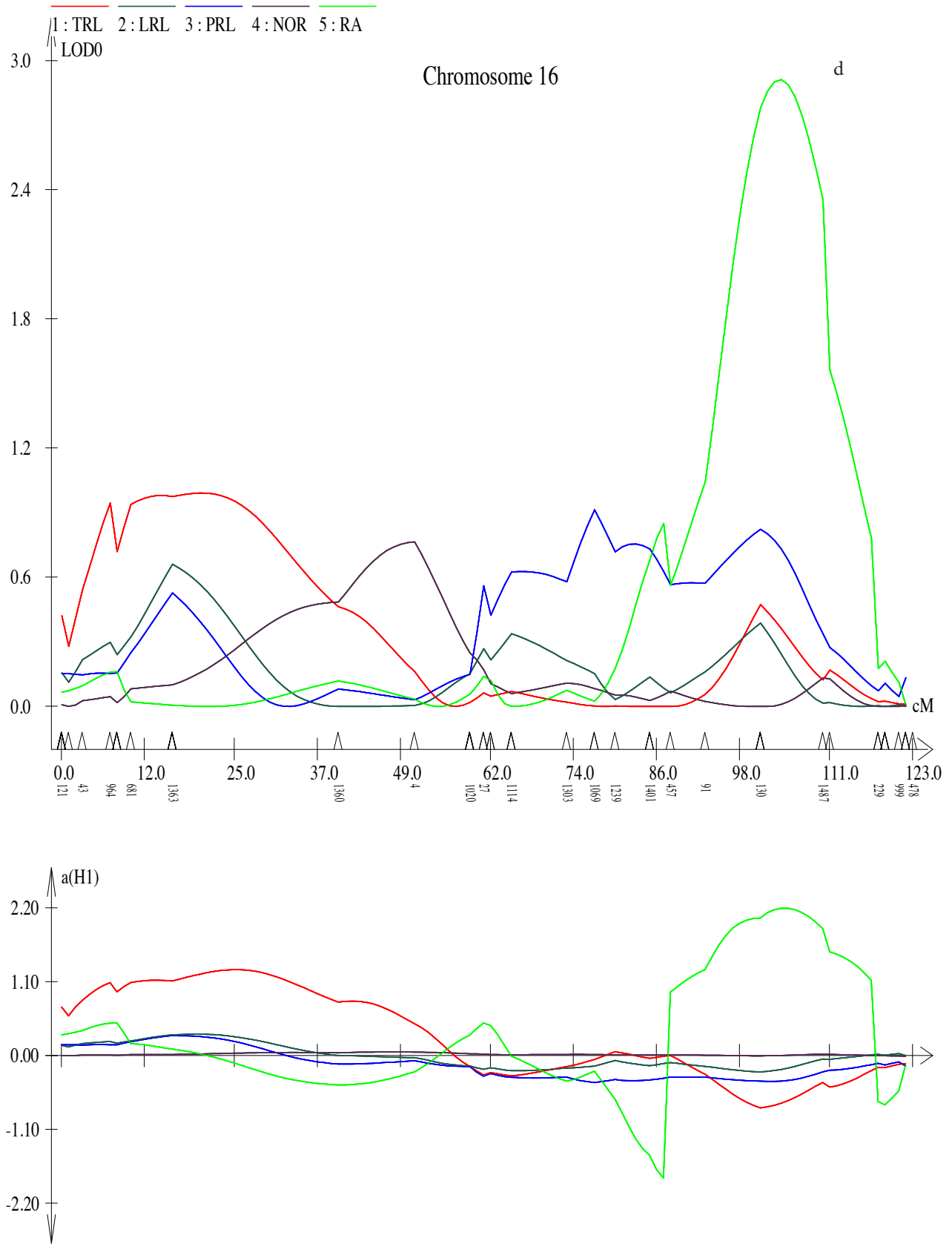

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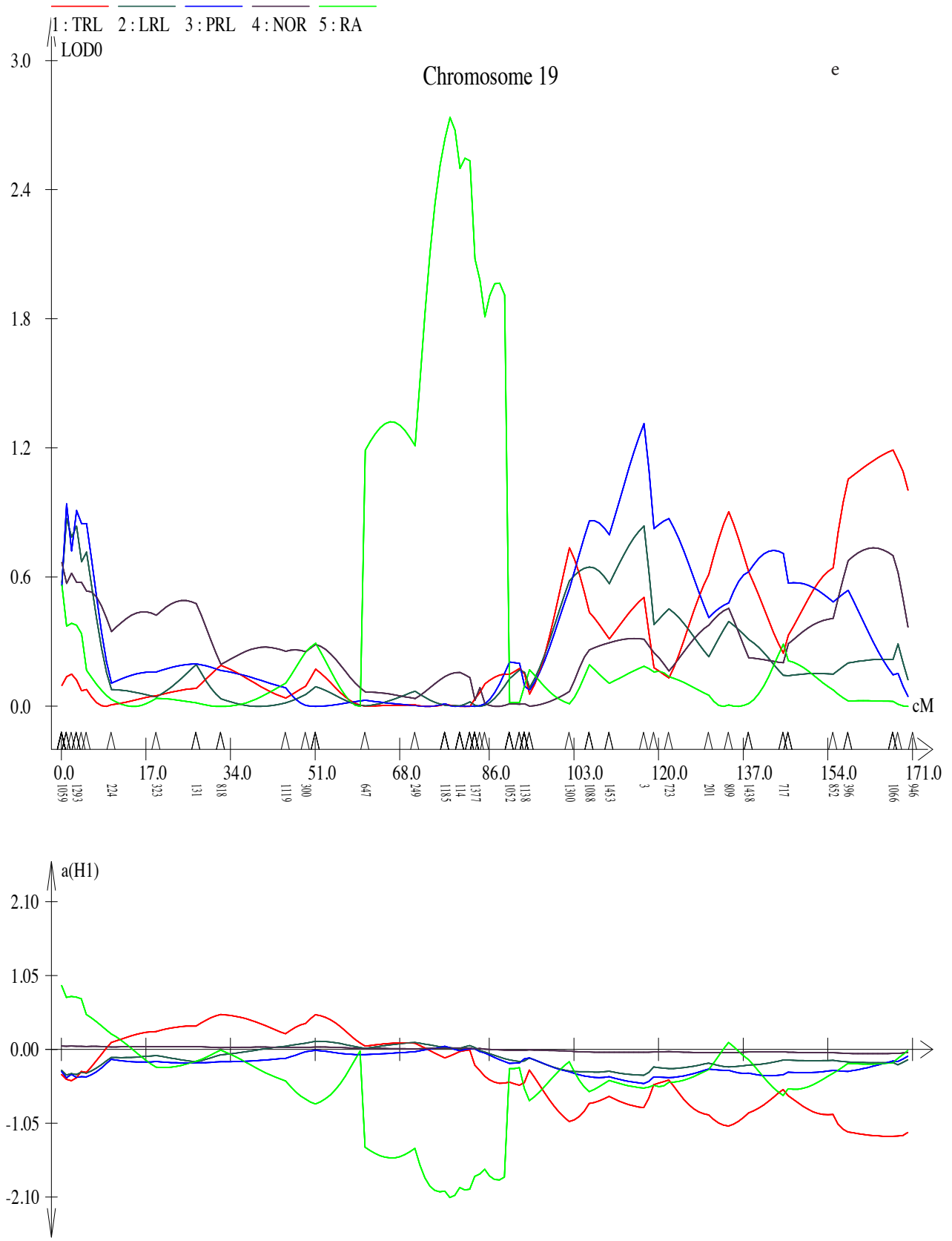

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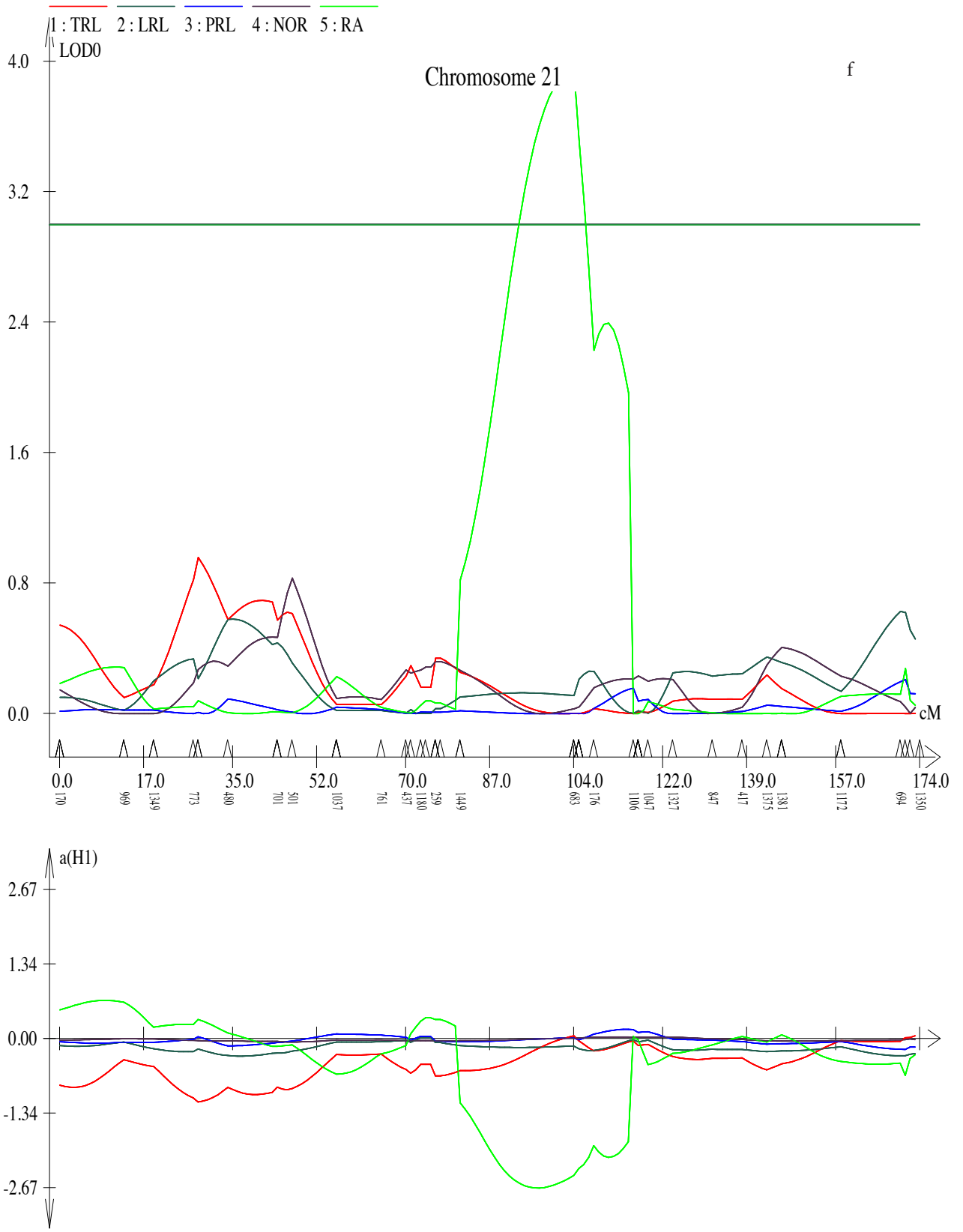

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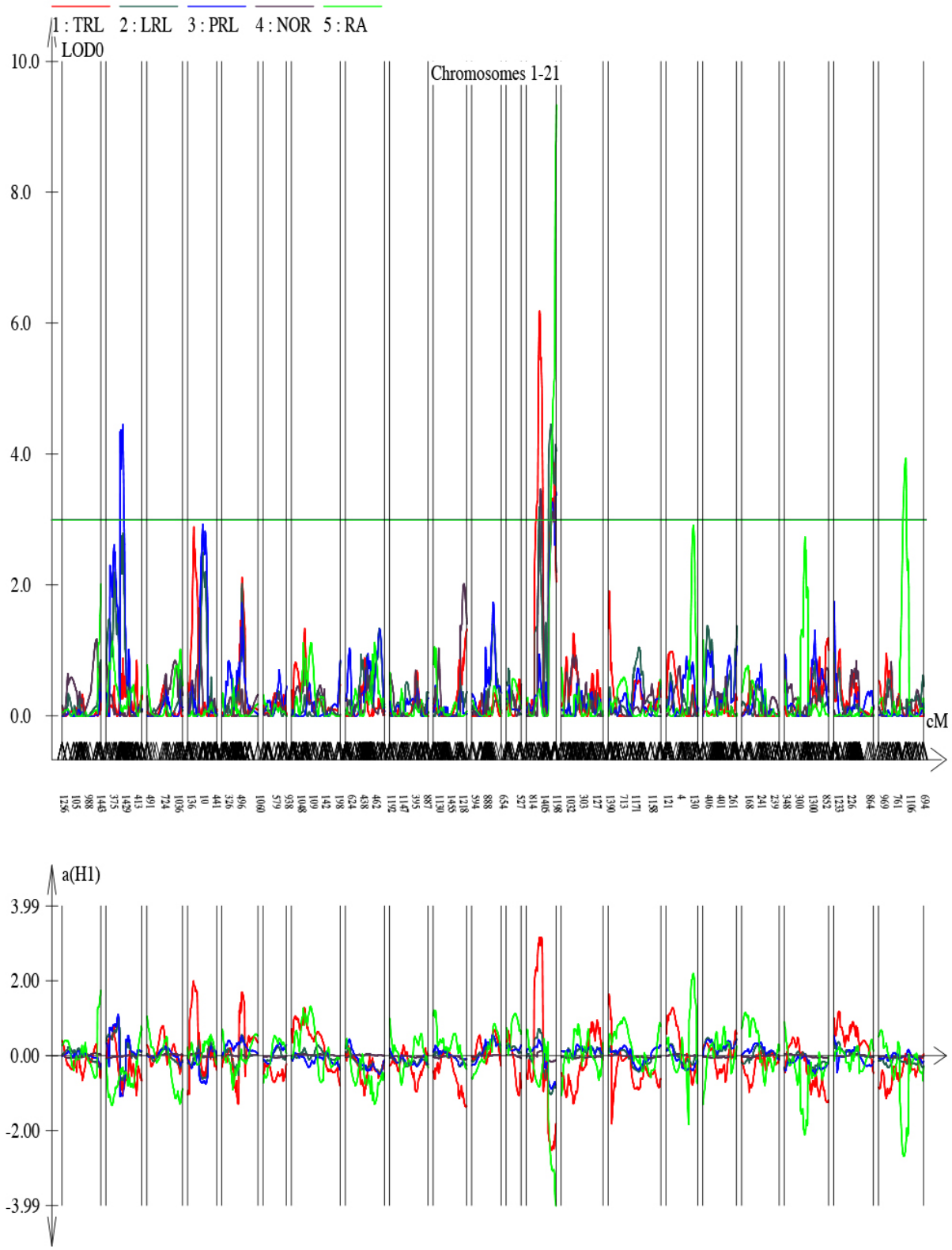


Figure 2. Whole-genome marker-trait association distribution on chromosomes 1B, 2A, 5A, 6A, 7A, and 7D for the seedling root architecture traits of total root length (TRL-red), longest root length (LRL-dark green), primary root length (PRL-blue), number of roots (NOR-purple) and seminal root growth angle (RA-green). A LOD significance threshold of 3.0 is used to call a QTL. Heritability levels for LRL and NOR were too low to consider these traits in QTL analysis.

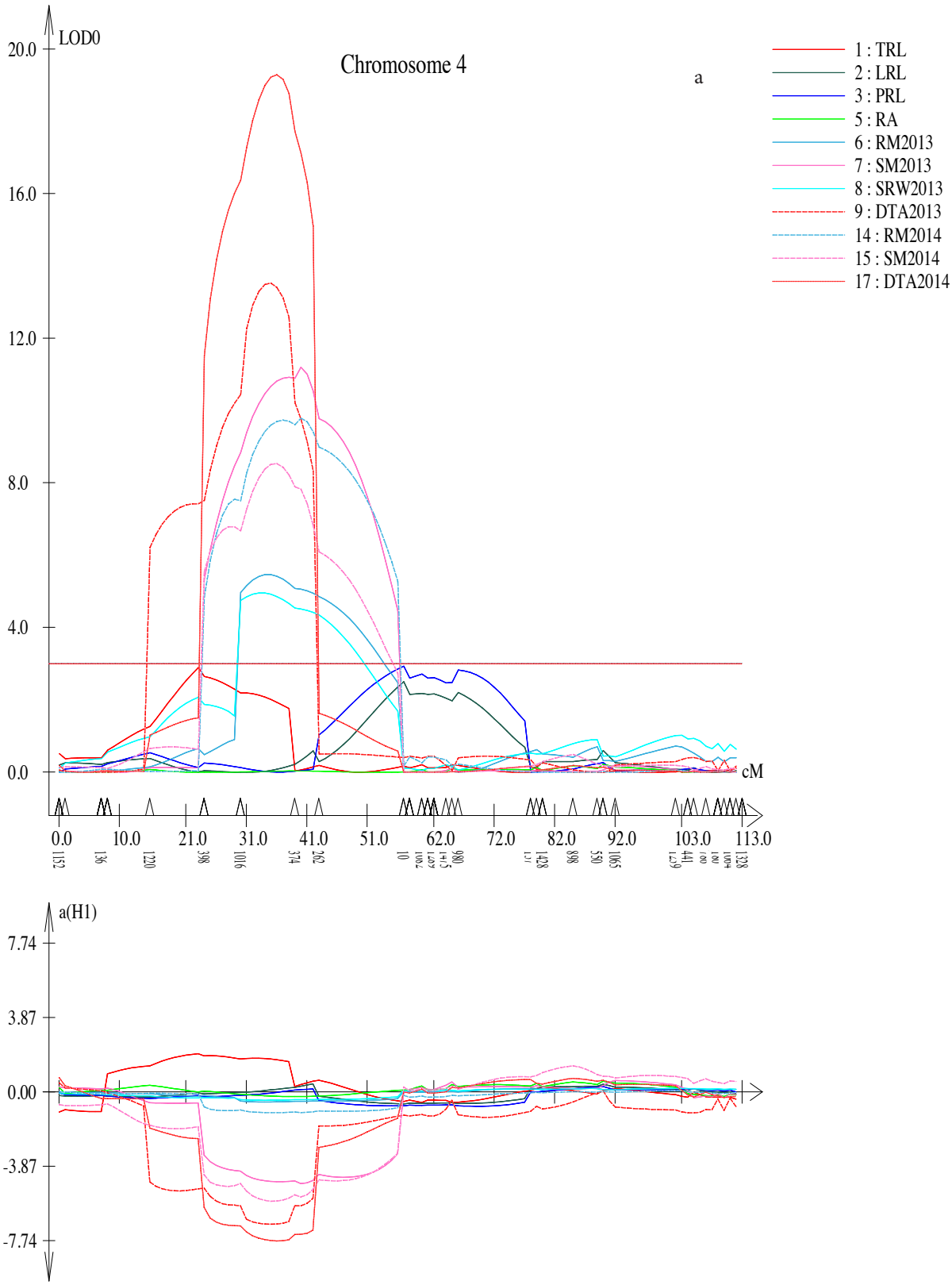
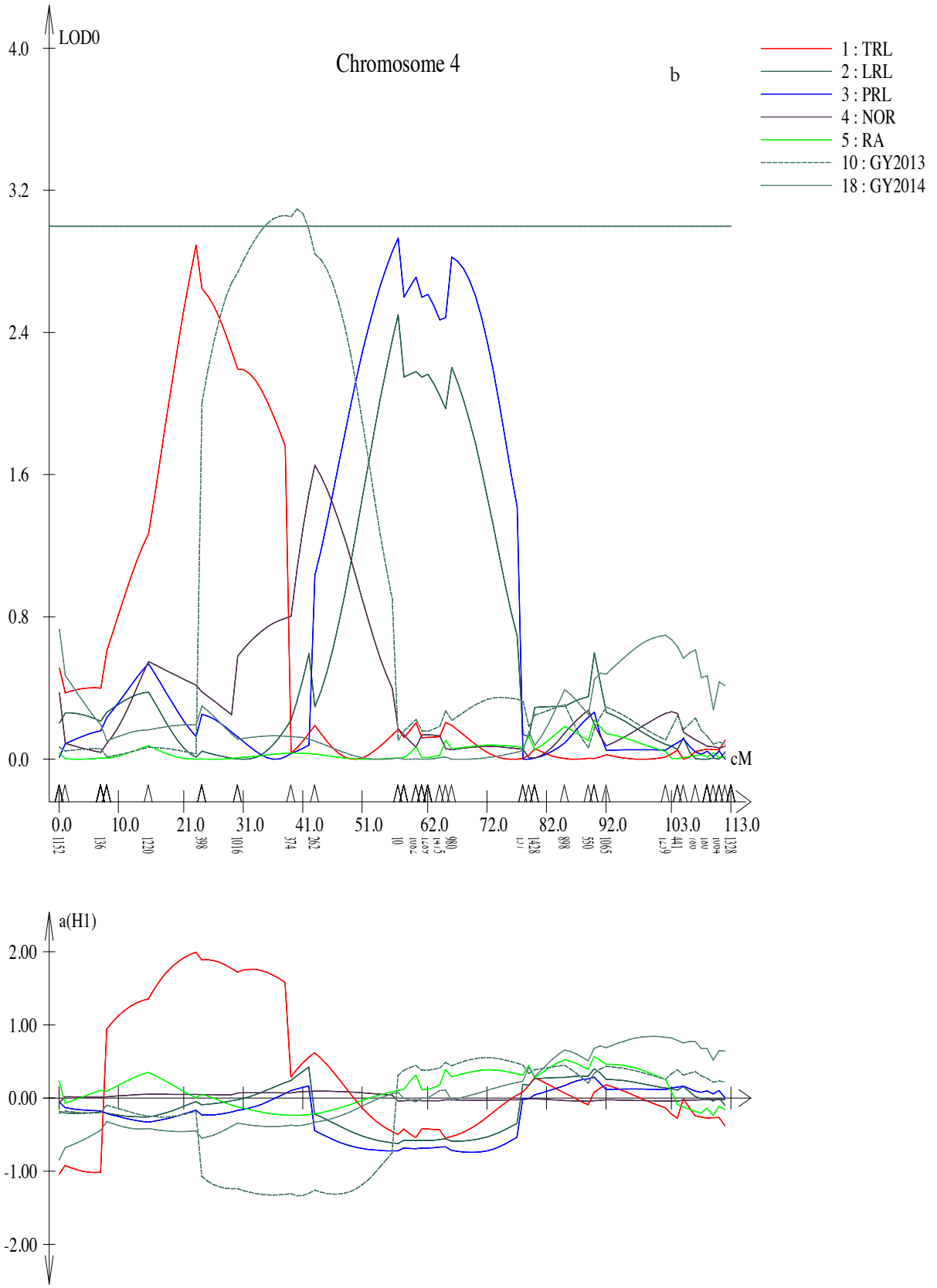


Figure 3. Colocated QTL for seedling and mature root traits for the SynOpDH biparental DH mapping population. Significant colocated marker-traits associations were obtained on chromosomes 2A (a–b), 5A (c), and 7D (d) when seedling and mature root-shoot traits were analyzed together for the QTL identification.



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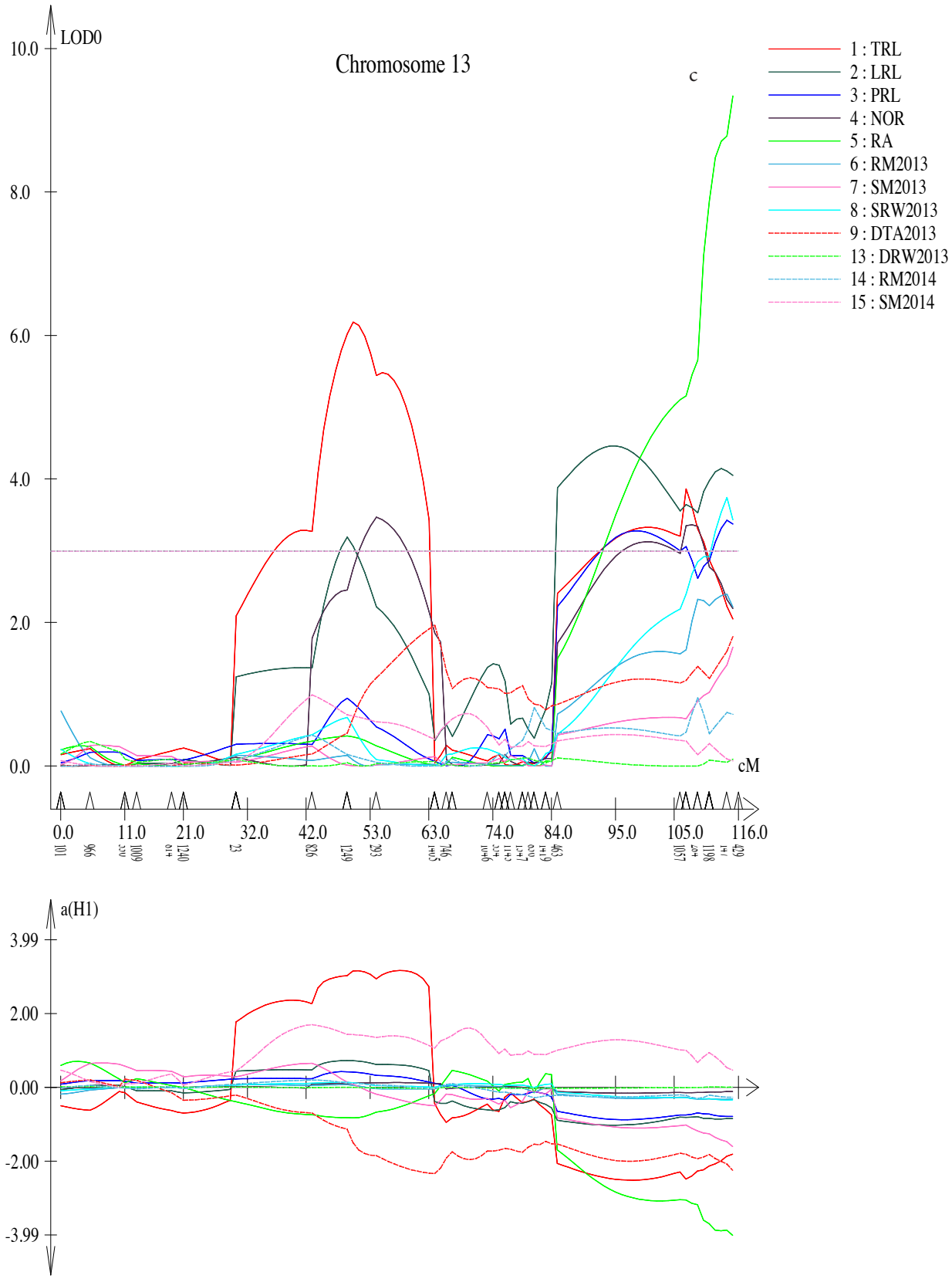

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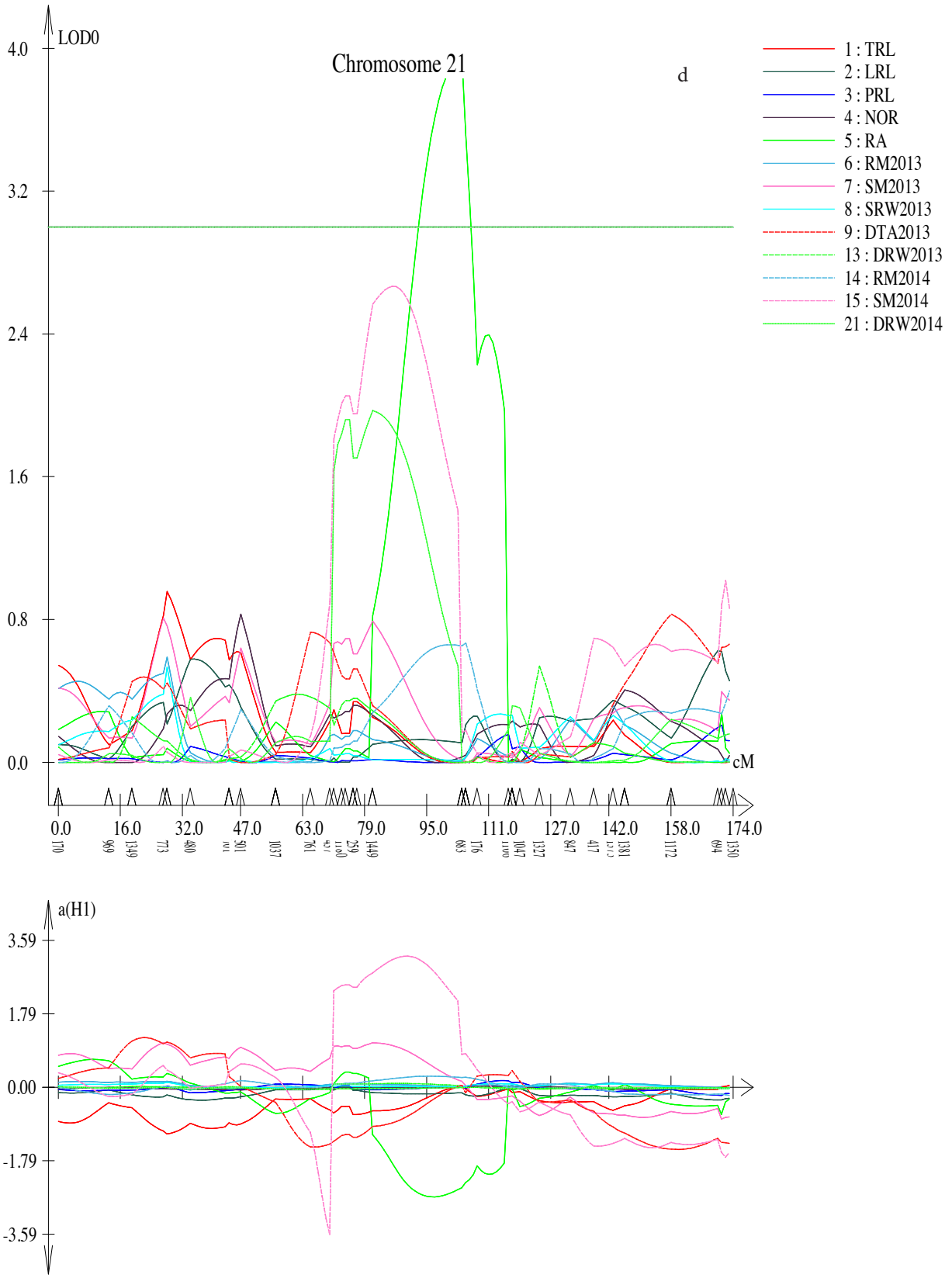

Figure 3. (Continued).

progeny of the SynOpDH population (Table). Two QTL on chromosomes 5A and 7D and two loci with LOD scores below 3.0 on chromosomes 6A and 7A (Figure 1) were identified. Mori et al. (2020) reported a terminal region on chromosome 6A with a QTL related to RA. Our results suggest a putative QTL for the same chromosome arm for RA. Similarly, Sanguineti et al. (2007) reported QTL for RA on chromosomes 3A, 4A, 5B, 6A in a study with durum (*Triticum turgidum* L. var. *durum*) wheat. Kabir et al. (2015) reported QTL on chromosomes 2A, 3A, 4D, 5A, and 6D for RA on DH and RIL populations. Chromosome 5A looks promising for the RA according to multiple reports on its effect on RA in wheat. There is a need for functional mapping and sequencing with the advantage of the bread wheat genome (Appels et al., 2018). A gene homologous to *DRO1* (Uga et al., 2013) would have the potential to shift the targets in wheat breeding for drought tolerance similar to rice (*Oryza sativa* L.) (Figueroa-Bustos et al., 2019).

4.2. Primary root length

Primary root length (PRL) defines plants' potential for rooting depth. The variation in PRL was in the range of 0.01 to 36.92 cm with a mean value of 22.30 cm. We identified two QTL on chromosomes 1B and 5A and one locus with a LOD score below 3.0 on chromosome 2A. Sanguineti et al. (2007) identified QTL on chromosomes 2A, 5A, and 7A for primary root length. Previous studies reported QTL for the longest/maximum root length on chromosomes in almost all linkage groups (Landjeva et al., 2008; Liu et al., 2013; Zhang et al., 2013b; Botwright Acuña et al., 2014; Kabir et al., 2015; Petrarulo et al., 2015). Two of the chromosomes (2A and 5A) identified in our study for PRL were previously reported for similar marker-trait associations and may be promising for further evaluations. Khalid et al. (2018) reported QTL in the SynOpRIL population for the root length on chromosomes 3A, 4D, and 7B. None of the QTL on the SynOpRIL population overlapped with our results. Additionally, TRL and RA were not reported in the SynOpRIL population. On the other hand, two of the loci we identified for PRL might be in a similar region to the ones reported by Kabir et al. (2015) on chromosomes 2A and 5A.

4.3. Total root length

Root system phenotyping at maturity is costly and difficult partly due to the plasticity (Ehdaie et al., 2012) of the root system. Identification of seedling root traits would provide cost-effective and timely results (Canè et al., 2014). The mean, minimum, and maximum values for the TRL were 55.40, 6.27, and 125.11 cm, respectively. Two major loci with LOD scores above 3.0 on chromosome 5A and one locus with a LOD score below 3.0 on chromosome 2A were identified. Previously TRL (Seedling or later growth stages) has been studied extensively and various reports identified QTL on chromosomes 1A, 1B, 2A, 2B, 3B, 4B, 4D, 5A, 5BS, 5D, 6A, 6B, 7A and 7D (Sanguineti et al., 2007; Li et al., 2011; Bai et al., 2013; Liu et al., 2013; Canè et al., 2014). Additionally, Kabir et al. (2015) reported QTL affecting TRL on chromosomes 2A, 2B, 3A, 3B, 4D, 5A, and 6D with 2.5 or higher LOD scores. A positive correlation between TRL and PRL (0.57) indicates a locus with possible pleiotropic effects. Liu et al. (2013) reported a colocated QTL for seminal root traits on chromosome 3B, and Kabir et al. (2015) reported QTL for TRL on chromosomes 2A, 3A, 4A, and 4D.

4.4. Overlapping loci for seedling and mature root traits

To find seedling and maturity interactions for root and shoot traits, data obtained in this study was reanalyzed with root and shoot biomass data from Bektas et al. (2020). Four different loci on chromosomes 2A, 5A, and 7D with possible pleiotropic effects were colocated between seedling and mature traits (Figures 3a–3d). The TRL, RM2013, and SRW2013 were colocated on the same loci and suggest an interaction between root length at seedling and root biomass at maturity. A further study at all growth stages would validate this interaction. A similar interaction, possibly pleiotropic, was located on chromosome 5A. The PRL and RA were within the same loci as RM2013 and SRW2013. Previous studies suggest that QTL for related traits is often colocated in close proximity (Tuberosa et al., 2002; Zhang et al., 2013a). Both colocated loci highlight promising interactions for root growth from seedling to maturity. The colocated QTL for seedling and mature traits, suggests the presence of a major QTL for root traits on chromosomes 2A and 5A. Chromosome 7D had a locus with a possible pleiotropic effect between RA, DRW2014, and SM2014. These loci may be promising to identify genes that affect the root system at both growth stages. Several loci on chromosome 2A were previously reported for root biomass and distribution (deep root ratio) (Ehdaie et al., 2016; Bektas et al., 2020). Bai et al. (2013) reported seedling and field trait correlations for wheat. Four loci identified in this study related to seedling and mature root traits on chromosomes 2A, 5A, and 7D are worth further evaluation, and QTL consistent at multiple studies may be a candidate for MAS.

5. Conclusion

Wheat as a staple crop can grow across the globe with wide adaptation. Nevertheless, improving grain yield and tolerance to abiotic and biotic stress factors is a continuous effort. Seedling vigor and deep root establishment may be promising traits to reduce the effect of drought stress (Rebetzke et al., 2014). Relatively high heritability on TRL (0.83), RA (0.49), and PRL (0.61) enabled good resolution QTL for these traits and looks promising for MAS in breeding. QTL identified at the seedling stage and

colocated QTL with the mature root and shoot traits are worth further validation at different scenarios including field conditions.

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Conflict of interest
The author declares no conflict of interest.

Author's Contribution
HB designed and performed the experiments, analyzed data, and wrote the manuscript.

Data availability statement
The data presented in this study are available on request from the corresponding author.

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