

Genetic Analysis of Soybean Plant Height, Hypocotyl and Internode Lengths

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Abstract

Diseases, mineral deficiencies, and water deficit reduce plant height and yield in many crop species. Conversely, plant growth regulators, water sufficiency and some diseases can increase plant height cause plants to lodge and may reduce yield. The aims of this study were to identify quantitative trait loci (QTL) for plant height (PLH), internode lengths (INL), and hypocotyls length (HYL) traits in soybean using the 'Essex' by 'Forrest' recombinant inbred line (RIL) population. Seedlings were grown in the greenhouse in replicated experiments. A total of 21 QTL for the 3 traits were located on 9 different linkage groups (LG). Sixteen QTL for INL (qINL1-16) were identified on LG A2, B1, C1, C2, D1b+W, D2, F, G, and K. LOD scores ranged from 2.64 to 4.5 and R^2 from 45.22 to 70.64 %. Three QTL for PLH (qPLH1-3) were identified on LG C2 and F. Their LOD scores ranged of 2.65 to 2.99 with R^2 ranging from 41.43 to 45.80 %. Two QTL for HYL (qHYL1-2) were identified on LG F with peak LOD scores of 2.51 and 2.85, and R^2 of 39.54 and 39.21 %, respectively. The traits studied here are components of yield and the QTL presented are important in soybean breeding programs to produce high yielding cultivars and germplasm.

Introduction

Soybean [*Glycine max* (L.) Merr.] is an important crop cultivated worldwide for its protein content, oil content and the numerous health benefits of its bioactive factors (Azadbakht et al., 2003; Chen et al., 2003; Desroches et al., 2004). Many agronomic traits such as plant height, internodes length, hypocotyls length, and disease resistance are complex and polygenic in nature; however their inheritance can be studied with the recent advances in plant genomics (Tanksley, 1993; Ashikari et al., 2005; SoyBase, 2007).

In the past decades, DNA-based molecular markers were extensively used to identify QTL for many important agronomic traits (Concibido et al., 2004; Kassem et al., 2004a,b, 2006, 2007a,b; Guzman et al., 2007; SoyBase, 2007), and to construct genetic and physical maps (Wu et al., 2004; Zhang et al., 2004; Song et al., 2004; Shultz et al., 2006; Kassem et al., 2006).

Plant height, internode length, and hypocotyl length of seedlings were reported to be correlated with high yield in many plant species such as maize (Pereira and Lee, 1995), wheat (Eriksen et al., 2003), barley (Scheurer et al., 2001), rice (Hittalmani et al., 2003; Ishimaru et al., 2004), sorghum (Pereira and Lee, 1995), sunflower (Bert et al., 2003), rye (Borner et al., 1999), cassava (Okogbenin and Fregene, 2003), poplar (Wu et al., 1998), cultivated lettuce (Argyris et al., 2005), and soybean (Orf et al., 1999a; Sebolt et al., 2000; Specht et al., 2001; Kabelka et al., 2004; Smalley et al., 2004; Zhang et al., 2004; Wang et al., 2004; Guzman et al., 2007; SoyBase, 2007).

Moreover, recent studies demonstrated the ability to use alleles from wild accessions and plant introductions to enhance yield in cultivated soybean cultivars (Orf et al., 1999a; Specht et al., 2001; Kabelka et al., 2004; Smalley et al., 2004; Concibido et al., 2003; Guzman et al., 2007).

To further examine the correlation of yield with seedling vigor in soybean this study sought; (1) to identify QTL for plant height, internodes length, and hypocotyls length using the 'Essex' by 'Forrest' recombinant inbred line (RIL) population; and (2) to compare the locations of these QTL with seed yield found in other genetic backgrounds.

Materials and Methods

Plant Material

The Essex by Forrest RIL population (EXF, $n = 100$) used in this study (Lightfoot et al., 2005) was provided in 2005 (at the F_{5:16}) by Prof. D.A. Lightfoot of SIUC.

DNA Isolation, Microsatellite Amplifications, and Map Construction

DNA purification, markers amplifications, and genetic map construction were performed as described earlier (Kassem et al., 2006, 2007a,b).

Growth Conditions and Trait Measurements

Growth conditions were performed as described in Jacobson et al. (2007). Briefly, one seed per pot, with 3 seed of each RIL, were grown in pots of 30 x 30 cm (diameter x depth) containing approximately 1 Kg of PRO-MIX soil. The PRO-MIX is a ready-made, peat based growing mix containing the Canadian Shpagnum Peat Moss (75-85% by volume), limestone (for pH adjustment), perlite, a wetting agent, and vermiculate. The seeds were planted in the summer (May – August, 2006) at KU, NJ and the experiment was repeated in the fall (September – December, 2006) at FSU, NC. The plants were kept in the greenhouse at 25±1°C under natural lighting and harvested at maturity of all RILs and parents Essex and Forrest. The plant heights, hypocotyl and internode lengths were measured at maturity of RILs and parents 'Essex' and 'Forrest', after day 112 (R8 growth stage). At that time, the number of internodes on each RIL ranged from 1 to 10 internodes (IN1-10).

QTL Mapping

To map plant height, hypocotyls length, and internodes length QTL, and to estimate their effects; the method of composite interval mapping (CIM) on WINQTL CART (Version 2.5) was used (Wang et al., 2005). The Model 6 was adopted. The control marker number and window size were 5 and 10 cM, respectively. A walk speed of 2 cM and the forward regression method were selected. LOD score peaks greater than 2.5 indicated the existence of QTL for the 3 traits reported in this study (Table 1). Experiment-wise threshold level to declare linkage was calculated from 1,000 permutations of each genotype marker against the phenotype in the population. Linkage was reported as significant if the two statistics for a marker were greater than the critical value at $P = 0.05$ as described earlier (Kassem et al., 2006, 2007a,b).

Table 1. Statistical analysis of the R8 stage hypocotyls length (HYL), internodes length (INL), and plant height (PLH) traits in the RIL population and the 'Essex' and 'Forrest' parents. Shown are averages and population ranges for these traits.

No., trait, and symbol	RIL	Population
	Average (cm)	Range (cm)
1. Hypocotyls Length (HYL)	6.64	5.4 – 9.5
2. First Internode (IN1)	5.35	2.8 – 10.2
3. Second Internode (IN2)	5.31	1.1 – 8.8
4. Third Internode (IN3)	4.85	1.2 – 8.6
5. Fourth Internode (IN4)	2.74	1.1 – 8.5
6. Fifth Internode (IN5)	3.42	1.2 – 10.1
7. Sixth Internode (IN6)	3.89	1.1 – 10.3
8. Seventh Internode (IN7)	3.62	1.0 – 15.1
9. Eighth Internode (IN8)	4.15	0.8 – 18.2
10. Ninth Internode (IN9)	3.89	0.5 – 16.7
11. Tenth Internode (IN10)	2.91	0.3 – 15.5
12. Plant Height (PLH)	47.54	28.1 – 93.3

Results

Polymorphism and Linkage

The genetic map was described earlier (Lightfoot et al., 2005; Kassem et al., 2006, 2007a,b). Briefly, the ExF genetic linkage map contained 368 markers (Lightfoot et al., 2005); however, 231 were high quality SSR markers that have been scored repeatedly (Lightfoot et al., 2005; Kassem et al., 2006, 2007a,b).

QTL Mapping

QTL mapping of plant height, hypocotyls length, and internodes length traits was performed using the CIM of WINQTL CART VER. 2.5 (Wang et al., 2005). A total of 21 QTL for the three traits were located on nine (9) different linkage groups (Table 2, Figures 1 and 2).

Internodes Length QTL

Sixteen QTL for INL were identified on LG A2, B1, C1, C2, D1b+W, D2, F, G, and K (Table 2, Figure 1). The first QTL (qIN1) was identified by the marker Satt208 on LG D2 and has a peak LOD score of 2.65 with an R^2 of 47.3% (Table 2, Figures 1 and 2). The second QTL (qIN2) was identified on LG C1 by the marker Sat_357 and had peak LOD score of 2.90 with an R^2 of 40.9% (Table 2, Figures 1 and 2). The third QTL (qIN3) was identified on LG C2 by the marker interval Satt307 – Sat_40H and had peak LOD score of 2.96 with an R^2 of 55.6% (Table 2, Figures 1 and 2). The fourth QTL (qIN6-1) was identified on LG A2 by the marker Satt424 and had peak LOD score of 2.70 with an R^2 of 45.7% (Table 2, Figures 1 and 2). The fifth QTL (qIN6-2) was identified on LG G by the marker Satt594 and had peak LOD score of 3.60 with an R^2 of 46.2% (Table 2, Figures 1 and 2). The sixth QTL (qIN6-3) was identified on LG K by the marker Satt260 and had peak LOD scores of 2.85 with an R^2 of 45.2% (Table 2, Figures 1 and 2). The seventh QTL (qIN7-1) was identified on LG A2 by the marker CAA16 and had peak LOD score of 2.82 with an R^2 of 51.4% (Table 2, Figures 1 and 2). The eighth QTL (qIN7-2) was identified on LG B1 by the marker interval S50TAA10 – Satt415 and had peak LOD score of 3.30 with an R^2 of 49.8% (Table 2, Figures 1 and 2). The ninth QTL (qIN7-3) was identified on LG G by the marker interval Satt356 – Satt570 and had peak LOD score of 2.66 with an R^2 of 48.9% (Table 2, Figures 1 and 2). The tenth QTL (qIN7-4) was identified on LG G by the marker Satt594 and had a peak LOD score of 3.25 with an R^2 of 51.9% (Table 2, Figures 1 and 2). The eleventh QTL (qIN8-1) was identified on LG C2 by the marker Satt307 and had peak LOD scores of 3.32 with an R^2 of 56.3% (Table 2, Figures 1 and 2). The twelfth QTL (qIN8-2) was identified on LG G by the marker interval Satt356 – Satt570 and had peak LOD score of 4.02 with an R^2 of

54.3% (Table 2, Figures 1 and 2). The thirteenth QTL (qIN9-1) was identified on LG G by the marker OEO2 and had peak LOD score of 3.20 with an R² of 52.0 % (Table 2, Figures 1 and 2). The fourteenth QTL (qIN9-2) was identified on LG G by the marker ACCCTC220 and had peak LOD score of 2.80 with an R² of 53.9 % (Table 2, Figures 1 and 2). The fifteenth QTL (qIN10-1) was identified on LG D1b+W by the marker Satt546 and had peak LOD score of 2.65 with an R² of 69.1 % (Table 2, Figures 1 and 2). The sixteenth QTL (qIN10-2) was identified on LG F by the marker interval Satt145 – CFR1 and had peak LOD score of 4.50 with an R² of 70.6 % (Table 2, Figures 1 and 2). No QTL were identified for the two traits IN4 and IN5.

Table 2. QTL for R8 plant height (PLH), hypocotyls length (HYL), and internodes length (IN1-10) traits in soybean. The QTL were found using the CIM of WINQTL CART., and reported with LOD scores equal or greater than 2.5 (Wang et al., 2005). QTL that underlie more than one trait are underlined.

Trait	QTL	LG	Marker/Interval	Position (cM)	LOD	Additive effect	R ² (%)
HYL	<u>qHYL1</u>	F	<u>Satt160</u>	<u>0.01</u>	<u>2.52</u>	<u>-0.44</u>	<u>39.54</u>
	<u>qHYL2</u>		<u>Satt145</u>	<u>21.01</u>	<u>2.85</u>	<u>-0.47</u>	<u>39.21</u>
IN1	qIN1	D2	Satt208	63.31	2.65	0.75	47.29
IN2	qIN2	C1	Sat_357	0.01	2.90	0.44	40.87
	<u>qIN3</u>	<u>C2</u>	<u>Satt307 – Sat_40H</u>	<u>52.31</u>	<u>2.96</u>	<u>0.55</u>	<u>55.60</u>
IN6	qIN6-1	A2	Satt424	74.91	2.70	0.63	45.70
	<u>qIN6-2</u>	<u>G</u>	<u>Satt594</u>	<u>81.31</u>	<u>3.60</u>	<u>-0.76</u>	<u>46.18</u>
	qIN6-3	K	Satt260	0.21	2.85	0.64	45.22
IN7	qIN7-1	A2	CAA16	3.81	2.82	0.85	51.37
	qIN7-2	B1	S50TAA10 – Satt415	58.31	3.30	-1.03	49.75
	qIN7-3	G	Satt356 – Satt570	63.61	2.66	0.98	48.95
	<u>qIN7-4</u>		<u>Satt594</u>	<u>81.31</u>	<u>3.25</u>	<u>-0.95</u>	<u>51.95</u>
IN8	qIN8-1	C2	Satt307	46.31	3.32	-1.30	56.31
	<u>qIN8-2</u>	<u>G</u>	<u>Satt356 – Satt570</u>	<u>63.61</u>	<u>4.02</u>	<u>1.72</u>	<u>54.31</u>
IN9	qIN9-1	G	OEO2	20.81	3.20	1.80	52.01
	qIN9-2		ACCCTC220	102.61	2.80	1.65	53.90
IN10	qIN10-1	D1b+W	Satt546	0.01	2.65	-1.36	69.06
	<u>qIN10-2</u>	<u>F</u>	<u>Satt145 – CFR1</u>	<u>45.01</u>	<u>4.50</u>	<u>2.00</u>	<u>70.64</u>
PLH	qPLH1	C2	Satt357 – Satt371	4.01	2.66	-5.35	43.22
	qPLH2		Sat_40H	56.01	2.80	5.65	41.43
	<u>qPLH3</u>	<u>F</u>	<u>Satt145 – CFR1</u>	<u>45.01</u>	<u>3.00</u>	<u>-6.50</u>	<u>45.80</u>

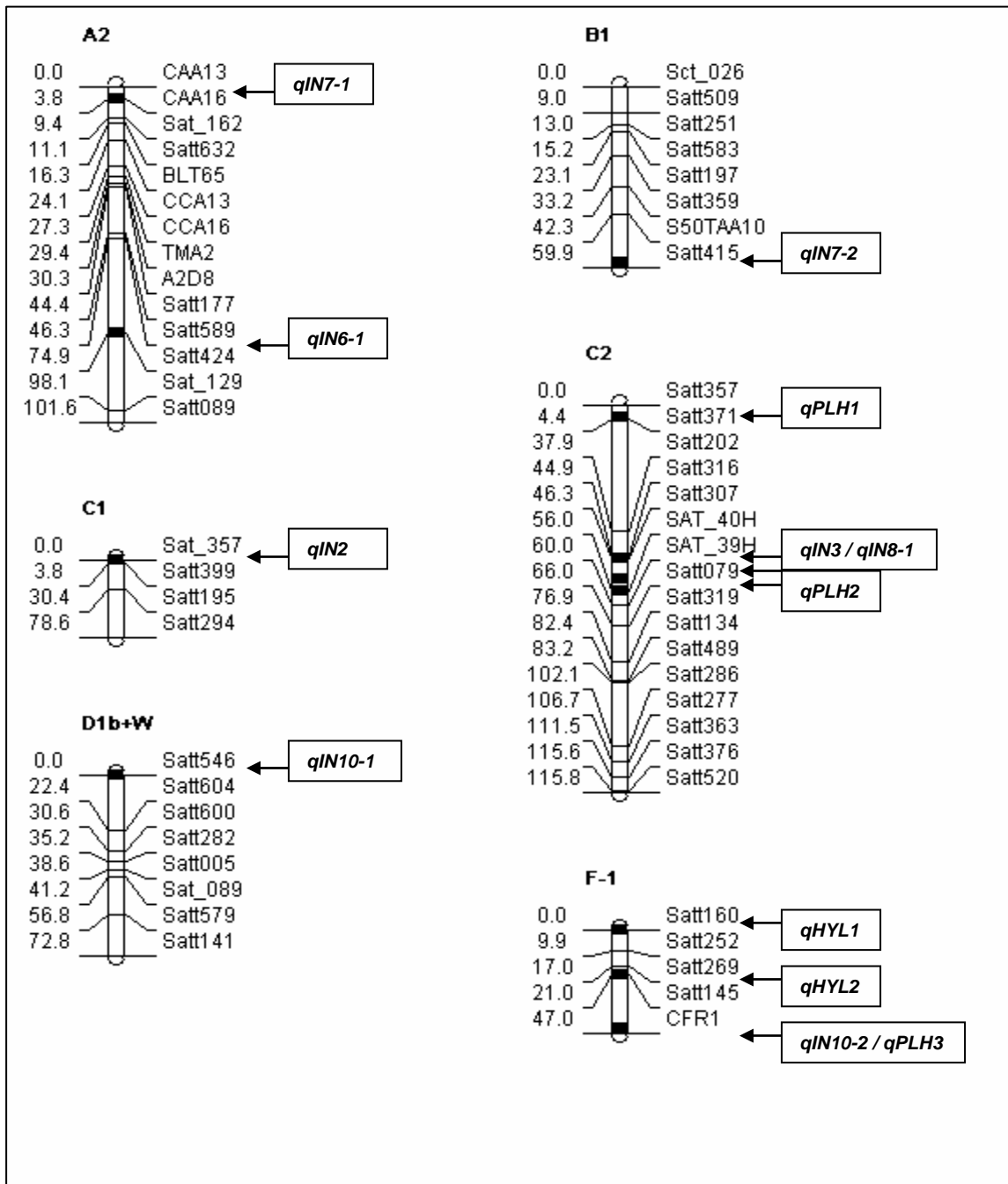


Figure 1. Locations of DNA markers and the QTL underlying plant height (PLH1-3), internodes length (IN1-10), and hypocotyls length (HYL1-2) in the soybean ExF RIL. The QTL were found using the CIM of WINQTL CART and reported with LOD scores equal or greater that 2.5 (Wang et al., 2005).

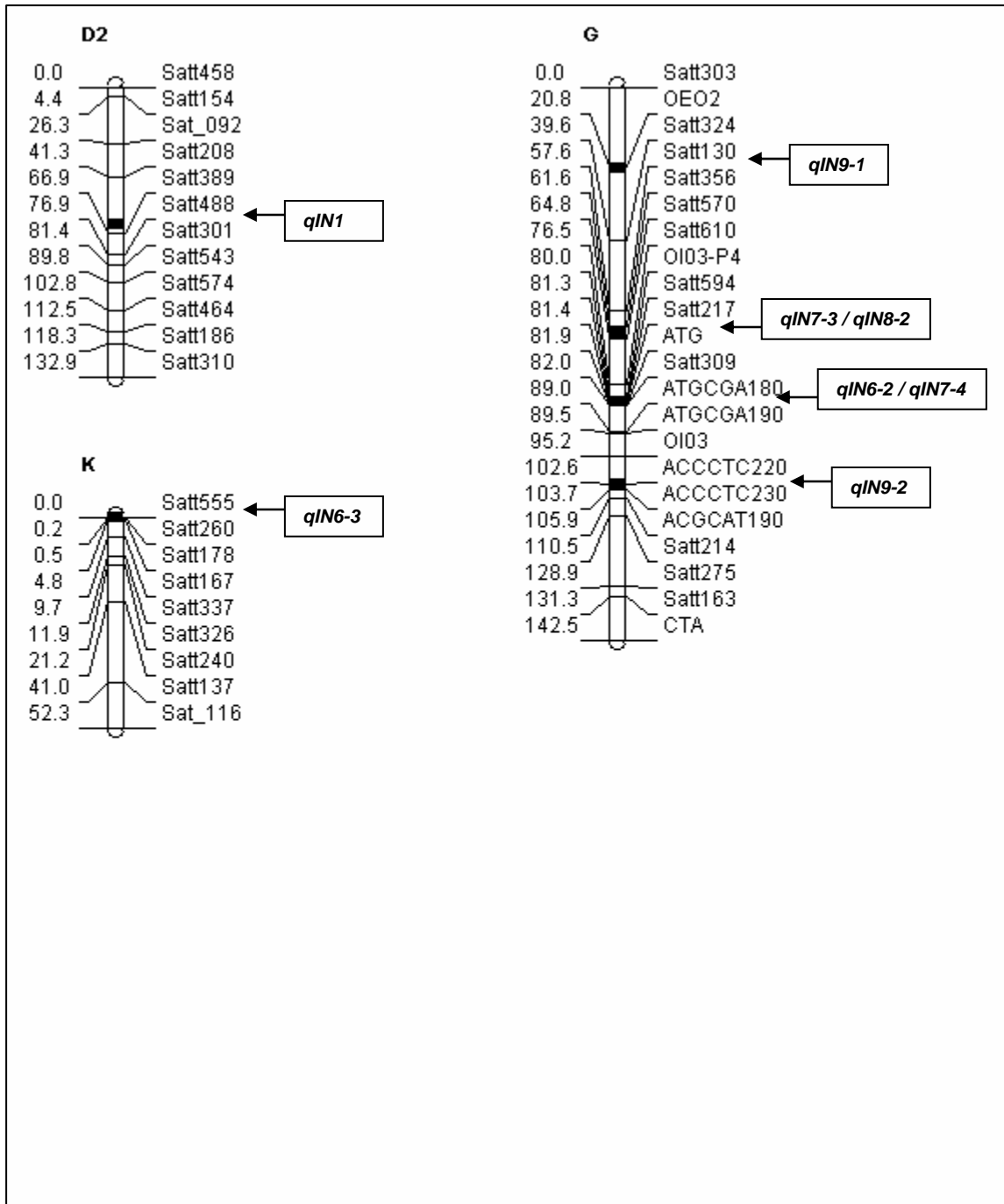


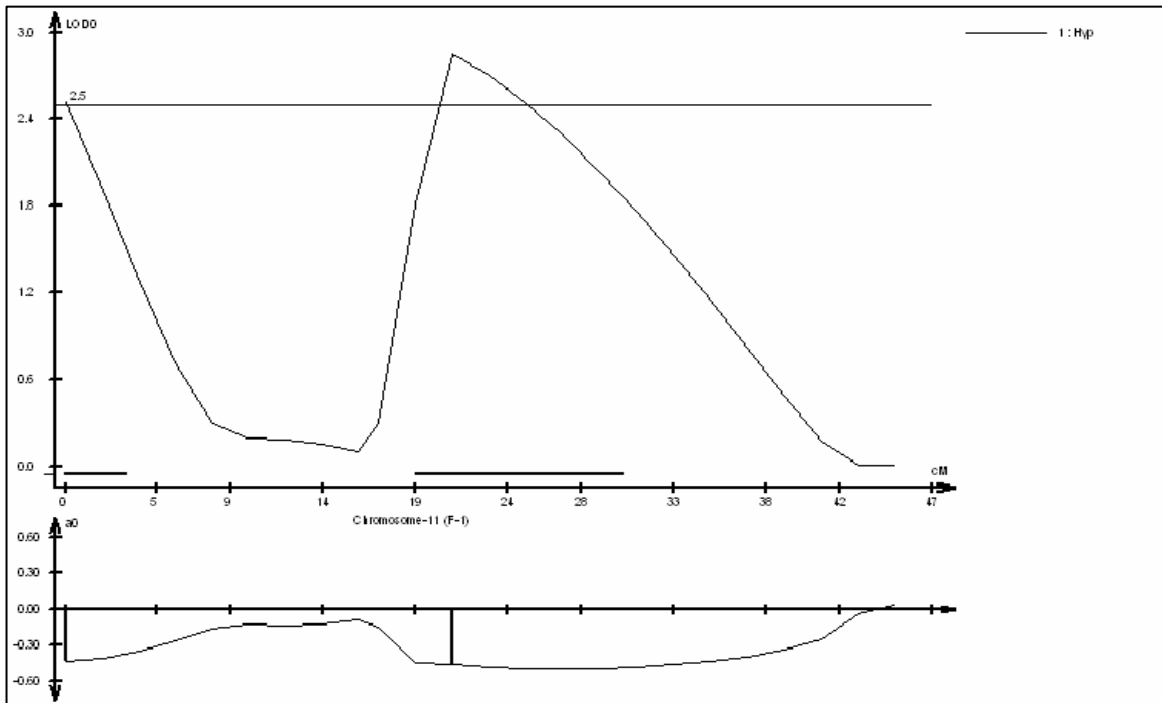
Figure 1. Continued.

Plant Height QTL

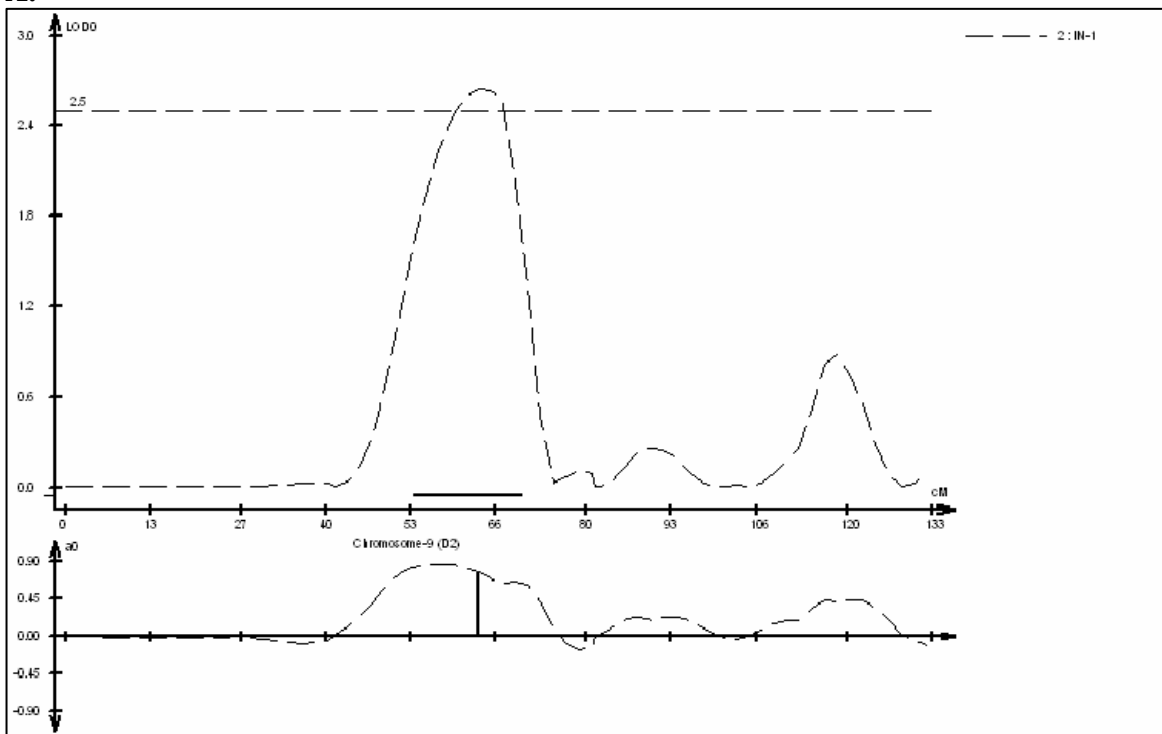
Three QTL for PLH (qPLH1-3) were identified on LG C2 and F (Table 2, Figures 1 and 2). The first QTL (qPLH1) was identified on LG C2 by the marker interval Satt357 – Satt371 and had peak LOD score of 2.66 with an R² of 43.2 % (Table 2, Figures 1 and 2). The second QTL (qPLH2) was identified on LG C2 by the marker Sat_40H and had peak LOD score of 2.80 with an R² of 41.4 % (Table 2, Figures 1 and 2). The third QTL (qPLH3) was identified on LG F by the marker interval Satt145 – CFR1 and had peak LOD score of 3.00 with an R² of 45.8 % (Table 2, Figures 1 and 2).

Hypocotyls Length QTL

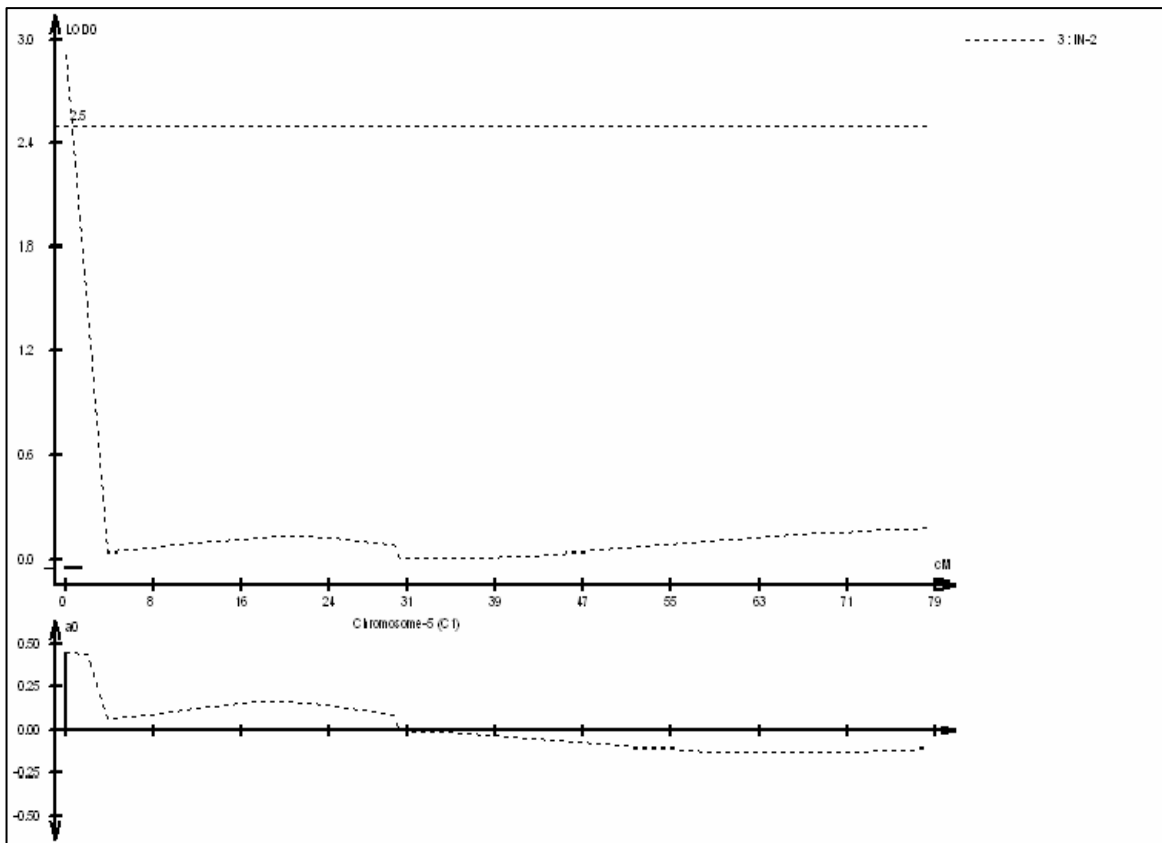
Two QTL for HYL (qHYL1-2) were identified on LG F (Table 2, Figures 1 and 2). The first QTL (qHYL1) was identified on LG F by the marker Satt160 and had peak LOD score of 2.52 with an R^2 of 39.54 % (Table 2, Figures 1 and 2). The second QTL (qHYL2) was identified on LG F by the marker Satt145 and had peak LOD score of 2.85 with an R^2 of 39.21 % (Table 2, Figures 1 and 2).



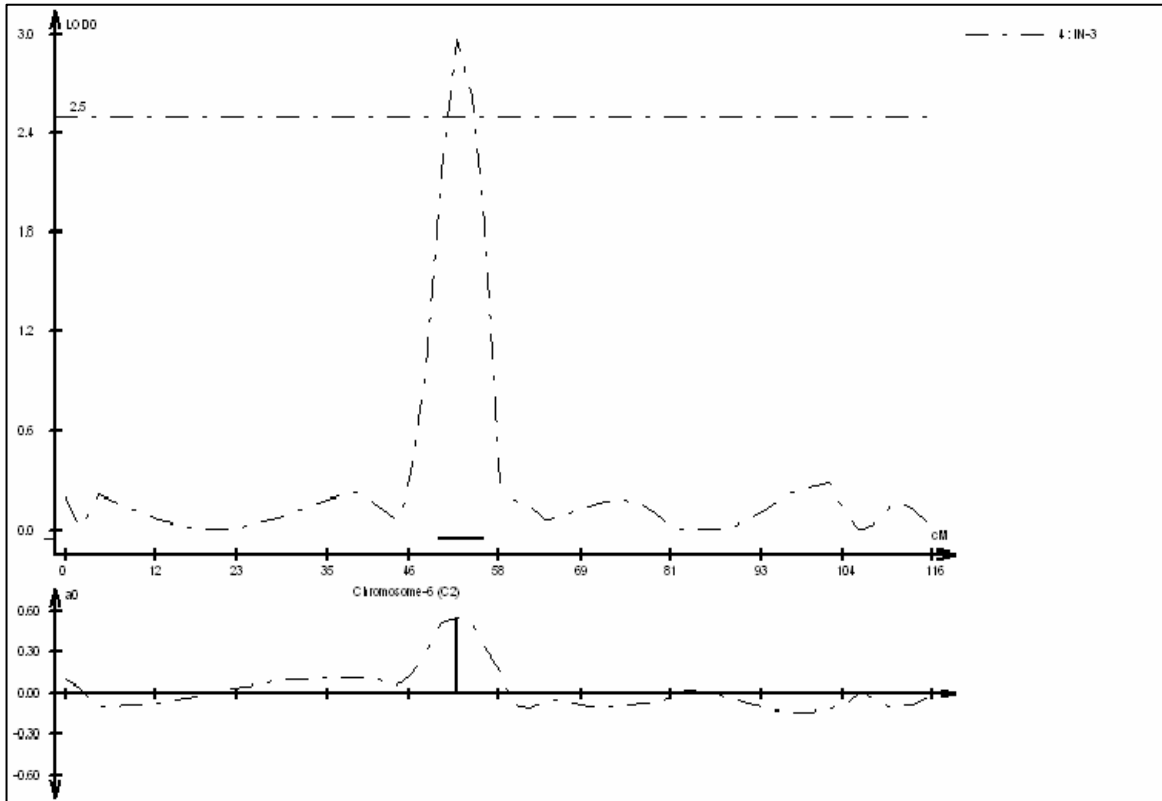
A.



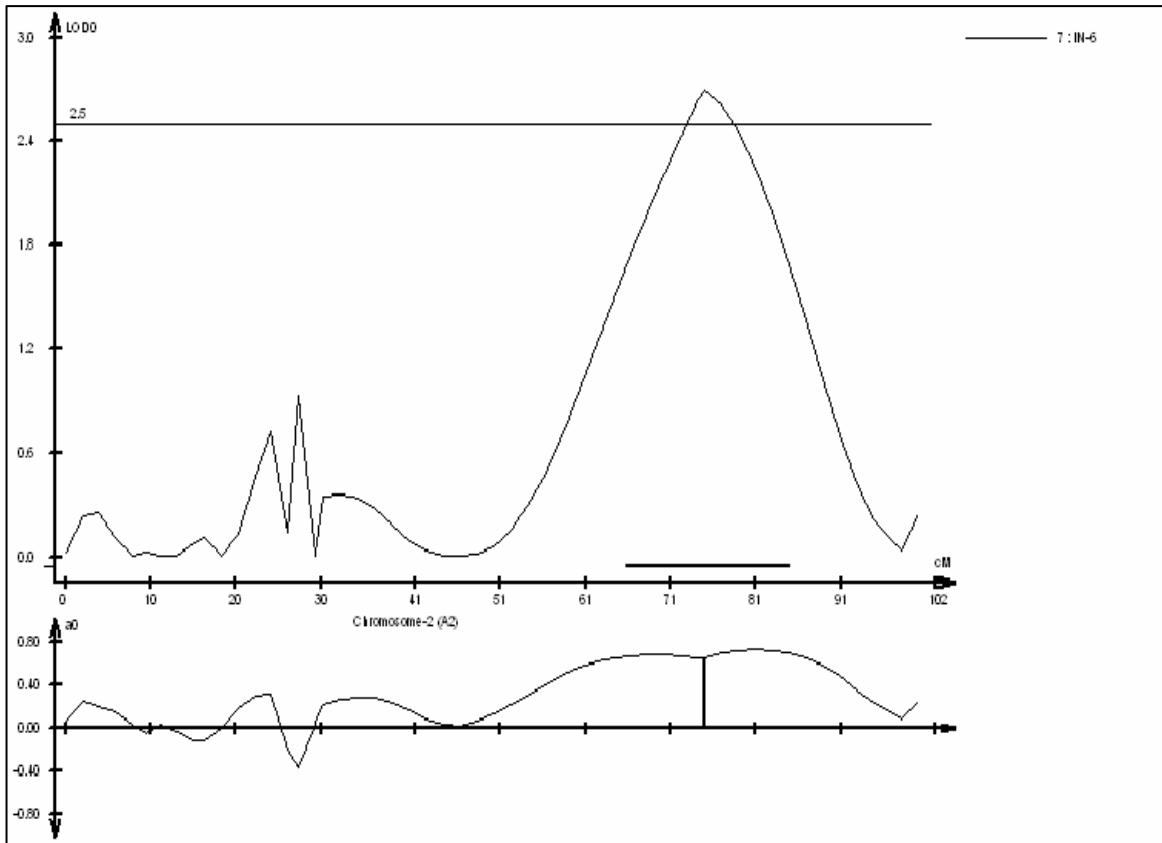
B.



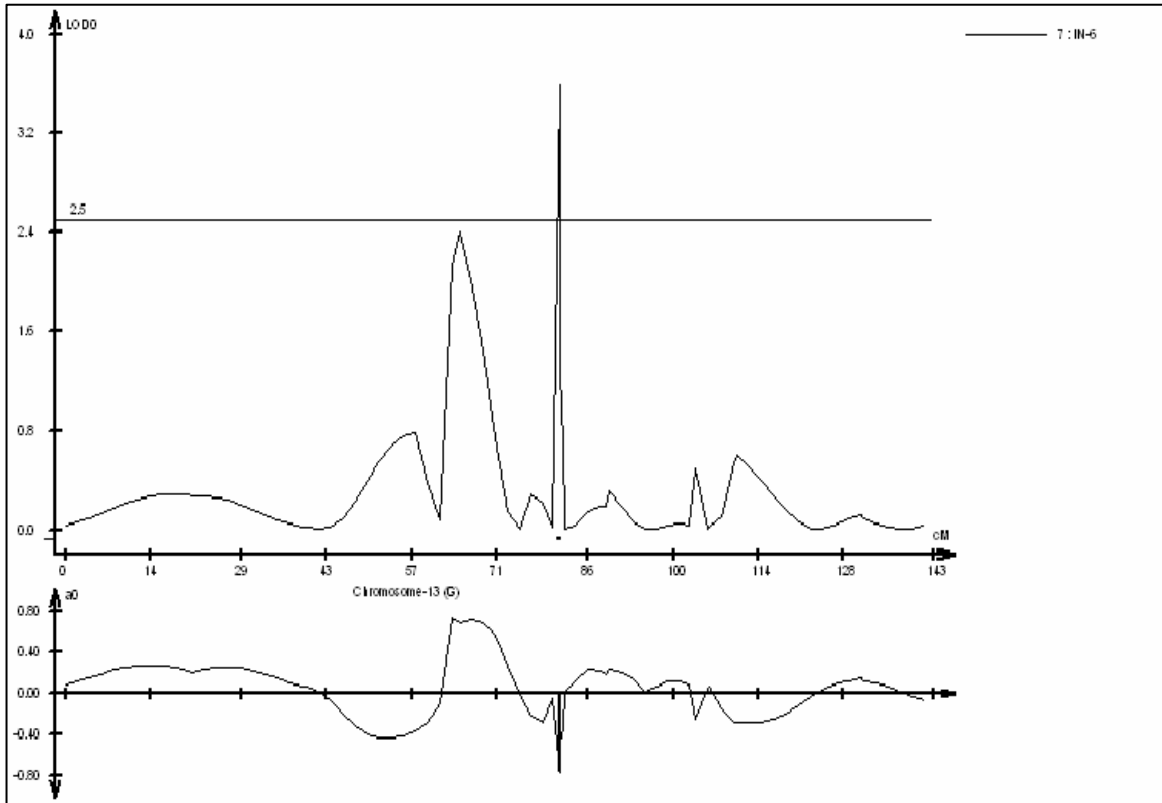
C.



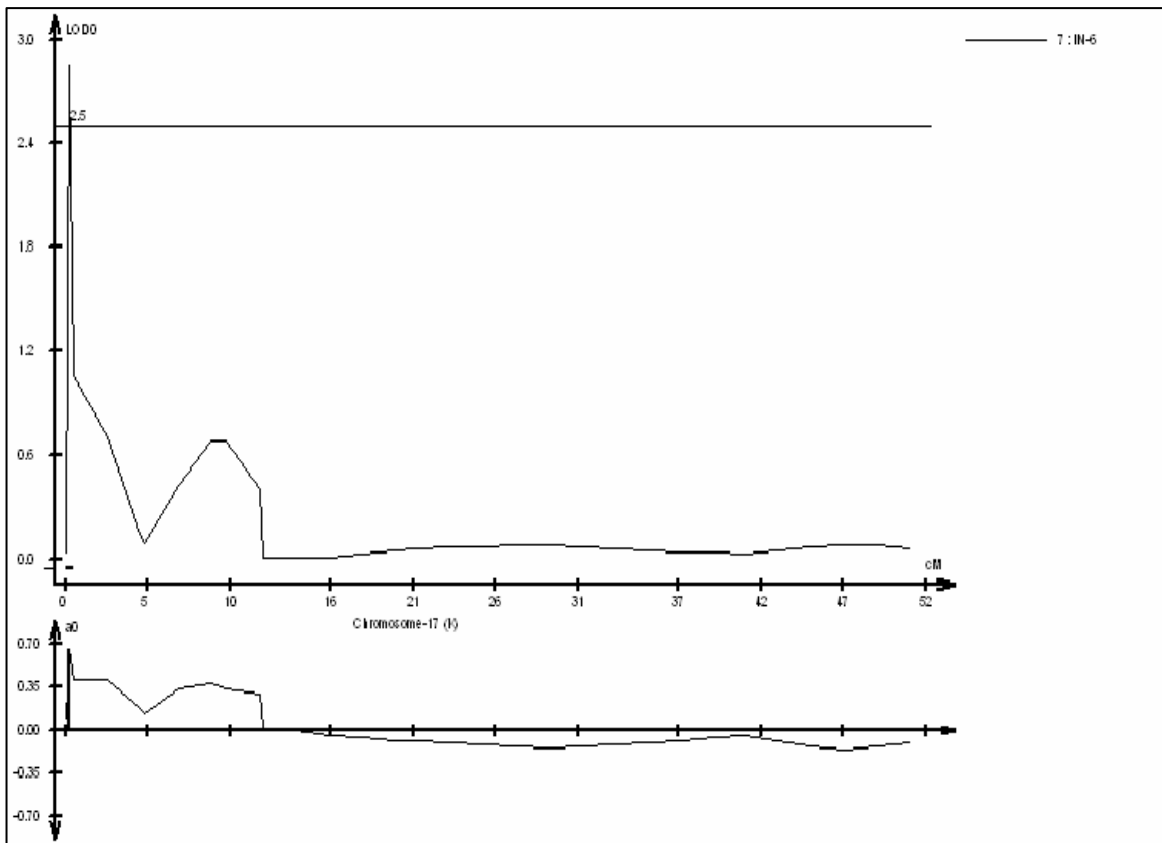
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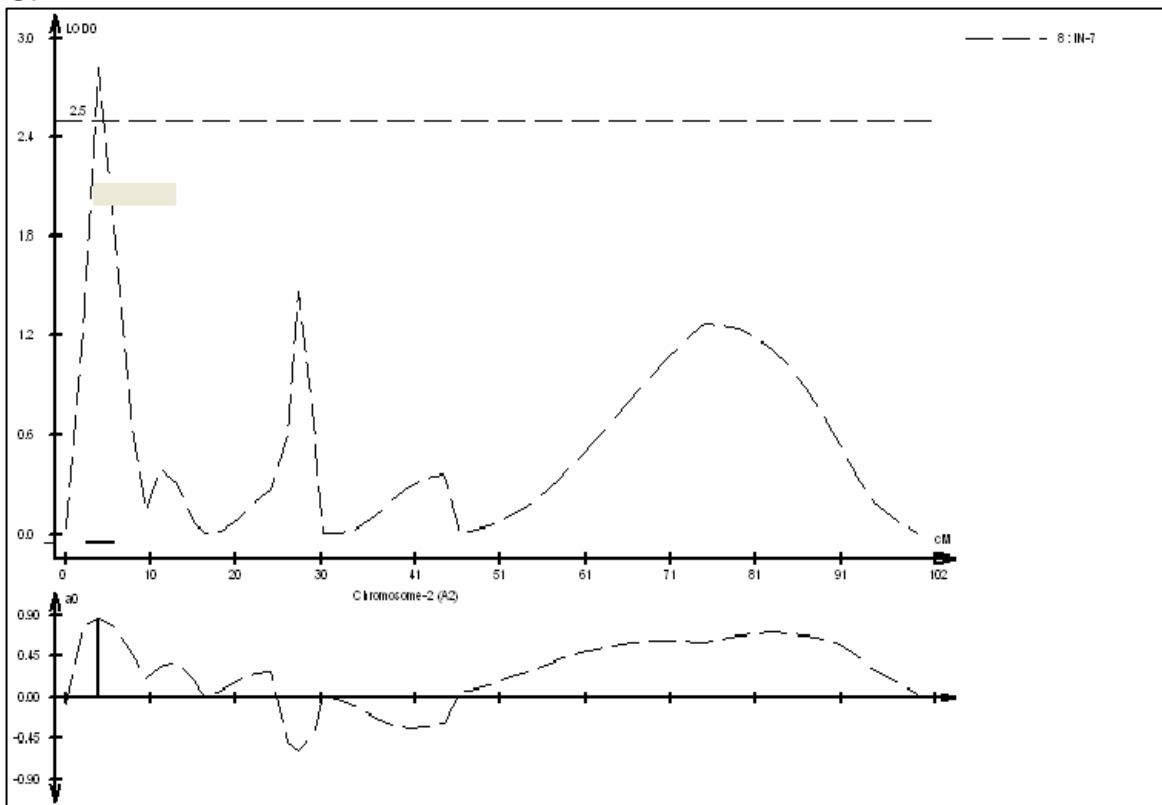
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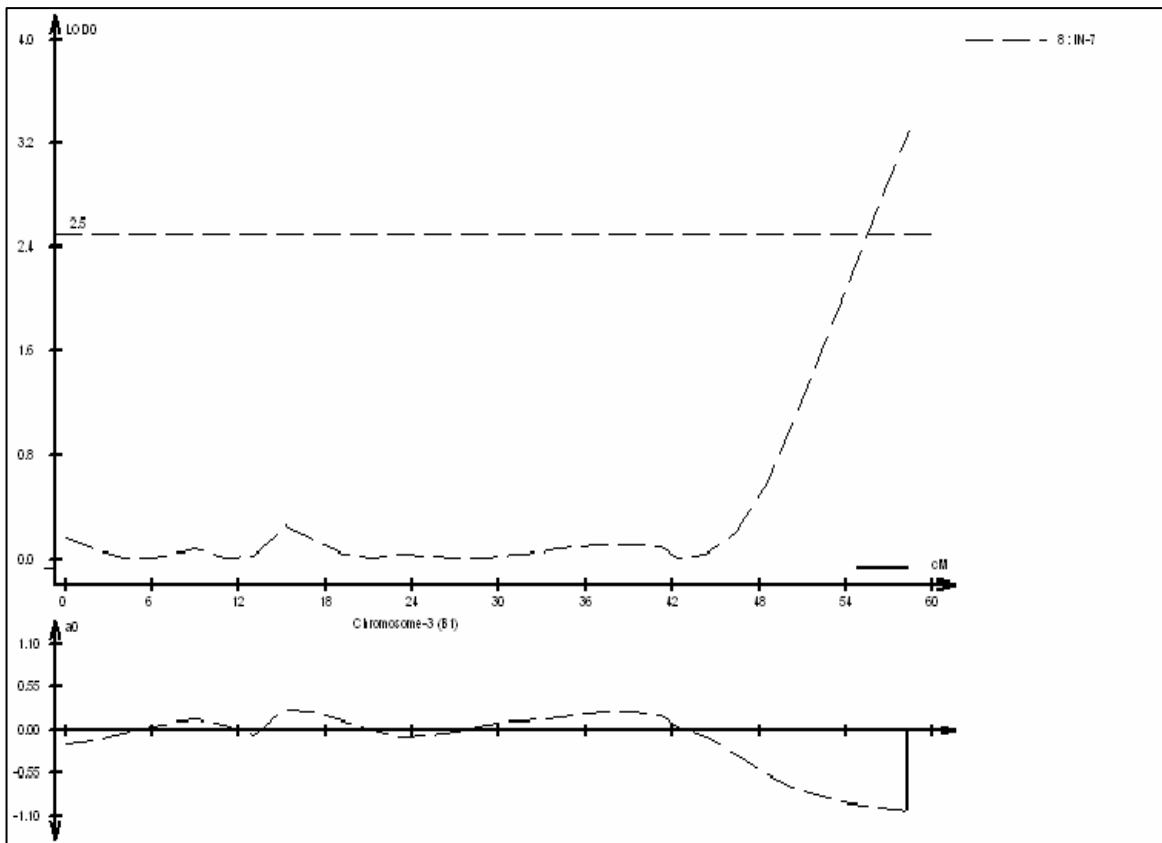
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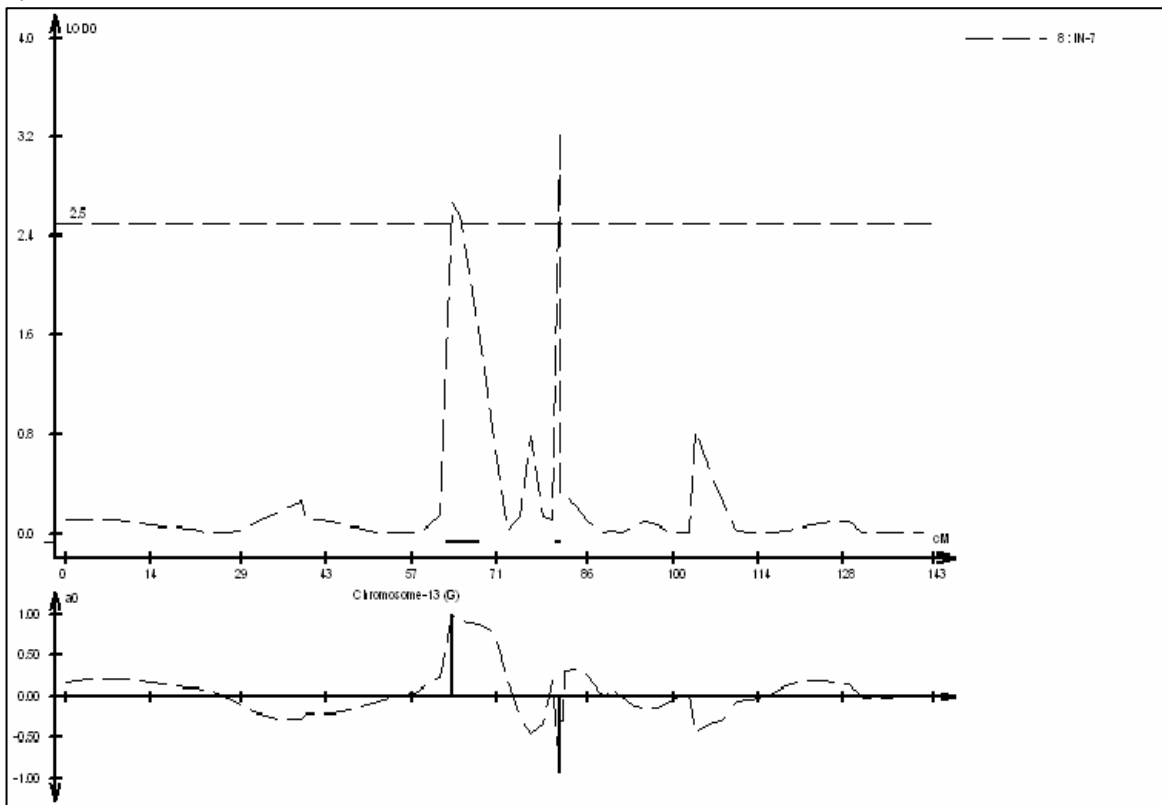
G.



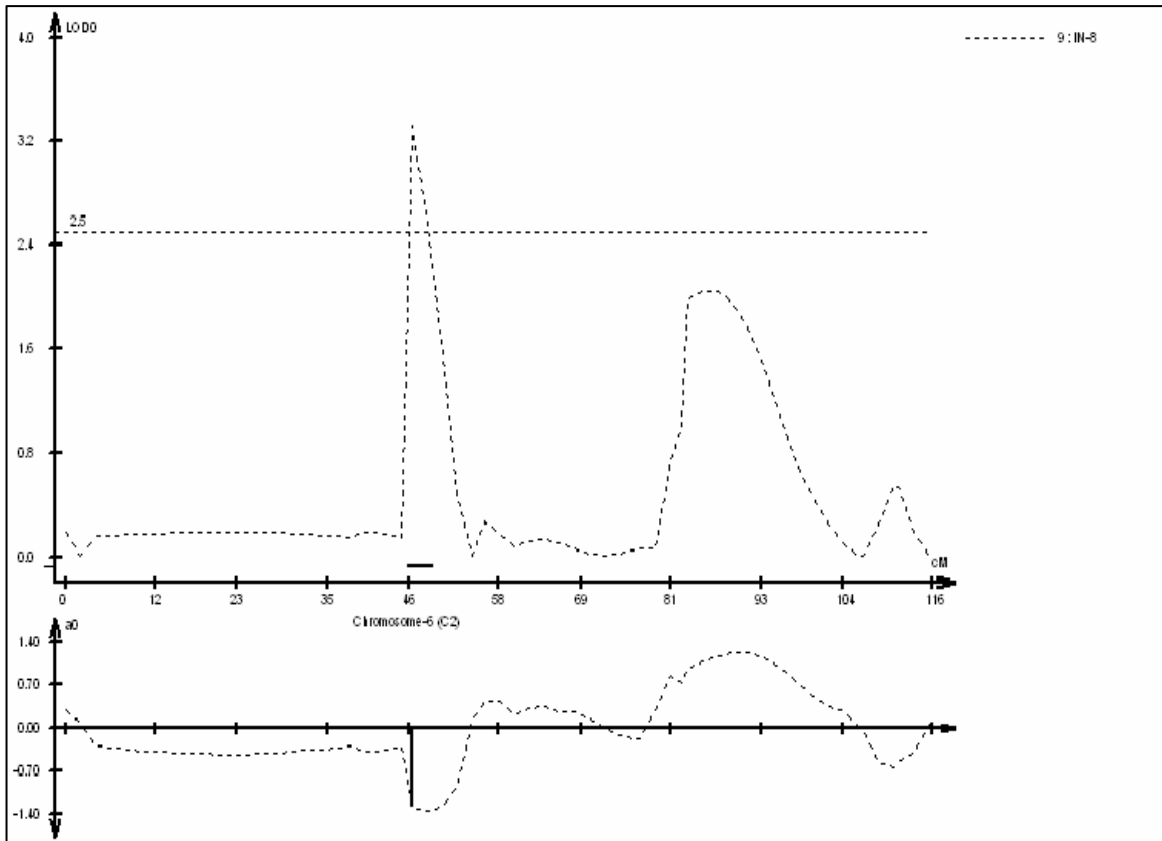
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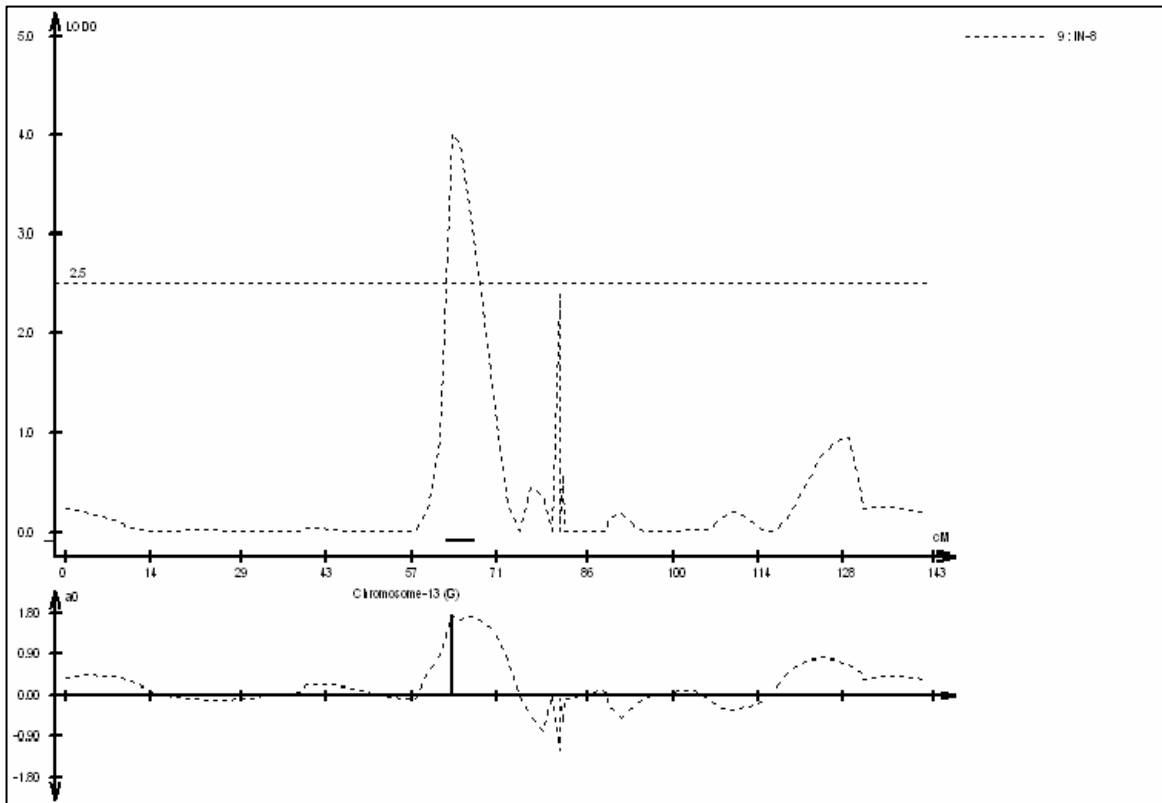
I.



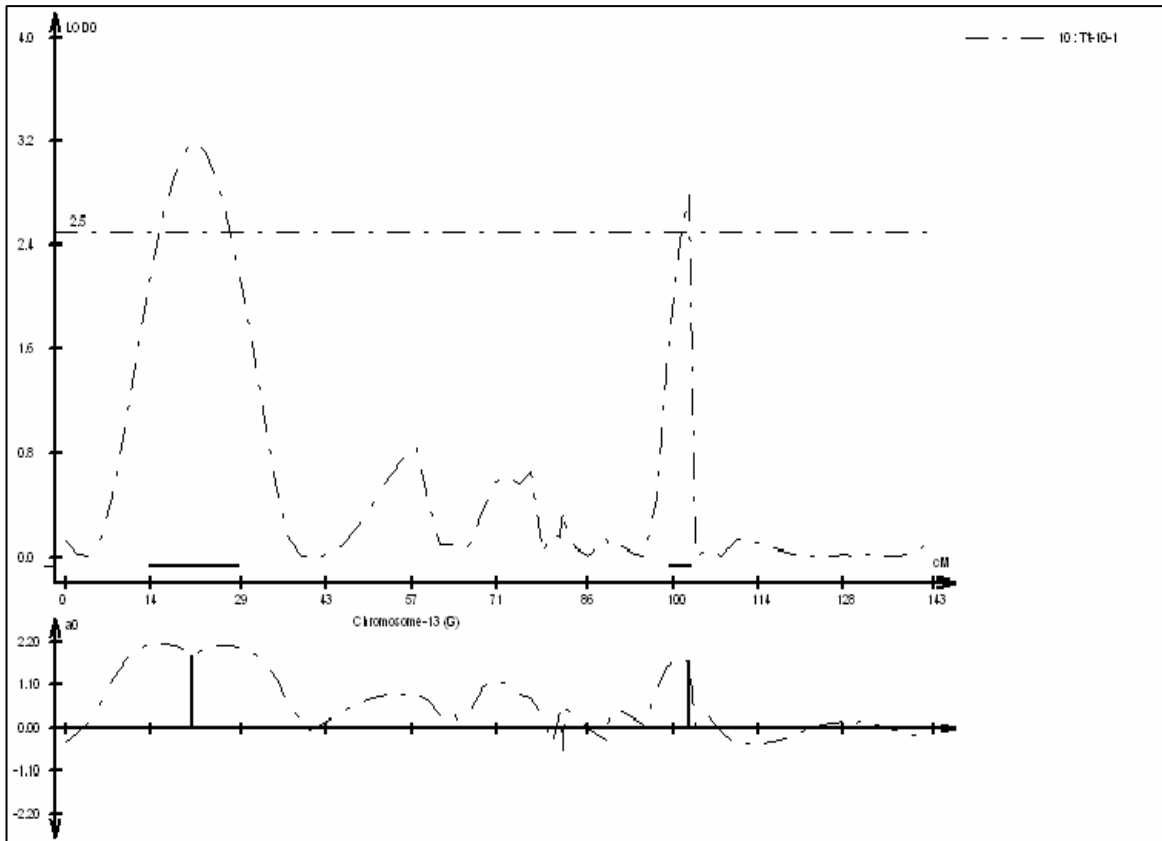
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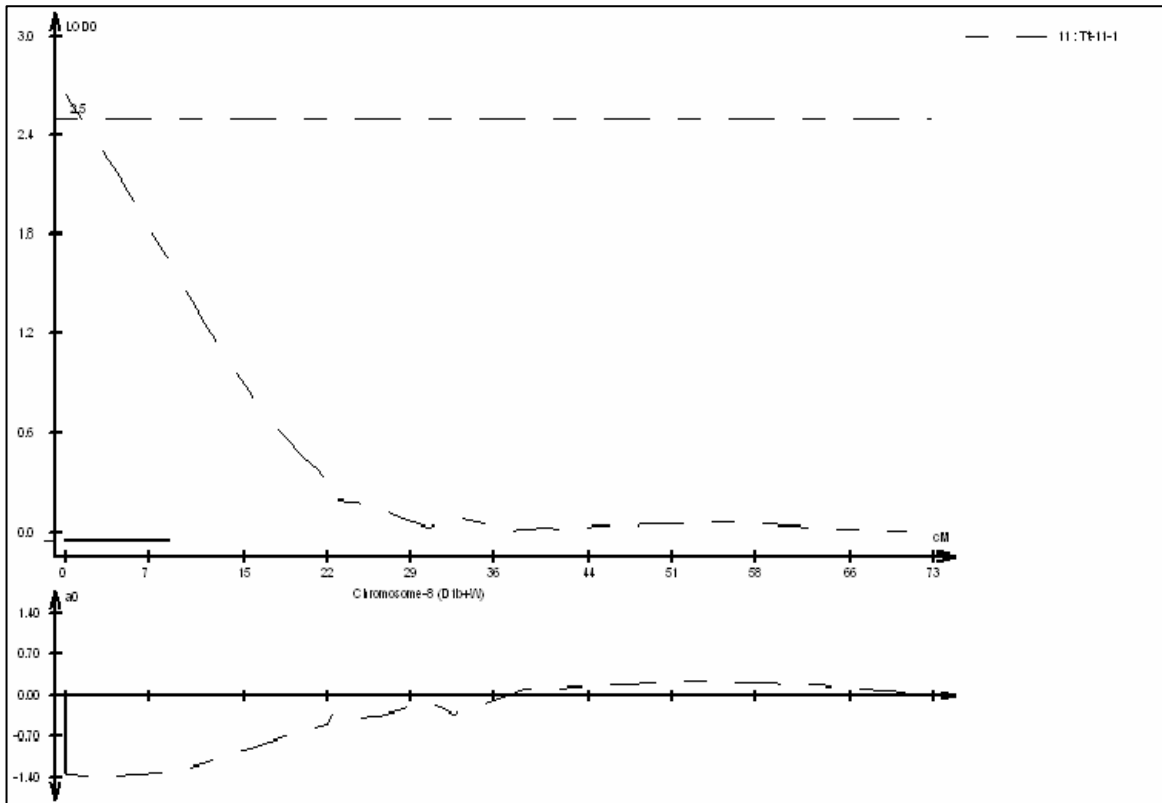
K.



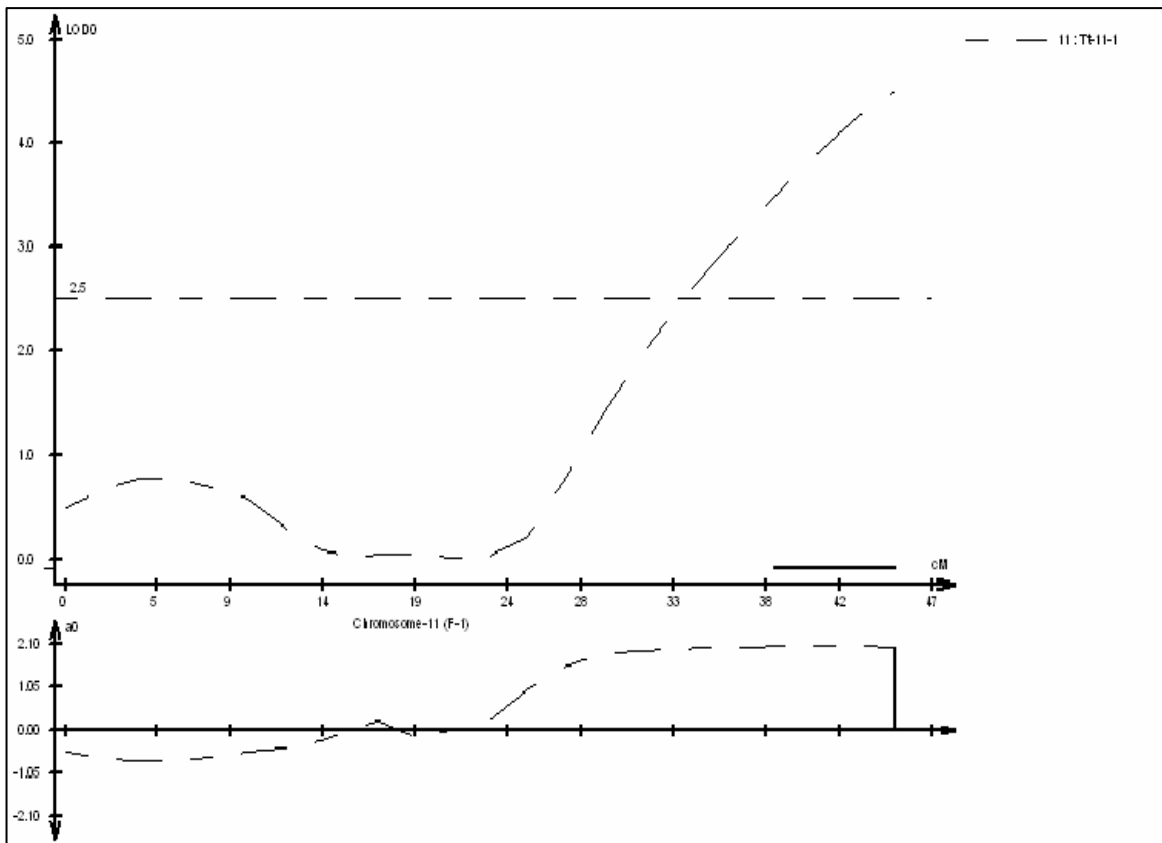
L.



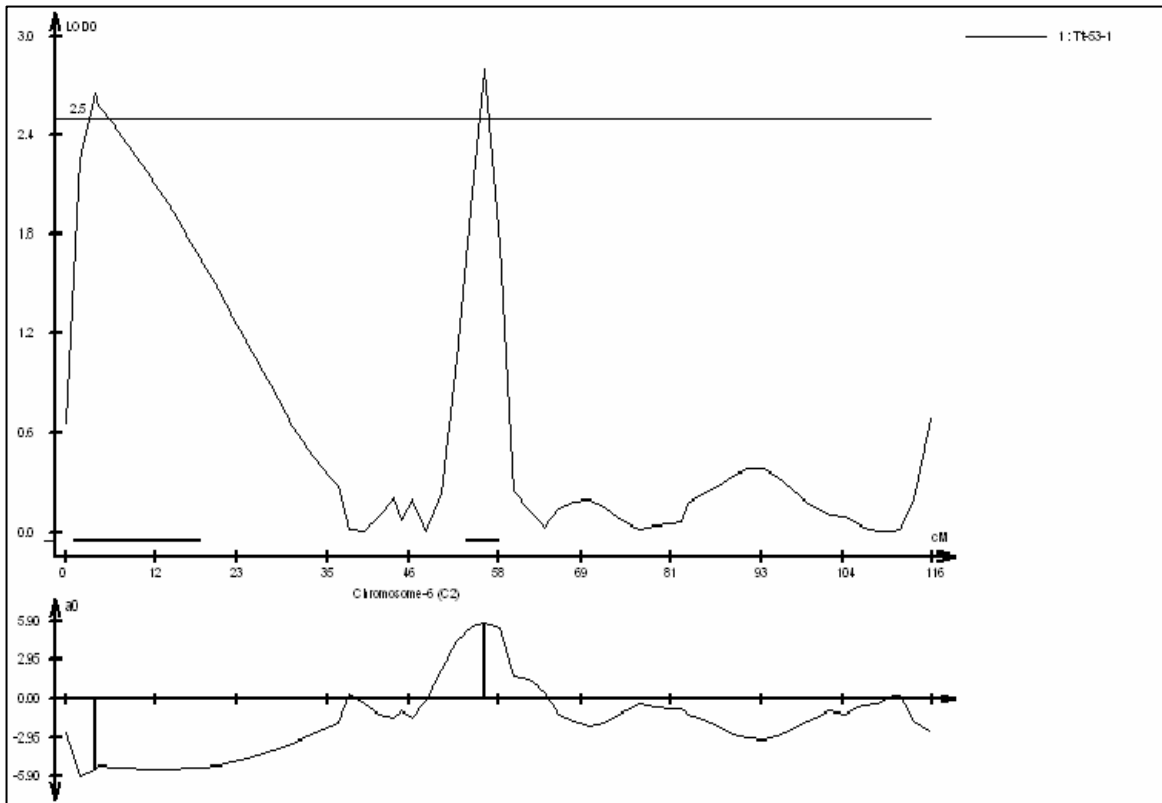
M.



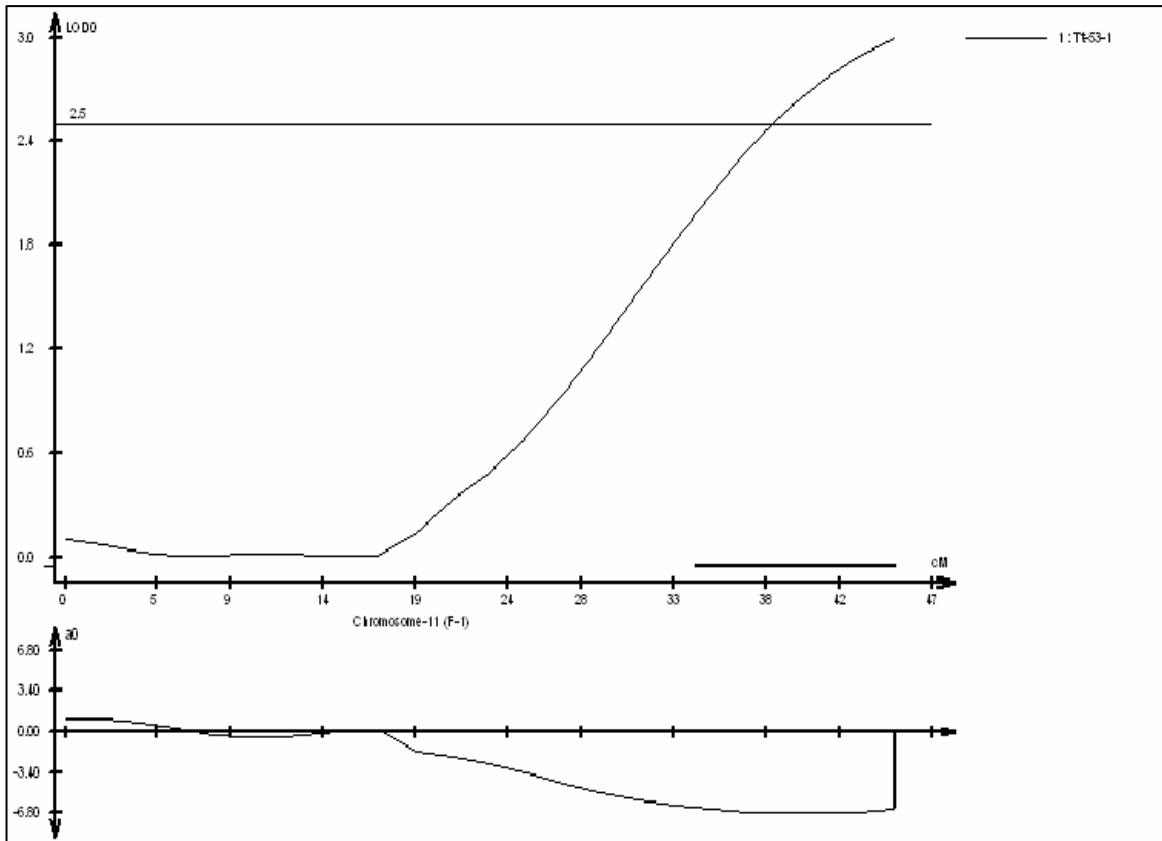
N.



O.



P.



Q.

Figure 2. The 21 QTL for (A.) hypocotyls length, (B. – O.) internodes length, and (P. – Q.) plant height found in the Essex by Forrest soybean RILs.

Discussion

The Essex by Forrest mapping population is among the most advanced based on southern US germplasm (Lightfoot et al., 2005; Kassem et al., 2006). The current ExF genetic map contains 1,053 BES derived simple sequence repeats (SSR), 13,747 sequence tagged sites (STS), and 417 previously mapped markers (Lightfoot et al., 2005; Kassem et al., 2006, 2007a,b).

In this report, sixteen QTL for internodes length (qIN1-10) were identified on LG A2, B1, C1, C2, D1b+W, D2, F, G, and K; two QTL for hypocotyls length (qHYL1-2) were identified on LG F; and three QTL for plant height (qPLH1-3) were identified on LG C2 and F. Except our previous study (Jacobson et al., 2007), no other studies reported QTL for internodes length in soybean (SoyBase, 2007). However, QTL for plant height, hypocotyls length, and flower color were identified and located on LG. A2, B1, C1, C2, (D1a+Q), (D1b+W), E, F, H, I, J, L, M, and N (Lark et al., 1995; Mansur et al., 1996; Lee et al., 1996a,b; Mian et al., 1998; Orf et al., 1999a,b; Sebolt et al., 2000; Specht et al., 2001).

Interestingly, QTL for soybean cyst nematode (SCN) resistance, and iron efficiency were identified within 20 cM of the internodes length QTL qIN7-1 reported here on LG A2 (Meksem et al., 1999, 2001; Concibido et al., 2004; Kassem et al., 2007a; SoyBase, 2007). At the same location of the QTL qIN6-1 on LG A2, QTL for plant height, SCN resistance, and internodes length were also reported (Concibido et al., 2004; Jacobson et al., 2007; SoyBase, 2007). Likewise on LG B1, QTL for plant height and SCN resistance were reported at the same location of the QTL qIN7-2 (Concibido et al., 2004; SoyBase, 2007). On LG C1, QTL for seed weight,

reproduction period, seed yield, and plant height were identified and located within 30 cM of the qIN2 reported here (Yuan et al., 2002; Kassem et al., 2006, 2007b; SoyBase, 2007). On LG C2, a gene rich region of 30 cM contains a cluster of QTL for sudden death syndrome (SDS) resistance, pod maturity, seed filling period, yield, plant height, and internodes length in addition to the QTL qPLH1, qPLH3, qIN3, and qIN8-1 reported here (Orf et al., 1999a,b; Iqbal et al., 2001; Wang et al., 2004; Smalley et al., 2004; Zhang et al., 2004; Kabelka et al., 2004; Kassem et al., 2006, 2007a; Jacobson et al., 2007; Guzman et al., 2007; SoyBase, 2007). The location of the new QTL supports the previous findings that genes and QTL are clustered in soybean (Meksem et al., 1999; Qiu et al., 1999; Kassem et al., 2006) and other plant species (Bert et al., 1999; Jiang et al., 1999; Teulat et al., 2001; Hittalmani et al., 2003). The same location of the internodes length (qIN10-1) reported here on LG D1b+W also underlies plant height and lodging (SoyBase, 2007). On LG D2 and within 5 cM of the qIN1, QTL for seed weight and oil content were also reported previously (SoyBase, 2007). The same QTL for hypocotyl length (qHYL1 and qHYL2) reported here on LG F, underlies also QTL for both hypocotyl length and seed weight detected in earlier studies of ExF (Jacobson et al., 2007; SoyBase, 2007). The same region contains also the QTL qIN10-2 and qPLH3. The region of LG F may contain a cluster of genes for plant growth and should be investigated further.

LG G is one of the most studied in soybean because it contains a cluster of QTL and genes for SDS resistance (Qrfs, QRfs1, Qrfs2, QRfs3; Meksem et al., 1999, 2001; Iqbal et al., 2001; Triwitayakorn et al., 2005; Kassem et al., 2006, 2007a), plant height, lodging, leaf ash, and internodes length (Jacobson et al., 2007; SoyBase, 2007) all within 20-30 cM from the QTL reported here qIN9-1, qIN7-3, qIN8-2, qIN6-2, qIN7-4, and qIN9-2.

Linkage group K has been associated with seed yield in many studies (Yuan et al., 2002; Kassem et al., 2006; Kazi et al., 2005, 2007). The same location of qIN6-3 identified on LG K also underlies pod maturity, seed weight, lodging, and internodes length traits (Jacobson et al., 2007; SoyBase, 2007).

Many studies reported that plant height, internodes length, and days to flowering are correlated with high yield in wheat (Eriksen et al., 2003), rice (Ishimaru et al., 2004), barley (Scheurer et al., 2001), sunflower (Bert et al., 2003), rye (Borner et al., 1999), cassava (Okogbenin and Fregene, 2003), cultivated lettuce (Argyris et al., 2005), and soybean (Sebolt et al., 2000; Specht et al., 2001; Yuan et al., 2002; Kabelka et al., 2004; Smalley et al., 2004; Wang et al., 2004; Guzman et al., 2007; SoyBase, 2007). Therefore, the plant height, internodes and hypocotyls lengths QTL found here are important when introduced in soybean breeding programs to produce superior high yielding cultivars and germplasm tolerant to drought and resistant to diseases. The genome sequence of soybean used in combination with the physical map (Shultz et al., 2006) will allow the intervals reported here to be examined for candidate genes.

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