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NaCl tolerance in *Lycopersicon pennellii* introgression lines: QTL related to physiological responses

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Abstract

The growth and ion content of salt sensitive *Lycopersicon esculentum* Mill. cv. M82 and salt tolerant *L. pennellii* Correll accession LA716 were examined under both control and stress conditions (150 mM NaCl). *L. esculentum* grew more vigorously than *L. pennellii* under optimal conditions, however, *L. pennellii* was able to maintain its growth better than cultivated tomato when the plants were exposed to salinity. Sodium content of both *L. esculentum* and *L. pennellii* increased as a result of NaCl stress. In addition, both species showed reduced potassium and calcium content due to salinity. The physiological traits were also measured in a population of 52 *L. pennellii* introgression lines grown under both normal and stress conditions. A total of 311 quantitative trait loci (QTL) were identified for the studied traits: plant height, stem diameter, leaf number, leaf and root fresh and dry mass, and sodium, potassium and calcium contents. Some of the loci (124) were identified under both control and stress conditions while 86 QTL were identified only under non-stress conditions and 101 loci were identified only under NaCl stress.

Additional key words: calcium, *Lycopersicon esculentum*, potassium, salinity, sodium, tomato.

Introduction

Salt stress tolerance is an extremely complex plant trait with multiple physiological, biochemical and genetic components (Xiong and Zhu 2002). Salinity tolerance may be expressed in more than one way including tolerance to osmotic stress, exclusion of damaging effects of sodium and chloride ions and/or tolerance to these ions (Munns and Tester 2008). When plants are first exposed to salt stress, ion homeostasis in the cell is maintained by pumping out of sodium ions at the plasma membrane and/or sequestration of these ions in the vacuole. In order to maintain growth, the plant must be able to tolerate toxic levels of sodium in its vacuoles and, at the same time, continue to take up essential ions such as potassium and calcium (Borsani *et al.* 2003). In addition to their roles in normal plant nutrition and metabolism, potassium and calcium are used for osmotic adjustment (Shabala and Cuin 2007) and to limit sodium entry into the cell (Demidchik and Maathuis 2007, Munns and Tester 2008) when the plant is under NaCl stress.

Cultivated tomato (*Lycopersicon esculentum*) is moderately sensitive to salinity at all stages of development (Maas 1986, Foolad 1996). At low concentrations of NaCl, tomato is able to exclude sodium ions (Foolad 1997) and the tolerant cultivars reduce sodium and increase potassium accumulation (Juan *et al.* 2005). Under high salinity, however, this system breaks down and a positive correlation between plant sodium content and the extent of damage is observed (Dasgan *et al.* 2002). In addition, plant growth and yield suffer as a result of the osmotic and oxidative stress and nutrient deficiency. Some of the wild relatives of cultivated tomato are salt tolerant. For example, *L. pennellii* accession LA716 has been reported as NaCl tolerant in several studies (Tal and Shannon 1983, Shalata and Tal 1998, Shalata *et al.* 2001, Mittova *et al.* 2002, 2003, 2004). Tomato salt tolerance is known to be a complex trait controlled by multiple genes with development and environment-specific loci associated

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Abbreviations: IL - introgression line; QTL - quantitative trait loci.
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with various components of tolerance (Foolad 2004). Thus, the genetic dissection of salt tolerance is difficult; however, it is necessary for the development of salt tolerant cultivars.

In this work, an introgression line population derived from a cross between the tolerant wild species *L. pennellii* LA716 and cultivated tomato (Eshed and Zamir 1995) was assayed for growth response and ion content under both control conditions and NaCl stress. Because these lines are genetically characterized, it was possible to identify and map genes related to plant growth and ion accumulation in response to NaCl stress. These loci may be useful for an increased understanding of plant salt tolerance and the future development of salt tolerant tomato cultivars.

Materials and methods

Salt-sensitive *Lycopersicon esculentum* Mill. cv. M82, salt-tolerant wild species *L. pennellii* Correll ass. LA716 and 52 *L. pennellii* × cultivated tomato introgression lines (ILs; Eshed and Zamir 1995) were used in the experiment. The IL population provides complete coverage of the *L. pennellii* genome as each IL contains a single introgression from the wild species in the genetic background of *L. esculentum* M82 (Eshed and Zamir 1995).

Seeds were germinated in peat and grown in aerated Hoagland's nutrient solution (Epstein 1972) with six replicates of each plant line. The experiment was performed in a greenhouse under natural irradiance and day/night temperatures of 27 - 29/23 - 25 °C and air humidity 45 - 51 %. At the seven true leaf stage, NaCl treatment started with the gradual addition of NaCl to the nutrient solution. The first increment of NaCl was 25 mM and additional increments of 25 mM NaCl were added each day until the NaCl concentration reached 150 mM. The plants were grown for 15 d at 150 mM NaCl. After the treatment period, plant height, stem diameter, and leaf number were determined for each plant. The leaves and roots were harvested and combined for each line to determine leaf and root fresh mass (g). After drying at 65 °C for 48 h, leaf and root dry mass were also determined. Additionally, leaf samples were analyzed for sodium, potassium and calcium content using the methods described by Chapman and Pratt (1961).

Student's *t*-test was used to compare treatment means for the parental lines and ILs at $P < 0.05$. The mean of each IL was compared with the mean for M82 under both control and stress conditions with this value expressed as a percentage (IL control mean/M82 control mean × 100). This value was then used to determine the difference in effect seen in the IL as compared to M82. This comparison with M82, the genetic background of the ILs, allowed the difference in effect to be attributed to the particular introgression carried by the IL. For this calculation, M82 was set as 0 % and 100 % was subtracted from the percent obtained for each IL. Thus, a value of 50 % in an IL would indicate that the introgression caused a 50 % increase in the trait as compared to M82. For detection of QTL, a threshold of 30 % was used. Thus, a QTL was assumed to be located in a particular introgression only if that introgression were associated with a 30 % change in the trait as compared to M82. The use of a 30 % threshold was chosen so that only QTL with large effects would be identified and agrees with the threshold used by Rousseaux *et al.* (2005) and Frary *et al*. (2011) in similar QTL detection studies in the IL population. Loci identified in only one of the treatments (control or NaCl) were assumed to be control- or NaCl-specific, respectively. QTL detected in both treatments were assumed to be important in controlling the trait of interest under both non-stress and stress conditions. QTL were located on the tomato map using the available IL molecular marker map (http://www.sgn.cornell.edu).

Results

Salt stress negatively affected all of the growth parameters measured in tomato cultivar M82 with the greatest decreases seen for root mass (Table 1). In *L. pennellii*, however, NaCl stress resulted in increases in plant height (1.2-fold) and stem diameter (1.3-fold) but decreases in the leaf and root traits. Leaf mass showed a greater negative response to NaCl stress in LA716 than M82 while root mass was more affected by stress in M82. Physiological parameter means for the ILs resembled M82 more than LA716 under both normal conditions and NaCl stress. Nevertheless, the ranges of values for these traits in the ILs usually spanned and exceeded the mean parental values. NaCl stress negatively affected growth in most of the ILs, however, for every trait, at least a small percentage of plants showed increased growth under stress (Table 1).

Ion content of M82 and LA716 showed similar responses to NaCl stress: sodium content increased while potassium and calcium contents decreased (Table 1). Despite this general similarity, LA716 showed much greater increases and decreases in sodium and potassium contents, respectively, than M82. As with the growth

parameters, ion content of the ILs exceeded the values of M82 and LA716. In addition, a significant proportion of the ILs had the opposite ion responses to NaCl stress as compared to their parents.

Table 1. Growth characteristics and ion content of M82, LA716 and IL lines under control conditions and NaCl stress. For the ILs, NaCl effect is the percentage of ILs showing increases and decreases in each parameter under NaCl stress as compared to non-stress conditions. Means ± SE, $n = 6$.

Parameter	M82 control	M82 NaCl	LA716 control	LA716 NaCl	ILs control	ILs NaCl	NaCl effect
Plant height [cm]	32.3 ± 3.7	23.7 ± 1.9	22.5 ± 4.0	18.3 ± 1.7	41.19 ± 1.57	31.36 ± 1.26	2 %
Stem diameter [mm]	6.7 ± 0.3	4.5 ± 0.3	4.1 ± 0.6	3.1 ± 0.4	5.03 ± 0.1	5.08 ± 0.12	17 %
Leaf number	9.0 ± 0.6	7.3 ± 0.3	11.0 ± 0.0	9.7 ± 0.3	8.80 ± 0.2	7.70 ± 0.2	9 %
Leaf f.m. [g]	12.54	10.03	5.53	1.52	21.67 ± 1.04	14.08 ± 0.81	8 %
Leaf d.m. [g]	1.52	1.10	0.47	0.15	1.34 ± 0.1	0.72 ± 0.08	10 %
Root f.m. [g]	38.42	14.23	4.03	2.76	18.24 ± 0.78	18.62 ± 1.04	58 %
Root d.m. [g]	1.68	0.25	0.16	0.18	0.53 ± 0.04	0.51 ± 0.05	42 %
Na^+ [% d.m.]	1.59	4.24	0.14	0.77	0.35 ± 0.008	1.47 ± 0.18	96 %
K^+ [% d.m.]	3.74	3.27	4.55	0.49	5.08 ± 0.25	3.09 ± 0.26	8 %
Ca^{2+} [% d.m.]	1.64	0.34	3.22	0.78	1.82 ± 0.11	1.57 ± 0.13	47 %

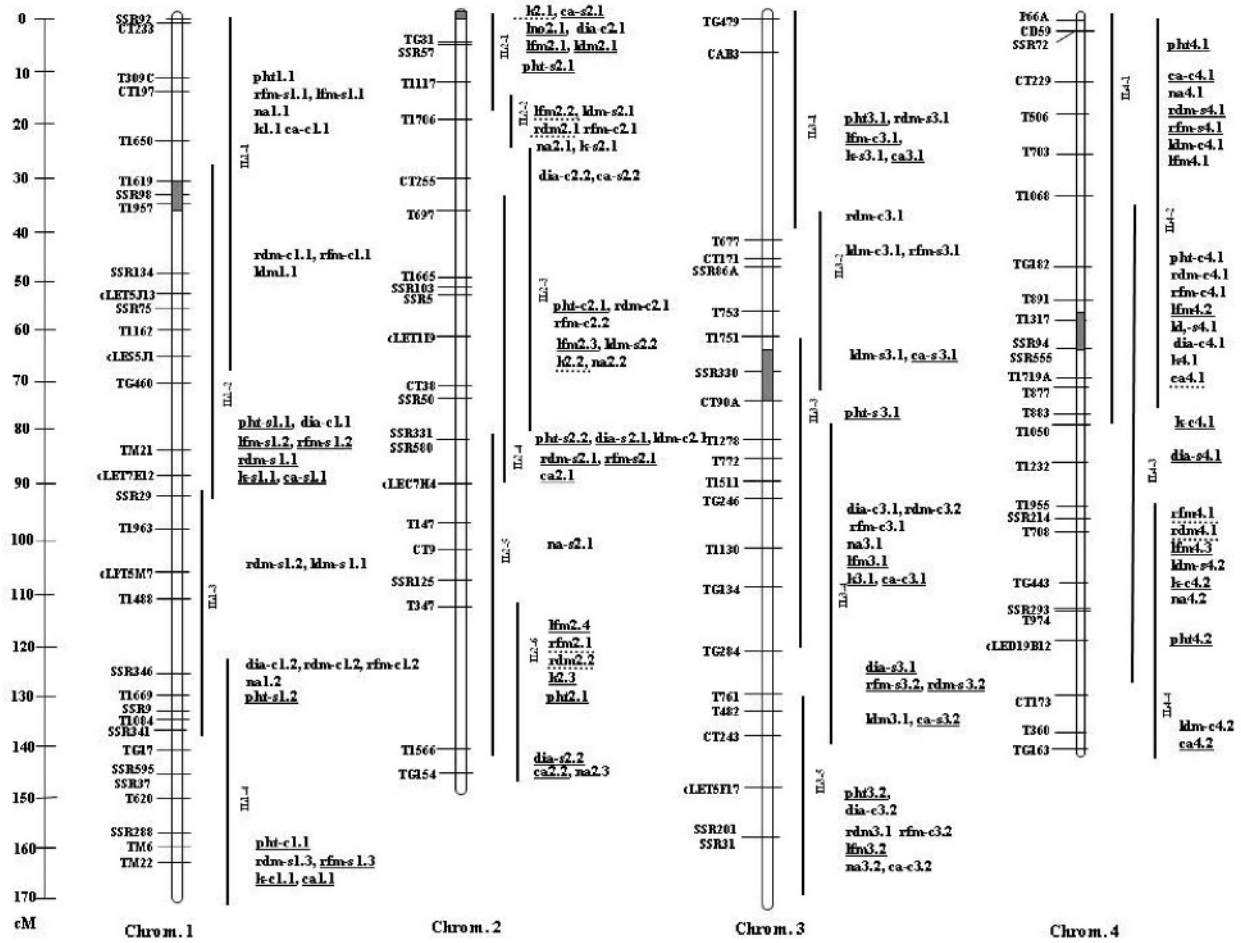

Fig. 1. Linkage map for the IL population showing the locations of QTL identified in this work. For loci that are underlined, *L. pennellii* alleles were associated with increased growth/ion content. Wild alleles for non-underlined loci were associated with decreased growth/ion content. Dotted underline indicates that the wild alleles were associated with both increased and decreased growth/ion content, depending on the environment (control or NaCl).

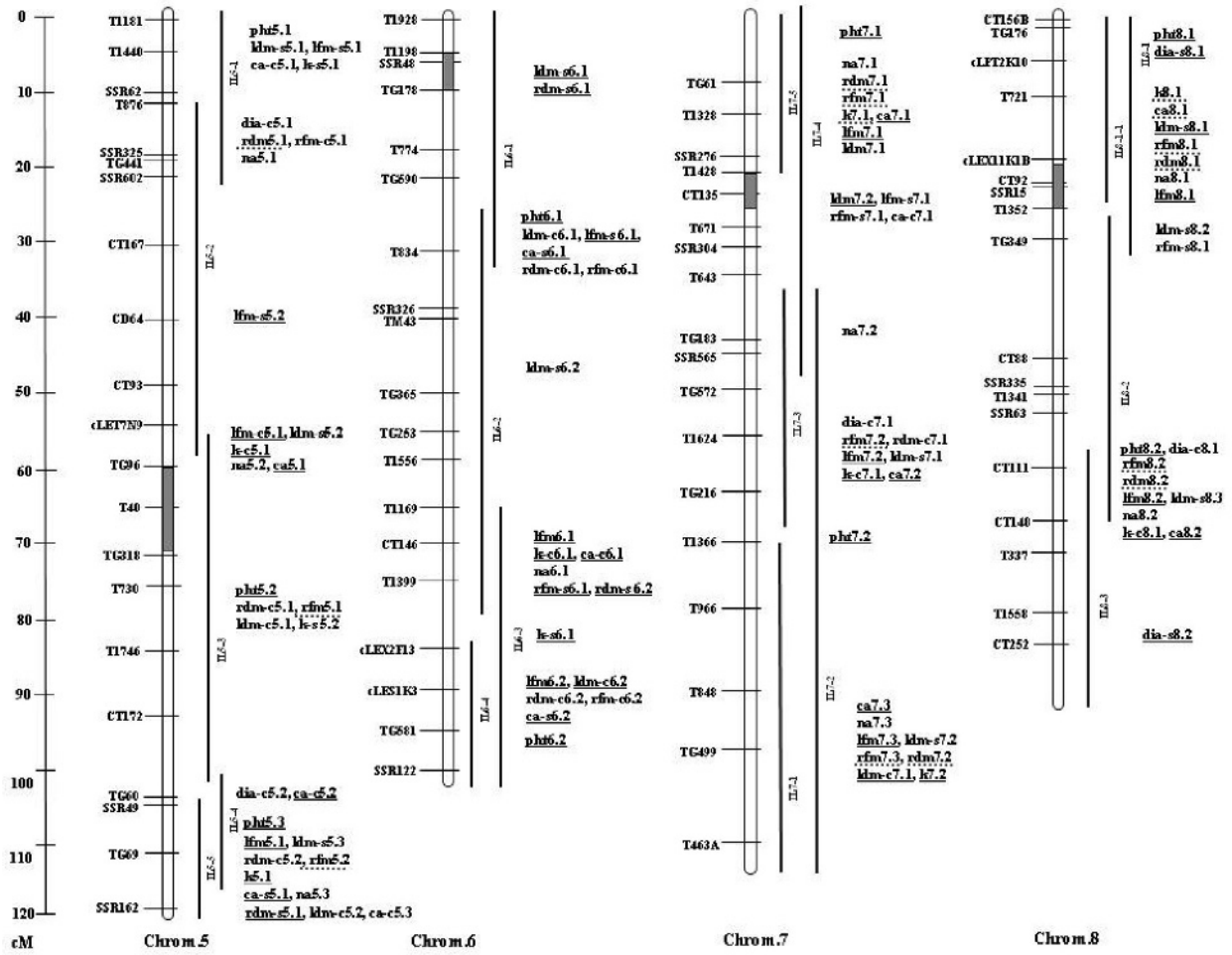

Fig. 1 (continued).

A total of 21 QTL altered plant height under both control and stress conditions in the ILs (Fig. 1). *L. pennellii* alleles for most of these loci (81 %) were associated with increases in plant height under both normal and stress conditions. The QTL with the strongest effect was *pht2.1* for which the wild alleles were associated with 71 and 78 % increases in plant height under control and stress conditions, respectively. In general, individual loci showed similar magnitudes of effect in stress and non-stress environments. Three QTL were identified for plant height under control conditions. For two of the loci, *L. pennellii* alleles were associated with increases in height. Six loci were detected that controlled height specifically under NaCl stress. *L. pennellii* alleles increased plant height under NaCl stress for five of the loci.

No QTL were detected that significantly affected stem diameter under both control and stress conditions. However, 13 loci were identified for stem diameter under control conditions (Fig. 1). *L. pennellii* alleles for these QTL were associated with decreased stem diameter. In addition, 8 loci were detected for stem diameter under NaCl stress. Interestingly, in contrast to the control QTL, the wild alleles for all of these loci were associated with increased stem diameter

One QTL was detected that controlled leaf number under both normal and stress conditions (Fig. 1). No loci were identified for this trait under control conditions and only one locus was detected for stress conditions. Like the other leaf number QTL, this locus had only a moderate effect on leaf number.

Leaf fresh mass was controlled by 22 QTL in both control and stress conditions (Fig. 1). Wild alleles for nearly all of these loci (91 %) were associated with increases in fresh mass. The greatest increases in leaf mass due to *L. pennellii* alleles were observed for *lfm2.1* (190 and 234 % increases for control and stress conditions, respectively). In general, QTL had lesser effects under stress conditions as compared to control conditions. Only 3 loci were identified for leaf fresh mass under control conditions and 10 QTL were detected for leaf fresh mass in stress conditions. *L. pennellii* alleles for these loci were equally divided between those for increased and decreased mass. Overall, increases in leaf fresh mass associated with wild alleles under NaCl stress were moderate.

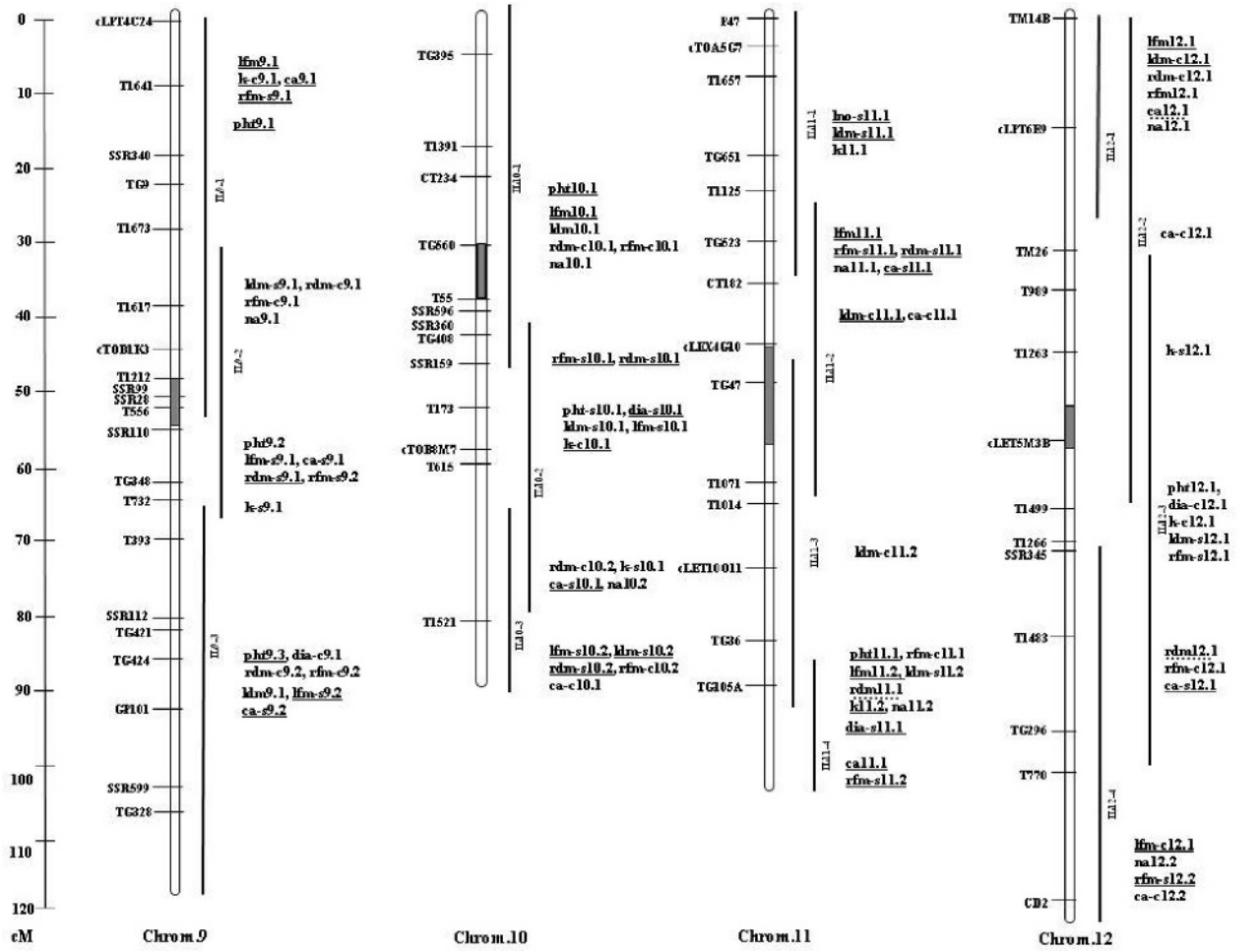

Fig. 1 (continued).

Seven QTL were identified that affected leaf dry mass under stress and non-stress conditions (Fig. 1). *L. pennellii* alleles were responsible for significant increases in leaf dry mass for only two loci. The greatest effect was observed for *ldm2.1* for which the wild allele increased leaf mass by 159 and 200 % under control and stress conditions, respectively. A total of 12 loci were identified for leaf dry mass under control conditions, while 22 loci were detected for the trait under stress conditions. Increased dry mass under NaCl stress was specified by wild alleles for four loci with *ldm-s11.1* having the greatest effect, a 100 % increase in mass as compared to M82.

Root fresh mass was associated with 10 QTL under both control and stress conditions (Fig. 1). For all but one locus, wild alleles were associated with a decrease in root mass when plants were grown in control conditions and an increase in mass when grown under stress. A total of 16 loci were identified for root fresh mass under control conditions. As with root dry mass, for all of these QTL, the *L. pennellii* alleles were associated with decreased root mass. Seventeen NaCl-specific loci were also identified for root fresh mass. *L. pennellii* alleles for most (65 %) of these QTL were associated with increased root mass under NaCl stress.

Eleven loci were identified that controlled root dry mass under stress and non-stress conditions (Fig. 1). Interestingly, *L. pennellii* alleles for most of the loci (91 %) were responsible for decreased root dry mass under control conditions and increased mass under NaCl stress. For five loci (*rdm2.1, rdm7.1, rdm11.1, rdm12.1*), wild alleles were associated with increases in mass of more than 200 % under stress conditions. Sixteen loci were identified for the trait specifically under control conditions. For all of these loci, the *L. pennellii* alleles were related with significant decreases in root mass. In contrast, for the 14 QTL that were detected for root dry mass only under stress conditions, 85 % showed increased root mass associated with wild alleles. Three loci (*rdm-s4.1, rdm-s10.1* and *rdm-s11.1*) showed increases in root mass of more than 300 % as compared to the M82 control grown under NaCl stress.

A total of 25 loci were identified for sodium content under both stress and non-stress growth (Fig. 1). For all of these QTL, *L. pennellii* alleles were associated with decreased sodium content in both environments. Wild

alleles decreased sodium content by as much as 100 % under control conditions and 98 % under NaCl stress. In general, for each QTL greater effects were seen under non-stress conditions than when plants were grown with NaCl. No sodium content QTL were detected specifically for control conditions and only one locus was specific for stress conditions.

A total of 12 loci were identified for potassium content under both experimental conditions (Fig. 1). The *L. pennellii* alleles for these loci showed every combination of effects. Ten loci were also identified for the trait only under control conditions. Wild alleles for these control-specific QTL were nearly always (90 %) associated with increased potassium levels. In addition, nine salt-specific loci were identified. For most (78 %) of these, the *L. pennellii* alleles were responsible for moderately decreased potassium content.

Fifteen QTL were detected for calcium content when plants were grown in stress and non-stress environments (Fig. 1). For most (80 %) of these loci, *L. pennellii* alleles were related with increased calcium content as compared to M82. While the effects of the QTL were moderate under control conditions, under NaCl stress *L. pennellii* alleles were associated with very dramatic increases in calcium content with seven loci showing increases of more than 500 % as compared to M82. A total of 13 QTL were identified for control-specific accumulation of calcium. Thirteen NaCl-specific QTL were also detected for calcium content. For all but two of these loci, *L. pennellii* alleles were responsible for very large increases in calcium content similar to those seen for the QTL identified under both stress and non-stress conditions. The greatest increases were observed in *ca-s6.2* and *ca-s3.1*, 700 and 713 %, respectively.

Discussion

Salt stress resulted in decreases in plant height, stem diameter, leaf number, leaf mass and root mass for both *L. esculentum* M82 and *L. pennellii* LA716. These changes were expected as it is known that plants tend to slow their growth in response to stress conditions (Kalefetoglu and Ekmekci 2005). With the exception of leaf mass, the reductions in the growth parameters were greater in M82 than in LA716. This difference was also expected as LA716 is tolerant to NaCl stress and therefore may be able to support a higher growth rate than M82 (salt sensitive) when exposed to NaCl stress. In addition, it was observed that the reduction in leaf mass was much greater than that of root mass in LA716. A similar response of tomato to salt stress was observed by Foolad (1997) who found that salt stress inhibited shoot growth more than root growth.

Although *L. pennellii* introgressions were generally associated with lower root mass than M82, 58 % of the ILs produced more roots under NaCl stress than under control conditions. This may indicate that *L. pennellii*-derived salt tolerance involves the production of more roots as a strategy to absorb more water in soil with low osmotic potential. An increased root to shoot ratio has been reported to be associated with NaCl stress in tomato (Maggio *et al.* 2004). The root to shoot ratio of M82 decreased by 2.2 and 2.5-fold for wet and dry mass, respectively, while that of LA716 increased by 2.5 and 3.5-fold, respectively. The ILs behaved like LA716 with only eight lines showing decreased root to shoot ratios under NaCl stress.

Salt stress resulted in increased sodium content in nearly all of the plants tested, however, the magnitude of the increase in *L. pennellii* LA716 (5.5-fold) was much greater than that seen in *L. esculentum* M82 (2.7-fold). According to Foolad (1997), *L. esculentum* responds to NaCl stress by excluding sodium ions. At high NaCl concentrations, however, this system breaks down. It is difficult to determine if NaCl exclusion was occurring in our experiment as M82 had much higher contents of sodium than LA716 even under control conditions. Only two ILs showed decreased sodium content under NaCl stress, IL2-1 and IL11-3. If these findings are verified by further experiments, they may indicate that these two lines are somehow deficient for sodium uptake. Such results would indicate that *L. pennellii* contains mutations for ion uptake/transport on chromosomes 2 and 11.

Potassium content of M82, LA716 and most of the ILs decreased under NaCl stress. Potassium and sodium ions rely on very similar systems for entry into plant cells including Na^+-coupled K^+ transporters, nonselective monovalent cation carriers and ion channels that mediate both K^+ and Na^+ transport (Cushman 2001). High affinity K^+ transporters have been identified in *Arabidopsis* that are blocked by high concentrations of sodium ions. Thus, growth in saline soils may lead to reduced uptake of potassium by plants. Potassium is required for osmotic adjustment to salinity and the activation of many enzymes which can also bind sodium ions (Shabala and Cuin 2007). If sodium ions are bound, normal metabolism is disrupted. Thus, the maintenance of a high K^+/Na^+ ratio in the cytosol is necessary for normal plant growth under NaCl stress.

Plants also require high concentrations of calcium for optimum growth under both normal and stress conditions (Demidchik and Maathuis 2007). In a saline environment, calcium can interfere with the movement of sodium ions into the plant through nonselective cation channels that are voltage independent (Demidchik and Maathuis 2007). In addition, calcium is an important signaling molecule and its increase in response to salinity is thought to trigger activation of Na^+/H^+ antiporters (Munns and Tester 2008). It has also been reported that salt tolerance

in *L. esculentum* is associated with the maintenance of calcium uptake and the exclusion of sodium ions (Ashraf 2004). In our study, calcium contents of M82 and LA716 were decreased by NaCl stress, however, the ILs had a mixed response with nearly equal numbers showing increases and decreases.

Salt tolerance is only partially determined by alterations in growth and ion concentration and it is possible that tolerance may be achieved in more than one way for these different parameters. Thus, different growth and ion exclusion, sequestration or uptake strategies may give the same result: salt tolerance. For example, some individuals may express tolerance as the ability to reduce shoot growth while maintaining root mass. Other plants may exhibit tolerance as the ability to continue shoot growth despite NaCl stress. Similarly when ion content is considered, salt tolerance may be the result of several factors either singly or in combination. Thus, exclusion of sodium ions, maintenance of potassium uptake in saline soils and/or increased calcium uptake are all strategies that may help a plant achieve salt tolerance.

Based on QTL analysis, the greatest increase in plant height under NaCl stress was conferred by a locus shared by IL1-3 and IL1-4. This QTL was responsible for an 87 % increase in plant height when the IL was compared to M82. IL11-1 and IL11-2 are also of special interest because these two lines harbored the most important loci for leaf number, leaf dry mass and root dry and fresh mass. *L. pennellii* alleles for these loci were responsible for 100 and 640 % increases in leaf and root dry mass, respectively, as compared to M82 under NaCl stress. Both of these ILs also contained a QTL for calcium content under NaCl stress for which the wild allele conferred a 363 % increase as compared to M82. In terms of ion content, IL2-5 is of interest because it harbors a locus for which the *L. pennellii* allele specified 83 % lower sodium content than M82 under salinity. IL6-3 was associated with loci for both potassium and calcium content under NaCl stress. The wild alleles for these loci or pleiotropic locus were associated with 74 and 700 % higher potassium and calcium contents, respectively.

Examination of Fig. 1 shows that many more QTL and ILs of interest to plant physiologists and breeders were identified in this work. Thus, this research may serve as a starting point for deeper investigations into the genetic control of and relationship between growth and ion responses to salt stress. For example, an IL with a locus or loci of interest may be selected and used to develop a population for fine mapping of the gene/genes responsible. Such populations can also be used for further introgression of QTL to breeding lines which is facilitated by the fact that the ILs contain single, well-defined introgressions in the cultivated tomato background. Such research may lead to the development of tomato cultivars with improved salt tolerance and a greater understanding of this increasingly important trait.

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