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Lettuce, a shallow-rooted crop, and *Lactuca serriola*, its wild progenitor, differ at QTL determining root architecture and deep soil water exploitation

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Abstract Wild plant species are often adapted to more stressful environments than their cultivated relatives. Roots are critical in exploiting soil resources that enable plants to withstand environmental stresses, but they are difficult to study. Cultivated lettuce (*Lactuca sativa L.*) and wild *L. serriola* L. differ greatly in both shoot and root characteristics. Approximately 100 $F_{2:3}$ families derived from an interspecific cross were evaluated in greenhouse and field experiments. In the greenhouse, root traits (taproot length, number of laterals emerging from the taproot, and biomass) and shoot biomass were measured 4 weeks after planting. In the field, plants were grown for 9 weeks (close to harvest maturity of the cultivated parent); mild drought stress was induced by withholding water for 1 week, and gravimetric moisture of soil was then determined for five depth increments between 0–100 cm. The families were genotyped using codominantly scored AFLP markers distributed throughout the genome. Composite interval mapping was used to analyze marker-trait associations. Quantitative trait loci were identified for differences between wild and cultivated lettuce for root architectural traits and water acquisition. Thirteen QTL were detected that each accounted for 28–83% of the phenotypic variation. The loci for taproot length (i.e., cm taproot length g^{-1} plant biomass) and the ability to extract water from deep in the soil profile co-localized in the genome. These coincident loci were identified in separate experiments. The wild *L. serriola* is therefore a potential source of agriculturally important alleles to optimize resource acquisition by cultivated lettuce, thereby minimizing water and fertilizer inputs and ultimately enhancing water quality.

Key words Root architecture · Soil water · Quantitative trait loci · Crop domestication · AFLP

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Introduction

There is a need for ecologically based management strategies to address the long-term environmental consequences of intensified production in agricultural ecosystems (Matson *et al.* 1997). Two major concerns are nitrate contamination of groundwater and the excessive consumption of limited water resources. Root systems that could efficiently acquire water and nutrients from the soil would minimize these problems. Wild progenitors of crop plants tend to have root systems that can exploit more unpredictable and stressful soil environments than their cultivated relatives (Chapin *et al.* 1989; Jackson and Koch 1997). Selection for high yields under high-input agricultural systems has resulted in cultivars with smaller root systems (Chapin *et al.* 1989; Jackson and Koch 1997; Siddique *et al.* 1990). Smaller root systems increase the propensity for movement and loss of soil resources beyond the reach of the roots.

Root architecture describes the spatial configuration of the root system, and includes both the topology of root axes and the distribution of roots in the soil (Lynch 1995). A plant with the minimum necessary fraction of its biomass in roots is optimal for annual crop productivity under the low environmental stress regimes typical of high-input agriculture (Chapin *et al.* 1989; Jackson and Koch 1997; Siddique *et al.* 1990), so that biomass is preferentially partitioned to the harvested organs. A root architecture that exploits the largest possible soil volume with the smallest possible root biomass would also be optimal for productivity under high-input growing conditions (Fitter 1994). Small, shallow root systems are unable to reach moisture and nutrients in lower layers of the

soil profile, so that frequent inputs of water and nutrients are applied to avoid plant stress. Increased rooting depth via changes in root architecture would promote a deeper recovery of soil resources. Of two plants with identical root biomass, the plant with a deeper root system will have access to deeper soil zones and thus a more abundant water and nutrient supply. Decreased inputs of water and fertilizer will be possible because less water and nutrients will tend to be leached below the root zone.

There are only limited data available on the effects of root architecture on the exploitation of soil resources (Fitter 1994; Eissenstat 1997; Berntson 1994). This has in part been due to the difficulties of measuring root characteristics and performance in soil. Some of the most detailed studies have been on lettuce (*Lactuca* spp.). Cultivated lettuce, *Lactuca sativa* L., is adapted to agricultural systems reliant on high inputs of nutrients and frequent irrigation (Lorenz and Maynard 1988), with the environmental consequences of nitrate leaching and, commonly, contaminated, lowered groundwater tables (Snow *et al*. 1988). It has a shallow root system with a short taproot and prolific lateral branches in the upper layers of the soil (Jackson 1995). Cultivated lettuce was probably domesticated from *Lactuca serriola* L. several thousand years ago (Kesseli *et al*. 1991), and the two taxa are fully interfertile. *L. serriola* is drought-tolerant (Werk and Ehleringer 1985), develops a long taproot, relies on water from deep soil zones during surface soil drought, and displays a lower level of developmental plasticity in its roots than cultivated lettuce (Jackson 1995; Gallardo *et al.* 1996). The differences in root architecture and root growth patterns between wild and cultivated lettuce suggest that inadvertent selection has occurred for root characteristics in *L. sativa* that result in rapid growth and shoot uniformity under cultivation (Jackson 1995) but potentially high losses of nutrients to below the root zone.

In this paper, we describe the analysis of an interspecific *L. sativa* × *L. serriola* population to identify quantitative trait locus or loci (QTL) for root architecture and water use patterns using co-dominant amplified fragment length polymorphic (AFLP) markers and composite interval mapping. Our results provide the opportunity for marker-assisted selection via the introgression of wild alleles into cultivated lettuce to improve soil water and nutrient acquisition from deeper soil zones.

Materials and methods

Plant material and linkage analysis

Randomly selected F_2 individuals from a cross between *L. sativa* cv. Salinas and *L. serriola* (UC92G489) originating from the collection of R.W. Michelmore (UC Davis) were self-pollinated to produce a population of over 100 $F_{2:3}$ families. Both *L. sativa* and *L. serriola* are highly autogamous and inbred. Plant material and DNA samples were prepared as described in Kesseli *et al*. (1994). A saturated molecular marker linkage map had been developed previously using 513 mostly co-dominant AFLP markers and a $F_{2:3}$ population of *L.*

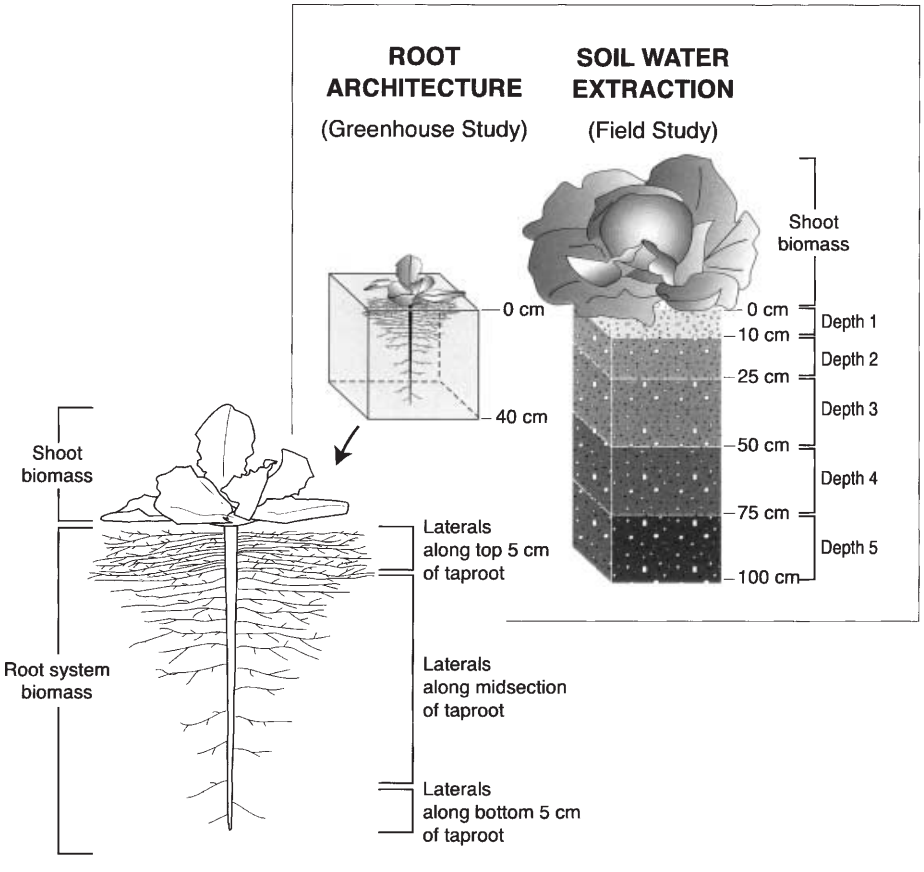

Fig. 1 Primary (directly measured) traits collected from the greenhouse and the field studies. Traits measured in the greenhouse include number of lateral roots along the taproot (top 5 cm, bottom 5 cm, midsection), root biomass, shoot biomass, and taproot length. Traits measured in the field study were shoot biomass and soil water content in five zones of the soil profile (0–10 cm, 10–25 cm, 25–50 cm, 50–75 cm, 75–100 cm)

Table 1 Traits examined in the *Lactuca sativa* cv. Salinas × *L. serriola* $F_{2:3}$ population. Bold font indicates the shortened names of traits as used in the text and figures

Trait
Primary traits from greenhouse study
Lateral roots along top 5 cm of taproot (no.); **(no. laterals in top 5 cm)**
Lateral roots along mid-section of taproot (no.); **(no. laterals in mid-section)**
Lateral roots along bottom 5 cm of taproot (no.); **(no. laterals in bottom 5 cm)**
Taproot length (cm); **(cm taproot length)**
Shoot dry weight (g plant^{-1}); **(g shoot biomass)**
Root dry weight (g plant^{-1}); **(g root biomass)**
Secondary traits from greenhouse study
g shoot biomass + g root biomass; **(g plant biomass)**
Number of laterals in top 5 cm g^{-1} shoot biomass
Number of laterals in top 5 cm g^{-1} root biomass
Number of laterals in top 5 cm g^{-1} plant biomass
Number of laterals in mid-section g^{-1} shoot biomass
Number of laterals in mid-section g^{-1} root biomass
Number of laterals in mid-section g^{-1} plant biomass
Number of laterals in bottom 5 cm g^{-1} shoot biomass
Number of laterals in bottom 5 cm g^{-1} root biomass
Number of laterals in bottom 5 cm g^{-1} plant biomass
Number of laterals in top 5 cm + no. laterals in mid-section + no. laterals in bottom 5 cm; **(no. laterals)**
Number of laterals g^{-1} shoot biomass
Number of laterals g^{-1} root biomass
Number of laterals g^{-1} plant biomass
Number of laterals cm^{-1} taproot length; **(no. laterals cm^{-1})**
cm taproot length g^{-1} shoot biomass
cm taproot length g^{-1} root biomass
cm taproot length g^{-1} plant biomass; **(cm taproot length g^{-1} plant biomass)**
(g root biomass g^{-1} plant biomass) · 100; **(% biomass in root)**
Primary traits from field study
g H_2O per m^3 at 0–10 cm soil depth; **(g H_2O per m^3 at 0–10 cm)**
g H_2O per m^3 at 10–25 cm soil depth; **(g H_2O per m^3 at 10–25 cm)**
g H_2O per m^3 at 25–50 cm soil depth; **(g H_2O per m^3 at 25–50 cm)**
g H_2O per m^3 at 50–75 cm soil depth; **(g H_2O per m^3 at 50–75 cm)**
g H_2O per m^3 at 75–100 cm soil depth; **(g H_2O per m^3 at 75–100 cm)**
Above-ground plant dry weight (g plant^{-1}); **(g shoot biomass)**
Secondary traits from field study
g H_2O per m^3 at 0–10 cm + g H_2O per m^3 at 10–25 cm + g H_2O per m^3 at 25–50 cm + g H_2O per m^3 at 50–75 cm + g H_2O per m^3 at 75–100 cm; **(total g H_2O per m^3)**
(g H_2O per m^3 at 50–75 cm + g H_2O per m^3 at 75–100 cm / total g H_2O per m^3) · 100; **(% total H_2O at 50–100 cm)**
(g H_2O per m^3 at 0–10 cm / total g H_2O per m^3) · 100
(g H_2O per m^3 at 10–25 cm / total g H_2O per m^3) · 100
(g H_2O per m^3 at 25–50 cm / total g H_2O per m^3) · 100; **(% total H_2O at 25–50 cm)**
(g H_2O per m^3 at 50–75 cm / total g H_2O per m^3) · 100
Total g H_2O per m^3 g^{-1} shoot biomass

sativa cv. Salinas × *L. serriola*. (R. Michelmore *et al*. unpublished). AFLP fingerprint patterns were obtained as described by Vos *et al*. (1995), visualized using a Fuji BAS/2000 phosphoimager, and scored co-dominantly with proprietary software developed by Keygene N.V. Molecular marker maps were generated using JOINMAP 2.0 (Stam and van Ooijen 1995). The 513 markers fell into ten linkage groups spanning 1342 cM (Kosambi) and provided markers throughout the genome. We chose a subset of 109 markers spaced approximately 10–15 cM apart to use as a framework map in QTL analysis. Framework markers were selected to maximize genome coverage and marker information content.

Collection of trait data

We measured root architectural traits in a greenhouse study and then analyzed the ability of the segregating families that were slightly water stressed to extract water in a field study (Fig. 1).

For the greenhouse study, F_3 plants were grown in non-sterile sand under natural lighting in 35-cm-deep pots that caused little impediment of the root growth of the lettuce plants at 4 weeks post-emergence. Irrigation was applied twice daily to avoid water stress. Nutrients (1/6 strength Hoagland's solution) were supplied at low, but non-limiting, levels beginning 10 days after planting. Four to seven plants for each of 97 F_3 families were evaluated; however, sufficient data for analysis of several traits was generated for approximately 75 families. Intact root systems were eluted, removed, and scored as described previously (Jackson 1995). Taproot length, number of laterals emerging from the taproot, and biomass were measured (Fig. 1). Careful assessment of root characteristics was time-consuming and had to be conducted over 5 days. Trait values that showed significant increases with time of harvest (P value of $R^2 \leq 0.05$) were normalized by assuming that a random sample of the families was assayed each day.

In the field study, 12 evenly spaced individuals (2 rows of 6 plants per m^2) from each of 89 F_3 families and the parental lines

were grown in plots replicated four times in a field at UC Davis in the Spring of 1997. Ammonium phosphate fertilizer (28 kg N and 32 kg P per hectare) was applied before planting to supply non-limiting amounts of N and P. The soil nitrate concentration was high in the field before planting so that 120 kg NO_3–N per hectare (0–100 cm depth) was present at the time of stand establishment. Intermittent furrow irrigation (approximately once a week) similar to actual cultivation practices was employed. To induce mild drought stress, we withheld irrigation for 1 week before scoring. The experiment was scored 62 days after planting when the cultivated parent, *L. sativa* cv. Salinas, had reached harvest maturity. Differences due to sampling over time were avoided by collecting all 430 soil samples in one 30-h period, with each of the four blocks sampled sequentially. Soil cores were collected from each replicate for each $F_{2:3}$ family at a location equidistant from 4 surrounding plants in the center of the beds. Soil cores were 4 cm in diameter. The shoots of the 4 surrounding plants were simultaneously harvested to obtain a measurement of dry weight after drying at 65°C. Soil samples from each soil depth increment (0–10 cm, 10–25 cm, 25–50 cm, 50–75 cm, 75–100 cm) were collected and stored in sealed containers. Volumetric moisture was calculated using the gravimetric moisture after drying 48 h at 105°C and bulk density (mg dry soil m^{-3}) for each soil depth increment.

Data analysis

Secondary traits were created to scale primary traits for shoot and root size in the greenhouse experiment and total soil volumetric water content in the field experiment (Table 1). To obtain information relevant to physiological associations between traits and to compensate for differences in seed weight (Jackson 1995) and photosynthetic rates (Gallardo *et al*. 1996) between *L. sativa* and *L. serriola*, we created a set of secondary traits in each experiment. Nineteen secondary traits were generated from the six primary traits measured in the greenhouse (Table 1). Each of the four primary root architectural traits (Fig. 1, Table 1) was scaled by root biomass, by shoot biomass, and by total plant biomass. In addition, the number of laterals per centimeter of taproot length and percentage biomass allocated to roots were calculated. For the field study, seven secondary traits were generated from the six primary traits. We did not scale water extraction by shoot biomass because there were large differences in plant growth habits, from compact heads to highly branched open canopies, that could have similar biomass but very different evapotranspiration rates. Therefore, we created secondary traits by dividing the volumetric moisture content in each portion of the soil profile by the total volumetric moisture content of the entire soil profile (0–100 cm) to detect differences in plant water use at various soil depths scaled by total water content.

QTL analysis

QTL were detected with the composite interval mapping (CIM) method (Zeng 1994) using the QTL CARTOGRAPHER software suite, version 1.12d (Basten, Weir, and Zeng, NC State University; http://statgen.ncsu.edu/qtlcart/cartographer.html). We used CIM for improved precision of QTL location estimates when more than 1 QTL for a single trait was present on a linkage group, and increased ability to detect QTL due to reduced sampling variance through the partial control of residual genetic variation (Churchill and Doerge 1994). The ZMAPQTL program, model 6, was used with a 10 cM window, controlling for the genetic background effects using the 10 markers with the strongest trait associations calculated by the SRMAPQTL program (stepwise linear regression). Thresholds for declaring QTL significance at $P \leq 0.05$ and $P \leq 0.01$ were estimated by permutation analysis (Churchill and Doerge 1994) for each trait using 1000 iterations (chosen for computational feasibility) of ZMAPQTL with randomly reassigned trait values and the same genetic model.

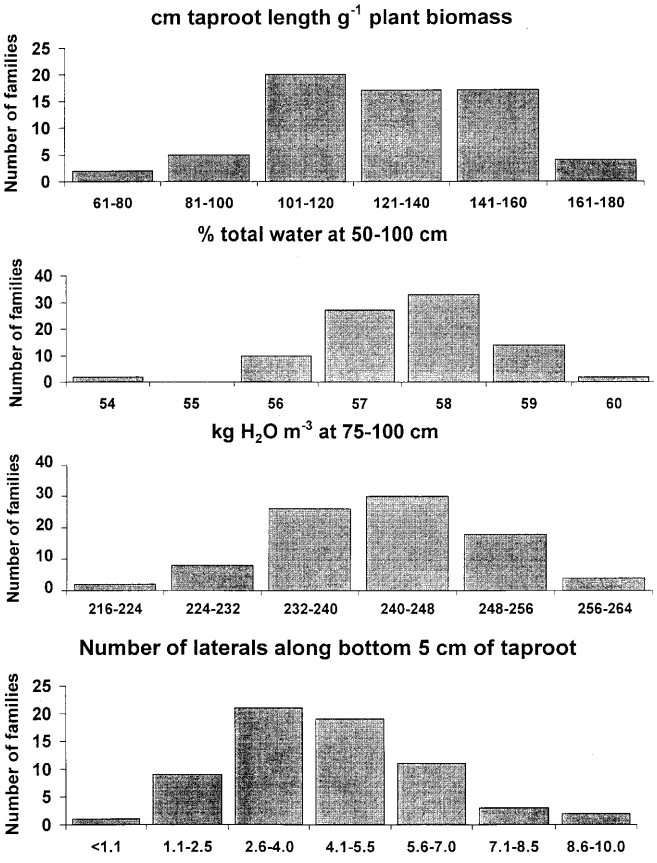

Fig. 2 Distributions of selected traits with QTL on LG2 and LG4 (**Fig. 3**) in $F_{2:3}$ families of *L. sativa* cv. Salinas × *L. serriola.* The means and coefficients of variation for the primary (directly measured) traits from which the secondary traits were derived are: taproot length, (cm) 31.1, 12%; total plant biomass (g), 0.25, 16%; total H_20 m^{-3} at 0–100 cm (kg), 212, 0.4%; H_20 m^{-3} at 50–100 cm (kg), 244, 0.4%; H_20 m^{-3} at 75–100 cm (kg), 242, 0.4%. At 75–100 cm depth, a sandier soil texture contributed to a lower water-holding capacity than observed higher in the profile

Results

QTL with large effects on root architecture and water-use patterns segregated in this interspecific cross. Phenotypic distributions for selected traits of this population are presented in Fig. 2. Thirteen significant QTL were detected, distributed on seven out of the ten linkage groups (Fig. 3, Table 2). Each QTL accounted for 28–83% of the phenotypic variation for 5 primary and 7 secondary traits (Fig. 3, Table 2). The greatest percentage of the phenotypic variance observed (83%) for all the 13 QTL detected was for the QTL on linkage group 4 determining the number of lateral roots along the bottom 5 cm of the taproot scaled for root biomass. The derivation of secondary traits permitted us to take into account differences in plant shoot and root size due to genetic and/or environmental variation. A maximum of 1 significant QTL was detected for the majority of traits; only 1 trait, number of laterals in the bottom 5 cm of the taproot scaled for root biomass in the greenhouse, identi-

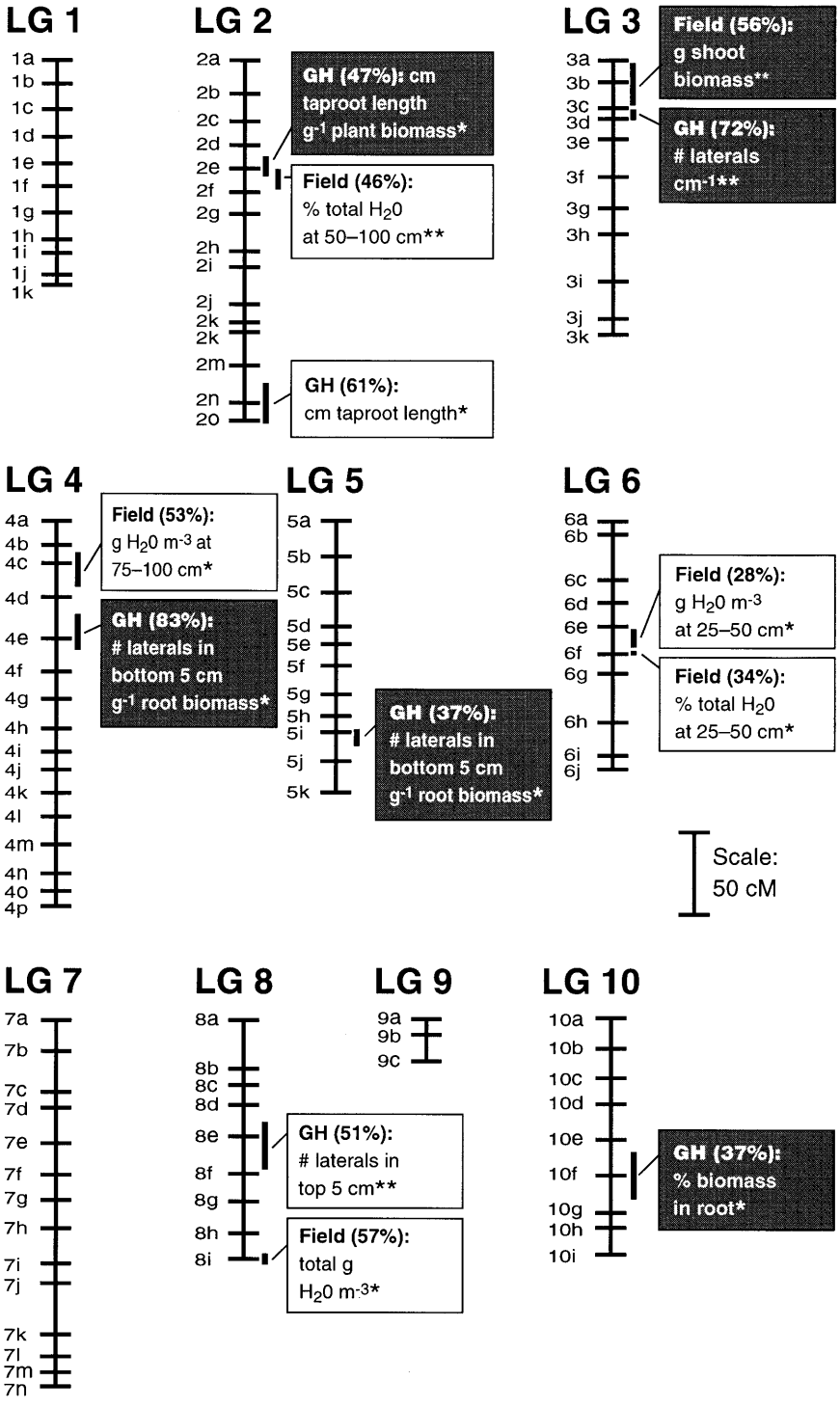

Fig. 3 The framework molecular marker linkage map with significant QTL for root architecture and soil water extraction. Linkage groups (*LG*) 1–10 are represented to scale by *vertical bars*. Individual framework markers (horizontal bars) are denoted in the text by the *linkage group number followed by a letter* designating the position within the group. Each QTL is represented by a *vertical bar* to the *right of a linkage group*; the *length of the bar* represents the region with test statistics exceeding $P<0.10$ significance threshold (see Table 2). Trait names and units are to the *right of the vertical bars*, followed by a number indicating the percentage variation in the trait accounted for by the genotype at the locus. Significance of QTL is indicated by * $P<0.05$ and ** $P<0.01$. *Boxes* indicate the parental allele resulting in increased trait values: *open* boxes represent *L. sativa* cv. Salinas alleles and *shaded boxes* represent *L. serriola* alleles

fied more than 1 QTL (linkage groups 4 and 5; Table 2, Fig. 3). These 13 QTL exceeded a $P<0.05$ experimentwise threshold level of significance calculated for each trait and included 12 of the 38 primary and secondary traits measured (Tables 1, 2). This population size and this stringent level of significance only allows the detection of QTL of large effect (van Ooijen 1992). It is probable that additional QTL are segregating in our population, but their effects were too small to exceed the significance threshold.

Co-localization of QTL for root architecture and ability to extract soil moisture was evident on linkage group 2 (Fig. 3, Table 2). A QTL at marker 2e conditioning the taproot length scaled for total plant biomass co-localized with a QTL at markers 2e-2f associated with the proportion of water in the lower soil zone (50–100 cm depth). The former was identified from the greenhouse experiment, while the latter was measured in the field study. Co-localization of these 2 QTL near markers 2e and 2f suggests the pleiotropic effects of a single gene or the ef-

Table 2 QTL identified in a *Lactuca sativa* cv. Salinas × *L. serriola* $F_{2:3}$ population for primary (1°) and secondary (2°) traits in the field and greenhouse (see Table 1 for listing). QTL were detected using composite interval mapping and permutated, trait-specific likelihood ratio (LR) test statistic thresholds. Bold font indicates the shortened names of traits as used in the text and figures.

Trait	QTL location[a]	Peak value[b]	Phenotypic variation %	Threshold 0.05	Threshold 0.01	Parental Allele[c]
Greenhouse traits (1°):						
Lateral roots along top 5 cm of taproot (no.); **(no. laterals in top 5 cm)**	8e**	25.5	51	21.2	25.1	Cultivated
Taproot length (cm); **(cm taproot length)**	2n-2o*	26.8	61	22.2	27.5	Cultivated (2n-2o)
Greenhouse traits (2°):						
Number of laterals in bottom 5 cm g^{-1} root biomass	4e*; 5i*	23.8, 23.6	83, 37	21.8	26.4	Wild (4e, 5i)
Number of laterals cm^{-1} taproot length; **(no. laterals cm^{-1})**	3d**	25.8	72	21.1	25.5	Wild
cm taproot length g^{-1} plant biomass; **(cm taproot length g^{-1} plant biomass)**	2e*	23.0	47	21.2	25.0	Wild
(g root biomass g^{-1} plant biomass) · 100; **(% biomass in root)**	10f*	22.6	37	20.5	25.5	Wild
Field traits (1°):						
g H_2O per m^3 at 25–50 cm soil depth; **(g H_2O per m^3 at 25–50 cm)**	6e-6f*	20.2	28	19.5	23.4	Cultivated
g H_2O per m^3 at 75–100 cm soil depth; **(g H_2O per m^3 at 75–100 cm)**	4c*	23.1	53	20.5	23.6	Cultivated
Above ground plant dry weight (g $plant^{-1}$); **(g shoot biomass)**	3b-3c**	27.6	56	20.3	23.5	Wild
Field Traits (2°):						
g H_2O per m^3 at 0–10 cm + g H_2O per m^3 at 10–25 cm + g H_2O per m^3 at 25–50 cm + g H_2O per m^3 at 50–75 cm + g H_2O per m^3 at 75–100 cm; **(total g H_2O per m^3)**	8i*	21.4	57	20.1	24.2	Cultivated
(g H_2O per m^3 at 50–75 cm + g H_2O per m^3 at 75–100 cm / total g H_2O per m^3) · 100; **(% total H_2O at 50–100 cm)**	2e-2f**	26.9	46	20.2	23.8	Cultivated
(g H_2O per m^3 at 25–50 cm / total g H_2O per m^3) · 100; **(% total H_2O at 25–50 cm)**	6f*	19.2	34	18.9	22.7	Cultivated

[a] QTL location estimate refers to the nearest molecular marker(s) on the framework map. The * and ** denote QTL significant at the 0.05 and 0.01 threshold levels, respectively

[b] Peak value is the maximum LR test statistic observed for the QTL in question; significant peak heights exceed trait-specific thresholds estimated through permutation analysis. To convert LR to LOD values, LOD=0.217 LR

[c] The parental [cultivated (*L. sativa*) or wild (*L. serriola*)] allele that causes an increase in the trait value

fects of a group of linked genes. The allele or haplotype from *L. serriola* encodes both increased taproot length in relation to plant size and a greater proportion of water uptake from deeper zones in the soil profile. The identification of these QTL in independent experiments implies that the longer the taproot in relation to plant size the greater the water use at soil depths greater than 50 cm.

On linkage group 4, 1 of the QTL determining the number of lateral roots along the bottom 5 cm of the taproot scaled for root dry weight was near a QTL influencing soil water content in the deepest portion of the soil profile (75–100 cm depth) (Table 2, Fig. 3). Differences in the location between these 2 QTL could be due to linkage of distinct genes, pleiotropy of a single gene, and/or imprecision of QTL mapping. The allele or haplotype from *L. serriola* determines a higher number of laterals in the terminal region of the taproot as well as greater water utilization in the deepest part of the soil profile. Greater proliferation of lateral roots near the tip of the taproot relative to root biomass may have consequences for water extraction below a depth of 75 cm.

QTL were co-located on two other linkage groups (Fig. 3, Table 2). On linkage group 6, QTL for the amount of water at 25–50 cm depth (a primary trait) and the proportion of total water in the profile at this depth (a derived secondary trait) co-located in the field experiment. For both QTL the *L. sativa* allele was associated with greater water remaining in the soil at this depth. On linkage group 3, 2 not obviously related traits, shoot biomass in the field and the number of laterals per centimeter in the greenhouse, were co-localized. The alleles for high shoot biomass and high frequency of root lateral branches were both from *L. serriola.*

The allelic contribution at each QTL was as expected, based on the parental phenotypes from prior studies (Jackson 1995), except for a QTL affecting taproot length at marker 2n. This exceptional QTL is an apparent case of heterozygote inferiority for taproot length. Average taproot length of plants homozygous for the *L. sativa* cv. Salinas allele at marker 2n was 33.8 cm, for plants homozygous for the *L. serriola* allele, 31.8 cm, and for 2n heterozygotes, 29.7 cm. *L. sativa* cv. Salinas acquires more of its water from the upper zones of the soil profile than does *L. serriola* (Gallardo *et al*. 1996). Alleles from the cultivated parent were associated with a high number of lateral roots along the top 5 cm of the taproot (8e), indicating a capacity to proliferate roots near the soil surface (Fig. 3). Three QTL for reduced water uptake below 25 cm of the 100-cm-deep soil profile (4c, 6e, 6f) were also associated with *L. sativa* cv. Salinas alleles, suggesting that the Salinas alleles contribute to a greater reliance on surface moisture (0–25 cm depth) than the corresponding alleles from wild lettuce. We also detected QTL in the greenhouse study for proportion of biomass in the roots (10f), number of laterals per unit taproot length (3d) and, in a second instance, lateral roots along the bottom 5 cm of the taproot, scaled for root biomass (5i), in which *L. serriola* alleles increased trait values (Table 2, Fig. 3).

Discussion

This study demonstrated an association between root architecture and resource utilization. Our present understanding of the genetic control of root branching patterns and distribution is poor but rapidly improving (Malamy and Benfy 1997; Yadav *et al*. 1997). Root distribution can also be influenced by preferential proliferation of roots in zones of high nutrient and water availability (plasticity); this increases a plant's ability to exploit resources with non-uniform distribution in the soil. Root phenotypic plasticity is also under genetic and environmental control (Zhang and Forde 1997). Despite the possibility of plastic responses, we were able to detect specific genomic regions that determined a large effect on root architecture (Fig. 3, Table 2) and to demonstrate a clear form-function relationship between the genes conditioning patterns of root growth and water acquisition.

Ideally, increased water extraction from the soil profile may be achieved by altering root architecture and distribution without increasing carbon expenditures to the root system. Higher carbon costs for root construction detract from shoot production and photosynthetic carbon gain. Selection for root systems with greater overall biomass would likely negatively impact yield. Therefore, we are searching for root architectural traits that increase the exploitation of resources with a minimal impact on root biomass allocation. This strategy has already been used for shoots; rice was selected for changes in shoot architecture (longer and more erect leaves to increase sunlight interception and photosynthesis) without increasing the carbon costs of producing greater leaf area (Mann 1999).

Marker-assisted breeding has been shown both theoretically (Hospital and Charcosset 1997; Gimelfarb and Lande 1995) and empirically (Young and Kelly 1996; Urrea *et al*. 1996; Romagosa *et al*. 1999) to be useful for selecting specific alleles. Alleles from wild relatives for increased rooting depth and acquisition of soil water and nutrients from lower zones of the soil profile could be introgressed to cultivated plants to help reduce total water use and nitrate leaching in commercial agriculture. This approach is applicable to a wide variety of economically and environmentally significant crops. It is particularly appropriate to apply this strategy to lettuce due to its high levels of nutrient and water use (Lorenz and Maynard 1988) and well-characterized root architectural patterns (Jackson 1995). Many of the potential useful alleles originated from the wild parent rather than the cultivated parent (Table 2); therefore *L. serriola* could be a rich source of agriculturally useful alleles. *L. serriola* alleles in several genomic regions (at markers 2e-f, 4c, 4e, 6e-6f) could be introgressed to increase the capacity of *L. sativa* to mine the deeper soil zones for water and nutrients. The *L. serriola* alleles for root biomass allocation (marker 10f), laterals per unit taproot length (marker 3d), and lateral roots along the bottom 5 cm of the taproot scaled for root biomass (markers 4e and 5i) could also be introgressed with the goal of enhancing acquisition of water from the soil profile. We are now introgressing *L. serriola* alleles for root architectural patterns using markers linked to the QTL into uniform cultivated genetic backgrounds of lettuce to study their individual and combined effects on plant growth form and biomass allocation.

The primary difficulty in analyzing and breeding for root characteristics is that they are extremely difficult to evaluate. The availability of markers linked to genes controlling root architectural traits provides a unique opportunity to develop genotypes having the above-ground performance of cultivated species but with at least some of the deeper rooting attributes of stress-adapted wild relatives through indirect selection on the marker genotypes. In crop species, however, high root distribution in the upper layer would be advantageous for efficient use of surface-applied nutrients. Therefore, higher biomass allocation to roots might be necessary to enable new cultivars to exploit both surface and deeper soil zones under agricultural conditions. However, it remains to be determined whether it is possible to generate cultivars with altered root architecture and/or higher root biomass allocation without prohibitively higher physiological costs that would slow the rapid plant growth necessary for commercial production.

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