ANNUAL REPORT

QTL mapping of drought resistance derived in wild barley, *Hordeum spontaneum*

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# TABLE OF CONTENTS

Executive summary.................................................................................................................. 3

SECTION I.................................................................................................................................. 3

A) RESEARCH OBJECTIVES..................................................................................................... 3

B) RESEARCH ACCOMPLISHMENTS OF ISRAELI AND KAZAKH RESEARCH GROUP........... 4

Material and Methods............................................................................................................. 4

(i) Plant material
(ii) Physiological characterization
(iii) Molecular-genetic characterization
(iv) QTL analysis

Results..................................................................................................................................... 5

1. Drought related traits
2. Molecular marker analysis.
3. Genetic map construction and preliminary QTL analysis

B2) DETAILED REPORT OF THE KAZAKH RESEARCH GROUP.............................................. 5

References............................................................................................................................... 6

III) SCIENTIFIC IMPACT OF COLLABORATION................................................................. 7

IV) DESCRIPTION OF PROJECT IMPACT................................................................................ 7

V) STRENGTHENING OF DEVELOPING COUNTRY INSTITUTIONS..................................... 8

VI) FUTURE WORK................................................................................................................... 8

SECTION II.................................................................................................................................. 9

A) Managerial Issues
B) Budget
C) Special concerns...
D) Collaboration, Travel, Training and Publications
E) Request for American Embassy Tel-Aviv or A.I.D. Actions.............................................. 10

APPENDIX................................................................................................................................ 11

Tables and figures
EXECUTIVE SUMMARY:

Project objectives: To reveal the genetic basis of unique resistance to water stress in wild barley, *Hordeum spontaneum*, from Israeli desert populations, as a potential source for a radical improvement of cereals drought resistance. This includes identification of physiological mechanisms of drought resistance of desert wild barley and genetic dissection (QTL mapping) of the revealed differences between resistant and susceptible genotypes.

Project findings over the second year: Significant differences were found between the parental genotypes of the mapping population (desert wild barley and cultivated barley) in response to drought stress, manifested in a few physiological traits, including osmotic adjustment in controlled environment. This was followed by a field experiment in two water regime (well watered and water stresses) that was conducted in Sede Boquer. Currently, a revised linkage map of 329 DNA markers have been constructed, and QTL analysis conducted using this more advanced molecular map. This allowed us to conduct a simultaneous mapping of laboratory physiological scores related to drought resistance and 20 field traits characterizing plant performance upon stressful conditions.

Contribution to the project objectives and international development: The results of the second year proved the efficiency of the chosen strategy of tagging unique drought resistance genes from Israeli desert barley. The final results will be of high theoretical and practical importance. The theoretical importance is due the need of understanding the molecular-genetic basis of plant survival at edge of life (extremely harsh desert environment: the used wild barley plants cope with as low as 100 mm year rainfall). The practical importance is in the fact that mapping of unique resistance to desert conditions will generate DNA markers flanking the target genes, enabling marker-assisted introgression of resistance from wild progenitor to modern cultivars and future map-based cloning.

Nature of collaboration: Fruitful relationships have been established between the partners based on complementation of the strong aspects of each group. This includes the Israeli experience of molecular marker analysis and genetic mapping, QTL mapping analysis, and drought resistance physiology at the cell and seedling levels. The Almaty group is good in field experimentation and plant physiology at the whole plant level. This complementation was already used to achieve some of the project objectives related to generation of new data. Likewise, members of the Almaty group participated during their training visits in molecular marker scoring. The equipment and chemicals purchased by the Almaty group within the framework of this project, combined with the experience obtained during the training visits, allowed them to conduct molecular marker analysis on their own mapping population derived from a cross between Israeli highly resistant desert ecotype of *H. spontaneum* and a local Kazakh barley cultivar.

SECTION I

A) RESEARCH OBJECTIVES:

Wild relatives of many cultivated plants, including wild barley, *Hordeum spontaneum*, have long evolved in the Near East Fertile Crescent across a wide ecological range. This generated a rich spectrum of adaptive diversity to multiple diseases, pests and ecological stresses, including drought (Nevo 1992). The objective of our research is to reveal the genetic basis of unique resistance to water stress in wild barley, *Hordeum spontaneum*, from Israeli desert populations, as a potential source for a radical improvement of drought resistance. This includes identification of physiological mechanisms responsible for drought resistance of desert ecotypes of *H. spontaneum* and genetic dissection (QTL mapping) of the revealed differences between resistant and susceptible genotypes.
B.1) RESEARCH ACCOMPLISHMENTS OF THE ISRAELI AND KAZAKH RESEARCH GROUPS:

Over the past twelve months, the research has been focused on (1) physiological phenotyping of the mapping population in the field and (2) saturation of the earlier constructed molecular map by additional DNA markers, both microsatellites (SSRs) and AFLP. This included:

(a) Testing the parental genotypes for polymorphism of molecular markers, SSRs (short sequence repeats).
(b) Scoring the mapping population for additional SSR markers and revising the molecular map.
(c) Field experiments at the Sede Boquer site under normal and minimal irrigation.
(d) Joint QTL analysis of quantitative traits: laboratory physiological traits and field traits characterizing drought tolerances and plant performance (e.g., changes in biomass and grain yield).

(d) Preparing a second mapping population based on a cross between Israeli desert genotype of *H. spontaneum* and Kazakh cultivar (including analysis of about 30 DNA markers conducted by Almaty group, see detailed report section B.2).

Important progress has been made, as shown in section Results (after the section of Material & Methods).

Material and Methods

**Plant material:** Wild barley (*H. spontaneum*) genotype 23-39, originated in Wadi Qilt, a desert population from Israel (100-250 mm annual rainfall) was crossed to *H. vulgare* cv. Mona (Swedish cultivar). A mapping population of 152 F4 families was established for QTL mapping of physiological characters related to drought stress.

**Physiological characterization:** Field experiment was conducted under two water levels (well watered and water stressed) in Sede Boquer. The recorded traits included flowering time, plant height, number of tillers, total grain yield, 100 seeds weight, and total biomass.

**Molecular marker analysis:** 60 SSRs, 7 STSs, and 2 Dhn genes, and 250 AFLPs were used for genotyping the population derived from the cross. Likewise, a second mapping population based on a cross between Israeli desert genotype of *H. spontaneum* and Kazakh cultivar is underway. In particular, analysis of 29 (18 SSR and 11 RAPD) DNA markers have been conducted by Almaty group.

**Map construction and QTL analysis:** Linkage map: the map was constructed using MAPMAKER, version 3.0. Due to the paucity of linkage information from dominant markers linked in repulsion phase (Peng et al. 2000), two map versions were constructed for each chromosome (see Fig. 1 in Appendix):

The Mona (M) map version consists of 48 SSRs, 66 AFLPs, 3 STSs, and 2 Dhn genes, spanning a distance of 1736.5 cM, with an average distance between markers of 15.0 cM.

The wild barley (W) map version consists of 51 SSRs, 60 AFLPs, 3 STSs, and 2 Dhn genes, being 1841.8 cM in length with an average interval of 16.4 cM.

**QTL detection:** Each of the measured traits was subjected to the scanning for putative QTL on the whole genome level using general interval mapping approach. In cases of significant deviation form normal distribution, the trait scores were log-transformed. An appropriate genetic model (pure additive, pure dominant, recessive, or heterotic effect) was chosen for each of the putative QTL; and the significance of LOD scores was determined using 1000 permutations. In addition, multitrait QTL analysis (Korol et al., 2001) was preliminarily conducted to show a few examples of simultaneous treatment of ten laboratory scores with two yield indices characterizing the change in plant performance under water stress relative to normal irrigation regime. The analysis was carried out using MultiQTL package.
RESULTS

Significant differences in resistance to drought stress under field conditions and osmotic stress at controlled environment (at -0.4MPa PEG), were found between wild barley inhabiting desert environments (Wadi Qilt 23-39) and cultivated barley (cv. Mona).

Single trait interval analysis revealed several QTLs affecting drought-tolerance related scores, at both seedling and whole-plant levels (see Table 1 in Appendix). These included traits scored in the lab: dry weight (chr. 4), dry weight after re-hydration (chr. 5 and 7), osmotic adjustment (chr. 2), root length (chrs. 3 and 5), and total root length (chr. 3, 4, and 7); and traits scored from field experiment: heading date under stress (chr. 2, 3 and 7), number of tillers (chr. 2), 100 seed weight (chr. 3 and 7), biomass (chr. 7) and tolerance index of biomass (chr. 2) (see also Fig. 1).

All possible variations in relationship between alleles at QTL were observed: either additive, dominant and recessive effects of the resistant parent allele, or positive and negative overdominance.

For most of the whole-plant level traits, a good correspondence of the results obtained for the two versions of the map was found, whereas some of the seedling-stage traits failed to display such a correspondence. This can presumably be explained by regional variation in maker information content, and a “conflict” in dominance-recessiveness at marker loci and QTL (when a dominant QTL is in repulsion phase with the flanking marker loci).

Two-trait and multiple trait analysis was conducted to increase the detection power and mapping resolution (Korol et al., 1995, 2001). As an example, the results of two-trait analysis of tolerance index for biomass and biomass at drought variant are shown in Fig. 2 (see Appendix). This analysis detected significant and coherent between the two map versions effects on chromosomes 2, 3, 4 and 7. Multiple-trait interval analysis of the seedling-stage traits revealed a few QTLs that have not been detected by single trait analysis (see Table 2 in Appendix). Joint analysis of these traits with tolerance index for biomass detected significant effects of chromosomes 2, 4 and 6. Some inconstancies between the results obtained on different groups of traits may partly derive from the large gaps on the maps and could be resolved by additional markers.

B.2) DETAILED REPORT OF THE KAZAKH RESEARCH GROUP:

Responsible researchers: Dr. Turuspekov, Dr. Abugalieva, Dr. Ryabushkina
Additional staff: Junior researcher Mrs. Dzhardemalieva.

Major objectives of the Year 2 were to study genetic diversity of wild and cultivated barley varieties from Kazakhstan and prepare the genetic material for localization of the major QTLs contributing to drought tolerance in barley.

1. Description of the wild barley plants *H. spontaneum* from Israel and Central Asia compared with varieties of cultivated barley *H. vulgare* from Kazakhstan.
A. Field data:
According to the Work Program, the barley varieties from Kazakhstan (Donetskii 8, Bereke 54, Arna, SK 43) and populations of *H. spontaneum* from Israel (Arad, Sede Boker, Yavne, Jericho) along with samples from Central Asia were sown in the fall of 1998 and 1999 and spring of 1999 and 2000. All wild barley accessions were tested for following traits: heading date, height of plant, color of spike and grain, number of productive spikes, weight of grains per one plant. In general, the lines from population Jericho were most adaptive to the conditions of the South East of Kazakhstan. Therefore, the majority of hybrid lines between *H. vulgare* and *H. spontaneum* were developed involving individual plants from population of Jericho.

B. Physiological analyses:
The objective of this investigation was to analyze the stomatal control in different barley cultivars and lines of wild species of *Hordeum spontaneum* K.

C. Results and discussion:
Line 3 (Jericho) of *H. spontaneum* and Arna showed two important features for drought avoidance (presumably along with some other traits which were not under present investigation). The first, shorter period of vegetative stage, (the time of the beginning the flowering stage). The second, line 3 from Jericho of *H. spontaneum* and Arna had the higher level of stomatal conductance and transpiration compared to other lines and cultivars. The influence of precocity, osmotic adjustment and stomatal conductance (Field Crop Res. 62:23-34) showed significant linear correlation between grain yield and stomatal conductance \((r=0.77, p=0.05)\) in stressed barley genotypes. We explained this observation by a smaller reduction in conductance, which may favor photosynthesis at critical stages in yield determination, and consequently increase yield under drought.

The next step of this investigation will be related to segregation analysis of F\(_2\) hybrid populations Bereke 54 × Jericho of *H. spontaneum* and South Kazakstan 43 × Jericho of *H. spontaneum*, which differ in time of the beginning of flowering and in stomatal conductance level.

D. Genetic diversity analysis:
1. Biochemical and molecular markers analysis: Both wild and cultivated barley accessions were screened using several biochemical markers, such as isozymes and storage proteins. The isozyme analysis of 10 barley varieties from Kazakhstan and *Hordeum spontaneum* K. from Israel was done for Esterase, Malate dehydrogenase, Acid phosphatase, Peroxidase, 6-Phosphogluconatedehydrogenase, Glutamate dehydrogenase. Comparative analysis of genetic diversity between Israeli and Central Asian population is underway. Population “Yavne” has been characterized by significant intrapopulational polymorphism on hordein components.

DNA analysis:
(i) **SSR (Simple sequence repetitions) analysis:** 96 wild plants *H. spontaneum* representing both Israel and Central Asia and Kazakh barley varieties were screened using 18 SSR primers
(ii) **RAPD (random amplified polymorphisms of DNA) analysis:** Ten cultivated barley varieties from Kazakhstan were analyzed using 11 PARD primers. Both SSR and RAPD data will be extended in order to develop genetic catalogue of barley varieties in Kazakhstan.

2. Preparation of plant material for genetic analysis: According to the Work program research group from Kazakhstan has prepared hybrid material from crosses between cultivated barley varieties from Kazakhstan and wild barley from Israel. F1 plants from the first year of the project were sown in order to obtain F\(_2\) segregation populations. Currently, we concentrate on two different F\(_2\) hybrid lines; *H. spontaneum* x Bereke 54 and *H. spontaneum* x South Kazakhstan 43.
References


c) SCIENTIFIC IMPACT OF COLLABORATION

Already the first year has demonstrated a fruitful collaboration between the partner teams proved by the richness of the generated data. In particular, this was manifested in a complementation of the strong aspects of each group. The Israeli team has accumulated a good experience of molecular marker analysis and maker mapping, QTL mapping analysis and drought resistance physiology at the cell and seedling levels. The Almaty group is strong in field experimentation and plant physiology at the whole plant level. Therefore, during the second year, the Almaty group contributed by in-depth analysis of field performance of barley genotypes contrasting for drought tolerance, i.e., desert H. spontaneum ecotypes and cultivated Kazakh barley. Their results were used in the scoring of the mapping populations, both in Israel and in Kazakhstan, for plant performance under drought stress. Once marker genotyping of the Kazakh mapping population is finished, the QTL mapping results obtained at both ends will allow us to address the QTL-environmental interaction problem.

D) DESCRIPTION OF PROJECT IMPACT

The final results of the project will be of high theoretical and practical importance. The theoretical importance is due primarily to the unique drought resistance manifested by the used Israeli desert genotypes of H. spontaneum. The genetic dissection of this resistance and testing for coincidence with already identified dehydrin genes will open the possibility to clone new unique alleles of drought resistance genes. We have already included several dehydrin genes into the mapping program aimed to look for their coincidental location with drought resistance and/or plant performance under stress. Once such coincidences are found, the next step will be testing the corresponding candidate genes for differential response to stress (assayed by expression analysis) between the parental genotypes as well as the alternative QTL groups of the mapping population defined by the flanking markers. Such an analysis could be considered as a genuine bridging between structural and functional genomics. The immediate practical importance of the obtained results is in the fact, that direct mapping of the unique
resistance will result in defining molecular markers flanking the key resistance genes, hence allowing for marker-assisted introgression of the resistance genes for the wild progenitor to modern cultivars.

V) STRENGTHENING OF DEVELOPING COUNTRY INSTITUTIONS

This project has manifold positive consequences for the Kazakh Institute, in particular, and for Biological and Agricultural Science of Kazakhstan, in general. These include:

1) **Purchasing modern equipment** to conduct Molecular Biology studies. They have got the money for equipment and chemicals that allowed them to initiate PCR analysis for genotyping their mapping population at Almaty.

2) **Training the personnel** was considered an important aspect of our collaboration. During the first year, two members of the Almaty team (Mr. Sersenbaev and Dr. Ryabushkina) visited Haifa, with total duration of the visits of about 5 months. We planned additional visits for the second year. The target of the planned visits was to continue training in molecular biology techniques and, in addition to experimental techniques, to learn how to use new software (MultiQTL package, see website www.MultiQTL.com) for QTL mapping developed by the Israeli PI. Due to technical problems these visits were postponed for the next year.

3) **Bridging between modern quantitative genetics and breeding** for crop resistance is one of the consequences of projects aimed to dissect genetically complex traits related to plant adaptation. Barley is a very important crop for Kazakhstan and resistance to drought stress is a limiting factor in productivity and yield stability of barley in this country. Therefore, the possibility to facilitate selection for drought resistance based on unique desert alleles of Israeli wild barley and developed molecular markers is a major contribution of this project to their agriculture. Moreover, the facilities, staff and know-how, that will be established in Almaty as a result of this project, will serve a basis for future development for other crops and other limiting factors of agriculture productivity in this region.

VI) FUTURE WORK

1) **Linkage map**: we still have to improve the density of markers in a few intervals where strong effects on drought-related traits have been detected. Simultaneously, two additional mapping populations will be characterized. Of these one is the population established by Kazakh group and derived from a cross between Israeli ecotype of *H. spontaneum* and a Kazakh cultivar of *H. vulgare*; the second population resulted from a cross between a mesic and a desert ecotypes of *H. spontaneum*, and is being analyzed by the Israeli group.

2) **Candidate genes**: a series of dehydrin genes (Choi et al., 1998) are now being mapped on our mapping population in order to relate the positions of the detected QTLs with those of candidate genes related to drought resistance (in particular, osmotic adjustment) and plant performance in the field upon drought stress. Likewise, we start to test the parents for differential expression of the candidate genes in response to drought stress.

3) **Drought resistance scoring**: further characterization of new resistance-related traits of the roots in the mapping population will be conducted.

4) **QTL analysis**: a detailed multiple trait analysis will be conducted using a revised map with added codominant markers and additional scores of resistance traits. Special attention will be paid to multiple trait analysis as a more powerful and precise technique of QTL mapping (Korol et al., 2001)

SECTION II

(A) Managerial Issues: (a) The Kazakh group required to assist in managing the training budget from Haifa. This problem was addressed to the Project Administrator Mr. Boaz Ayalon who approved this application.
(B) **Budget:** The financial part of the report will be provided the next week by the management of the Research Authority of the University of Haifa (by 3-5 of July).

(C) **Special concerns:** No such issues have arisen.

(D) **Collaboration, Travel, Training and Publications**

1. **Collaboration:** Fruitful collaborative relationships have been established between the participating groups. In particular, this was manifested in a complementation of the strong aspects of each group. The Israeli team has accumulated a good experience of molecular marker analysis and maker mapping, QTL mapping analysis, and drought resistance physiology at the cell and seedling levels. The Almaty group is strong in field experimentation and plant physiology at the whole plant level. This complementary expertise was already used to achieve the project objectives of the first year. Namely, the first mapping population that was established by Haifa group has been characterized at Haifa for molecular markers and cell and seedling level resistance traits, whereas whole plant traits were partly characterized at Almaty. Likewise, a thorough test of several candidate mapping populations established by crossing of Israeli resistance genotypes of barley to Kazakh cultivars, is conducted at Almaty.

2. **Publications:** The obtained results demonstrate a success of the project: already after the first year we have produced a preliminary QTL map for drought resistance evolved in a desert ecotype of *H. spontaneum*. During the second year the last results were presented at a European conference on Plant Genomics (Gatersleben) Plant & Animal Genome conference at San Diego USA at January 2001 (see Appendix 2 for the Abstract of the presentation). We expect that the first manuscript will be submitted soon. Here is the list of publications resulted from the project:


E) **Request for American Embassy Tel-Aviv or A.I.D. Actions.** We have no special requests. The helpful assistance of the Project Administration is highly appreciated.
Appendix to the annual report
Fig. 1. QTL Mapping of drought resistance derived from wild barley, Hordeum spontaneum. The mapping population consisted of 152 F4 families resulted from a cross between H. spontaneum genotype from a desert population Wadi Qilt and H. vulgare cv. Mona (Swedish cultivar). M and W denotes two versions of the map based on codominant markers and dominant markers in coupling phase. The locations of putative QTLs are marked by vertical bars; symbols of the traits are listed in Table 1.
Table 1. Putative drought tolerance QTLs detected by single-QTL analysis

<table>
<thead>
<tr>
<th>No.</th>
<th>Trait (under drought)</th>
<th>Chromosome interval</th>
<th>M map LOD²</th>
<th>PVE(%)</th>
<th>Mode of Action</th>
<th>Effect d</th>
<th>h</th>
<th>Chromosome interval</th>
<th>W map LOD²</th>
<th>PVE(%)</th>
<th>Mode of Action</th>
<th>Effect d</th>
<th>h</th>
</tr>
</thead>
<tbody>
<tr>
<td>S1</td>
<td>Dry weight</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>CHR5-15</td>
<td>4.3*</td>
<td>H</td>
<td>0</td>
<td>0.054</td>
<td></td>
<td>CHR4-3</td>
<td>3.3**</td>
<td>18</td>
<td>R</td>
<td>-0.08</td>
</tr>
<tr>
<td>S3</td>
<td>Dry weight after re-hydration</td>
<td></td>
<td>CHR7-4</td>
<td>5.5**</td>
<td>H</td>
<td>20</td>
<td>-61</td>
<td></td>
<td>CHR5-16</td>
<td>4.0*</td>
<td>22</td>
<td>H</td>
<td>0</td>
</tr>
<tr>
<td>S4</td>
<td>Osmotic adjustment</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>CHR2-8</td>
<td>3.8*</td>
<td>45</td>
<td>H</td>
<td>0.12</td>
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<tr>
<td>S7</td>
<td>Survival (%)</td>
<td></td>
<td>CHR7-4</td>
<td>5.0*</td>
<td>H</td>
<td>0</td>
<td>88</td>
<td></td>
<td>CHR3-16</td>
<td>3.4*</td>
<td>34</td>
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<td>0</td>
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<tr>
<td>S8</td>
<td>Root length</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>CHR5-10</td>
<td>4.8**</td>
<td>46</td>
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<tr>
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<td>Root number</td>
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<td></td>
<td></td>
<td></td>
<td>CHR5-10</td>
<td>4.8**</td>
<td>46</td>
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</tr>
<tr>
<td>S10</td>
<td>Total root length</td>
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<td>-389</td>
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<td>CHR3-16</td>
<td>8.5*</td>
<td>63</td>
<td>H</td>
<td>0</td>
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<td></td>
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<td>H</td>
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<td></td>
<td>CHR4-6</td>
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<td>45</td>
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<tr>
<td>P22</td>
<td>Heading date</td>
<td></td>
<td>CHR2-4</td>
<td>4.0***</td>
<td>R</td>
<td>6.0</td>
<td></td>
<td></td>
<td>CHR2-14</td>
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<td></td>
<td>CHR3-18</td>
<td>2.9**</td>
<td>D</td>
<td>3.9</td>
<td></td>
<td></td>
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<td>4.0*</td>
<td>29</td>
<td>H</td>
<td>4.9</td>
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<td></td>
<td></td>
<td></td>
<td>CHR7-4</td>
<td>4.4***</td>
<td>A</td>
<td>11.1</td>
<td></td>
<td></td>
<td>CHR7-4</td>
<td>3.8**</td>
<td>18</td>
<td>R</td>
<td>4.6</td>
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<tr>
<td>P24</td>
<td>Number of tiller</td>
<td></td>
<td>CHR2-1</td>
<td>3.5***</td>
<td>D</td>
<td>-1.3</td>
<td></td>
<td></td>
<td>CHR2-13</td>
<td>3.5**</td>
<td>40</td>
<td>H</td>
<td>-1.4</td>
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<td>P26</td>
<td>100 seeds weight</td>
<td></td>
<td>CHR7-4</td>
<td>4.0**</td>
<td>D</td>
<td>1.0</td>
<td></td>
<td></td>
<td>CHR7-6</td>
<td>5.2**</td>
<td>28</td>
<td>D</td>
<td>1.06</td>
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<tr>
<td>P27</td>
<td>Biomass</td>
<td></td>
<td>CHR7-4</td>
<td>3.0**</td>
<td>A</td>
<td>5.6</td>
<td></td>
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<td>CHR3-18</td>
<td>3.4**</td>
<td>11</td>
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<td>0.43</td>
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<td>P29</td>
<td>T&lt;sup&gt;+&lt;/sup&gt;&lt;sub&gt;1&lt;/sub&gt; of heading date</td>
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<td>CHR2-11</td>
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<td>0.05</td>
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<td>CHR7-6</td>
<td>3.3*</td>
<td>30</td>
<td>D</td>
<td>0.004</td>
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<tr>
<td>P34</td>
<td>T&lt;sup&gt;+&lt;/sup&gt;&lt;sub&gt;1&lt;/sub&gt; of biomass</td>
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</tbody>
</table>

1 No.- Trait number, as located on the linkage map (S1-S10,...-scored at seedling stage, P11-P34,...-scored at whole plant level)
2 LOD significance: *, **, *** 5%,1%,0.1% respectively, based on permutation test (Doerge & Churchill, 1996)
3 Mode of action: D-dominant, R-recessive, A-additive, H-heterosis
4 T<sub>I</sub> - Tolerance index = S/C ratio (Stress mean value / Control mean value)
Table 2. The results of joint analysis of the seedling stage traits (SST) and biomass tolerance index (BTI) with SST

<table>
<thead>
<tr>
<th>Chromosome</th>
<th>interval</th>
<th>LOD</th>
<th>Traits</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>(a) Seedling stage traits (SST)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>W2</td>
<td>2</td>
<td>39.3*</td>
<td>S2,S3,S8,S9</td>
</tr>
<tr>
<td>M3</td>
<td>15</td>
<td>75.5***</td>
<td>S1,S2,S3,S8</td>
</tr>
<tr>
<td>W3</td>
<td>15</td>
<td>75.5***</td>
<td>S1,S2,S3,S8</td>
</tr>
<tr>
<td>M4</td>
<td>6,15</td>
<td>47.0**</td>
<td>S1,S2,S3,S8</td>
</tr>
<tr>
<td>W4</td>
<td>14</td>
<td>26.8*</td>
<td>S1,S2,S3,S8</td>
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<tr>
<td>W5</td>
<td>10</td>
<td>72.4***</td>
<td>S2,S3,S8,S9</td>
</tr>
<tr>
<td>M6</td>
<td>17</td>
<td>82.3***</td>
<td>S1,S2,S3,S8</td>
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<tr>
<td>W6</td>
<td>3</td>
<td>43.4**</td>
<td>S1,S2,S3,S9</td>
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<tr>
<td>M7</td>
<td>5</td>
<td>62.2***</td>
<td>S1,S2,S3,S8</td>
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<tr>
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<td>2</td>
<td>56.9**</td>
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<tr>
<td><strong>(b) SST combined with biomass tolerance index (BTI)</strong></td>
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<tr>
<td>M2</td>
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<td>15.9**</td>
<td>S1,S2,S3,S8,P34</td>
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<tr>
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<td>34.6**</td>
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<tr>
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<td>63.7</td>
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</tr>
</tbody>
</table>

1 For group (a), *, **, *** and **** denote significance of the detected QTL based on permutation test at the level of 5%, 1%, 0.1% respectively; for group (b), the significance of the detected QTL effect on TIB, based on permutation test as described in Korol et al. (2001)

2 Symbols of traits are listed in Table 1, except of S2-Dry weight under stress/ dry weight after dehydration (%)