Environmental and Experimental Botany 64 (2008) 33–42

Contents lists available at ScienceDirect

Environmental and Experimental Botany

journal homepage: www.elsevier.com/locate/envexpbot

Insights on the role of tillering in salt tolerance of spring wheat from detillering

Yuefeng Ruan, Yuncai Hu*, Urs Schmidhalter

Department of Plant Sciences, Technical University of Munich, Am Hochanger 2, 85350 Freising-Weihenstephan, Germany

ARTICLE INFO

Article history:
Received 18 April 2007
Received in revised form 11 April 2008
Accepted 22 April 2008

Keywords:
Detillering
Wheat genotypes
Salt tolerance
Tillering

ABSTRACT

Tillering is reduced by salinity, with the primary and secondary tillers being more affected than is the mainstem. To understand the importance of tillering in the salt tolerance of wheat plants, two contrasting genotypes of spring wheat (*Triticum aestivum* L.) were grown in a greenhouse under saline or non-saline conditions and were subjected to five progressive levels of detillering. Regardless of the genotype and salinity, shoot dry weight, seed yield and seed number per plant were all significantly decreased in the treatments where only one or two tillers per plant remained compared with the untouched treatment (more than three tillers), whereas these same variables per tiller tended to be increased on a per tiller (mainstem or substem tiller) basis. The increased seed yield per tiller observed with tiller reduction may be attributed to the enhanced seed number within the spikelet. Under saline conditions, the reductions in shoot dry weight, seed yield and seed number per plant for the salt-tolerant genotype Kharchia were of a greater magnitude in the treatments where only one or two tillers per plant were present compared with the untouched treatment, whereas the magnitude of this reduction in the salt-sensitive genotype Sakha 61 was decreased.

1. Introduction

Tillers are important for seed yield in wheat (*Triticum aestivum* L.) as well as in other cereals, but are also sensitive to environmental stresses. In saline environments (e.g. soil salinized by the saline water), the growth of the mainstem and substem tillers is reduced, which usually results in the reduced seed yield. However, to complicate matters, salinity affects the growth of mainstem and substem tillers differentially in wheat. To improve the salt tolerance of wheat plants, therefore, a better understanding of these differential effects of salinity is required.

In the plant, the early growth of substem tillers is supported entirely with photoassimilates and nutrients from the mainstem in wheat (Kirby et al., 1985). Even after the anthesis, the substem tillers are still supplied with assimilates from the flag leaf and other leaves on the mainstem (Thorne, 1982; MacKown et al., 1989). There is also evidence to support the existence of competition between the mainstem and substem tillers in wheat (Mohamed and Marshall, 1979; Martinez-Carrasco and Thorne, 1979). Compared with the substem tillers, the mainstem is less susceptible to salt stress during the period of growth (Maas et al., 1994; Hu et al., 1997). Several hypotheses exist to explain these observations: (1) the carbohydrate supply is reduced more by salinity in the substem tillers than in the mainstem, thereby inhibiting the growth of the former to a greater degree (Grieve et al., 1992); (2) the mainstem may retain more photosynthates for its own growth rather than exporting source reserves to the substem tillers under saline conditions (Thorne, 1982; Maas et al., 1994); (3) the mainstem competes with the substem tillers to obtain more nutritional ions to lessen nutrient deficiency and/or imbalance caused by toxic ions (Thorne and Wood, 1987; Maas and Grieve, 1990). Recently, Zeng et al. (2002) and El-Hendawy et al. (2005a) have demonstrated that different wheat and rice genotypes exhibited various responses to salinity according to the three agronomic variables: tiller number, leaf number and leaf area per plant. In both wheat and rice, the salt-sensitive genotypes accumulate harmful ions (Na^+ and Cl^-) in concentrations which lead to the toxicity, resulting in a greater reduction in tiller number and biomass when compared to the salt-tolerant genotypes that exclude toxic ions from the shoots. These results suggest that the mainstem and substem tillers of salt-tolerant and salt-sensitive genotypes respond differently to salinity due to different mechanisms of tolerance of genotypes to salinity (Zeng et al., 2002; El-Hendawy et al., 2005a). Thus, by comparing the growth of the mainstem and substem tillers in the contrasting genotypes, the effects of salinity on tillering may be clarified.

Only a few studies have investigated the relationship among genotype, tiller and seed yield. Papadakis (1940) reported that high-tillering genotypes have a greater potential to increase seed

* Corresponding author. Tel.: +49 8161 713394; fax: +49 8161 714500.
E-mail address: hu@wzw.tum.de (Y. Hu).

0098-8472/$ – see front matter © 2008 Elsevier B.V. All rights reserved.
doi:10.1016/j.envexpbot.2008.04.004

yield on poor soil conditions than do low-tillering ones. Hucl and Baker (1991) supported this conclusion, finding that increasing the tillering capacity of genotypes could increase seed yield in semiarid environments. Within a given genotype, however, Jones and Kirby (1977) indicated that restricting tiller number of plants in semiarid environments tended to increase seed yield compared to free-tillering plants due to the enhanced water-use efficiency. Benbelkacem et al. (1984) have ever observed that breeding for high-tillering genotypes increased efficiency (i.e. added spike-bearing tillers) by only 36% for barley.

All the above studies investigated the relationship between tiller number and seed yield only. No information exists about the effects of tillering on salt tolerance and seed yield in contrasting wheat genotypes under saline conditions. Yet, exactly this information may be of great benefit to breeding programs designed to improve salt tolerance in wheat. However, according to Kirby (1973), morphological development was found to be similar in the artificial and mutant uniculms in barley. Therefore, tillering was manipulated in the present study by artificial tiller removal, which proved to be a superior method in the absence of isogenic lines.

The objectives of this study, therefore, were to investigate how the tiller number affects the growth, both of the individual tiller and of the whole wheat plant under saline conditions at different growth stages, and to understand the impact of different tiller number of plants on salt tolerance in two contrasting wheat genotypes.

2. Materials and methods

2.1. Plant materials and growth conditions

Thirty seeds for each of salt-tolerant genotype Kharchia and salt-sensitive genotype Sakha 61 (El-Hendawy et al., 2005a) were germinated at room temperature for 2 days, and then were sown in 11-L plastic pots containing 10 kg of dry loamy soil that was salinized or not. Twelve days after sowing, the seedlings were thinned to 22 plants per pot. The plastic pot was with a 24-cm diameter and with a depth of 18.5 cm. There was a 9-cm space between pots. In this study, we maintained uniform spacing among the plants within the pots during the experiment and the same among all the plants in all the detillering treatments. Loamy soil was collected from a soil surface (0–15 cm), air-dried, sieved through a 5-mm screen. The soil consisted of 23% clay, 48% silt and 29% sand. The initially air-dried soil with 4.6% gravimetric water content was filled layer-wise in pots with four layers (a 4-cm soil thickness per layer). To reach a final soil water content of 25% on a dry soil basis, tap water or NaCl solution was added to the non-saline or saline treatment. For the saline treatment, in order to avoid an osmotic shock for seedling emergence, the first three soil layers starting from the bottom in pots was salinized by adding 120 mM NaCl solutions to each soil layer, and the top layer was salinized at day 10 after sowing (i.e. at the early two-leaf stage). A final electrical conductivity (EC) of approximately 5.6 dS m^{-1} was achieved in the soil solution of the potted soil according to a preliminary experiment. Only a moderate salinity was applied in this study because it was found that high salinity could cause tillers to be omitted in the plant based on a set of the preliminary experiments. In order to avoid water loss by evaporation, the pots were covered by the perforated plastic foil and the plants grew through the small holes in the foil. There was no drainage at the bottom. The pots were weighed daily and the water loss was replaced by adding tap water during the experiment as necessary. Soil water content was maintained at a 25% dry soil basis by replacing any water lost through evapotranspiration. The plants were grown in a growth chamber at 23/18 °C (day/night) with 16-h light period of photon flux density (PPFD)

Table 1
Effect of detillering on leaf number and leaf area (cm^2/tiller or plant) of the mainstem and substem tillers in the salt-tolerant (Kharchia) and salt-sensitive (Sakha 61) genotypes subjected to salinity

Treatments		Kharchia							Sakha 61							
Detillering	Stress	Tiller number	Mainstem		T1		T2		Total leaf area	Tiller number	Mainstem		T1		T2		Total leaf area
			Leaf number	Leaf area	Leaf number	Leaf area	Leaf number	Leaf area			Leaf number	Leaf area	Leaf number	Leaf area	Leaf number	Leaf area	
Untouched	No salt	5	10	189	6	87.6	5	70.5	347	6	10	148	7	83.6	6	78	316
	Salt	4	9	153	6	76.8	5	58.0	288	4	9	123	6	75.6	5	50.5	249
MS	No salt	1	10	232					232	1	10	192					192
	Salt	1	9	186					186	1	9	149					149
T1	No salt	1			6	124			124	1			7	119			119
	Salt	1			6	109			109	1			6	90.6			90.6
MST1	No salt	2	10	201	6	103			304	2	10	162	6	96.0			258
	Salt	2	9	170	6	94.2			264	2	9	131	6	84.0			215
T1T2	No salt	2			6	97.2	5	75.0	172	2			7	113	6	93.6	206
	Salt	2			6	90.0	5	70.0	160	2			6	89.4	5	63.5	153
LSD ($P \leq 0.05$)		–	–	17	–	12.2	–	9.8	30	–	–	17	–	9.1	–	13.2	25.6

550 μmol photon m^{-2} s^{-1} until the first tiller emerged, and then transferred to a greenhouse.

The preliminary experiments also showed that the optimal soil nutrient was obtained by applying 0.57 g NH_4NO_3 per pot initially, with an additional 0.57 g NH_4NO_3 per pot being added at the third, sixth, eighth and tenth weeks after sowing. In addition, 0.1 g KH_2PO_4 and K_2SO_4 per pot were added at the sixth and eighth weeks after sowing, respectively.

2.2. Experimental design and sampling

The experiment was arranged as a randomized complete block design and consisted of five detillering treatments each replicated three times. The processes of tillering in wheat can be summarized generally as: (1) the mainstem produces the primary tillers (T1, T2, ..., TN) from the buds of its leaf axils; (2) the primary tillers likewise bear secondary tillers (T10, T11, ...) from their leaf axils; (3) the secondary tillers can occasionally also produce tertiary tillers from their leaf buds. In order to simplify the tillering system, the mainstem is classed as the mainstem tiller, and all other tillers (i.e. primary tillers, secondary tillers, tertiary tillers, and so on) are named substem tillers (Mitchell, 1954; Christen and Lovett, 1993). According to this scheme of tiller appearance, the detillering treatments that we employed were:

(1) Untouched: mainstem and all substem tillers were left intact;
(2) MS: mainstem was left intact; all substem tillers were removed;
(3) MST1: mainstem and the primary tiller from leaf 1 on the mainstem (substem tiller T1) were left intact; all other substem tillers were removed;
(4) T1: substem tiller T1 was left intact; the mainstem and all other substem tillers were removed;
(5) T1T2: the primary tillers from the first two leaves on the mainstem (substem tiller T1 and substem tiller T2) were left intact; the mainstem and all other substem tillers were removed.

To identify substem tillers as they emerged, the substem tillers were circled with the different colored wires. The unwanted tiller

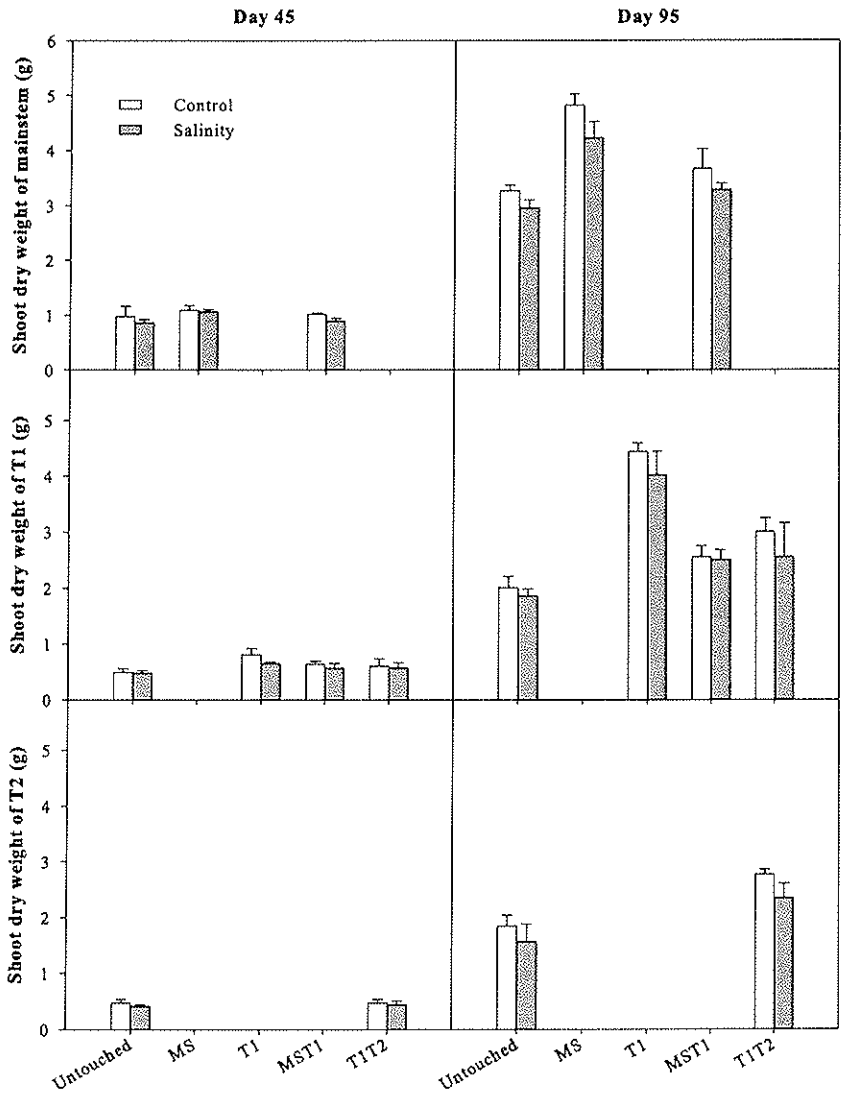

Fig. 1. Shoot dry weights of mainstem, T1 and T2 in the different detillering treatments of the salt-tolerant genotype Kharchia with or without salinity at two harvest times.

buds were broken off by a blunt needle at the base of the leaf as soon as they became visible; the mainstem was excised by a surgical scalpel from the plant when the second leaf of the youngest substem tiller that was left intact was fully expanded (Kirby and Jones, 1977; Alaoui et al., 1988). The mainstem and substem tiller buds were removed two times due to the growth of the meristem.

During plant growth, leaf numbers of the mainstem and substem tillers T1 and T2 were recorded. Leaves of the mainstem and substem tillers T1 and T2 were harvested from 10 plants at day 45 after sowing (flag-leaf stage) and from the remaining plants at day 95 after sowing (mature stage). At day 45 after sowing, after leaf area was measured in the leaves of the mainstem, substem tiller T1 and substem tiller T2, respectively, the plant materials were dried at 65 °C for 48 h to determine shoot dry weight for them and the whole-plant. At day 95 after sowing, shoot dry weight, seed yield, seed number and spikelet number were measured in the mainstem, substem tiller T1, substem tiller T2 and the whole-plant, respectively, after the plant materials were dried as above.

2.3. Statistical analysis

Data were analyzed by analysis of variance (ANOVA) using the PROC GLM procedure of The SAS System v9.1. Means separation on the data was conducted using LSD multiple range tests. Terms were considered significant at $P \leq 0.05$.

3. Results

3.1. Association of mainstem growth with detillering treatments

Effects of salinity on leaf area and leaf number on mainstem were observed in both salt-tolerant and salt-sensitive genotypes (Table 1). Compared with the untouched treatment, the mainstem leaf area under saline or non-saline conditions was increased in the MS and MST1 treatments for Kharchia and in the MS treatment for Sakha 61. However, a larger reduction due to salinity compared with the untouched treatment was observed for the MS treatment of Kharchia and for the MS and MST1 treatments of Sakha 61 (Table 1). Furthermore, the number of

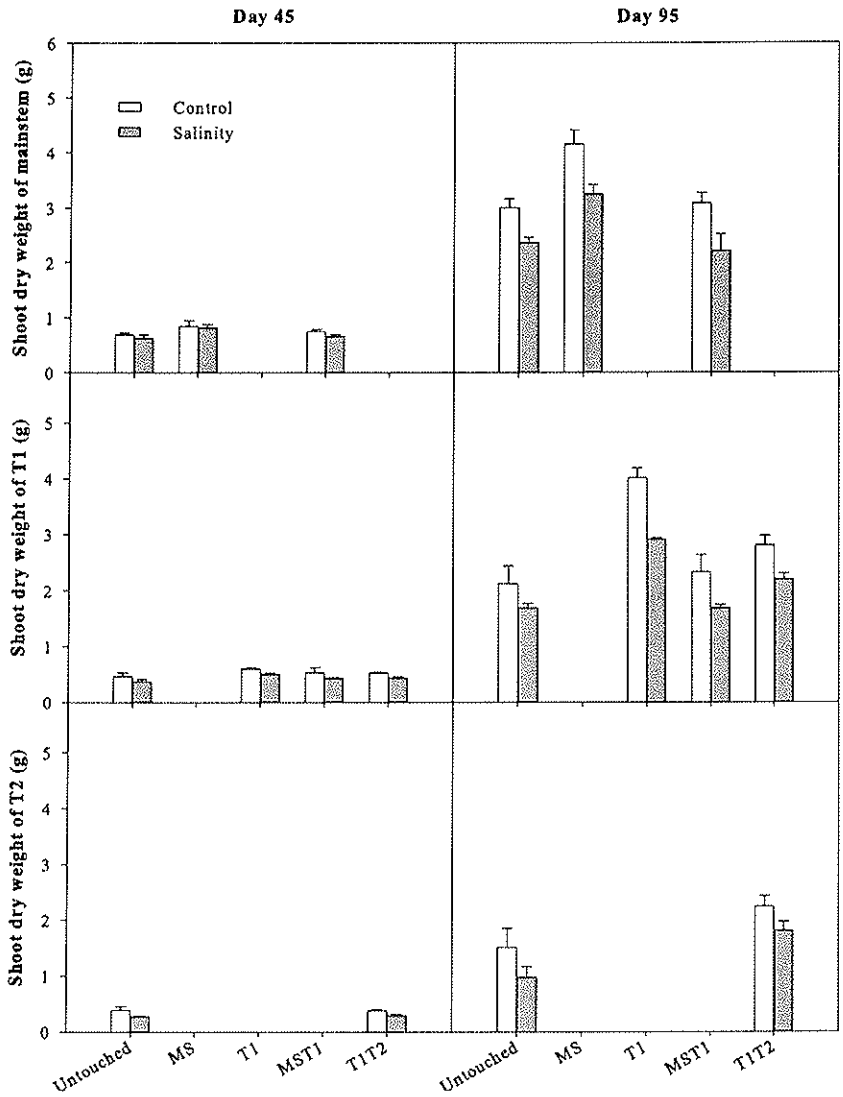

Fig. 2. Shoot dry weights of mainstem, T1 and T2 in the different detillering treatments of the salt-sensitive genotype Sakha 61 with or without salinity at two harvest times.

leaves in the MS and MST1 treatments was the same as in the untouched treatment for both genotypes regardless of salinity (Table 1).

The effects of salinity on shoot dry weight, seed yield, seed number and spikelet number on the mainstem are presented in Figs. 1–5 and Table 2. Regardless of salt level, shoot dry weight, seed yield and seed number on the mainstem at maturity were significantly greater in the MS than in the untouched treatment in the MS treatments of both genotypes, but only slightly in the MST1 treatment of Kharchia (Figs. 1–4). Under saline conditions, the reductions in the average shoot dry weight, seed yield, seed number and spikelet number on the mainstem were observed in both the salt-tolerant and salt-sensitive genotypes, with the magnitude being genotype dependent, i.e. there was a smaller reduction in these variables on the mainstem of the salt-tolerant genotype than in the salt-sensitive genotype regardless of treatments (Figs. 1–5; Table 2). At maturity, i.e. day 95 after sowing, the greatest reduction in shoot dry weight on the mainstem of Sakha 61 under saline conditions was found in the MST1 treatment relative to the untouched treatment. For Kharchia, the reduction was slightly greater in the detillered treatments as compared to the untouched treatment, with the largest reduction occurring in the MS treatment (Figs. 1 and 2; Table 2). Similarly, compared with the untouched treatment, the reduction in average seed yield on the mainstem by salinity was greater in the MST1 treatment of Sakha 61 (33% cf. 25%) and MS treatment of Kharchia (10% cf. 7%), but smaller in the MS treatment of Sakha 61 (24% cf. 25%) and the MST1 treatment of Kharchia (6% cf. 7%).

Compared with the salt-tolerant genotype, salinity always resulted in a greater reduction in seed number on the mainstem of the salt-sensitive genotype, e.g. 23% higher in the untouched treatment (Fig. 4). For both genotypes, however, decreases in tiller number also increased spikelet number of the mainstem under saline conditions compared to the untouched treatment as witnessed, for example, by maintaining the spikelet number but increasing seed number on the salt-stressed Sakha 61 mainstem in the MS treatment (Figs. 4 and 5; Tables 1 and 2).

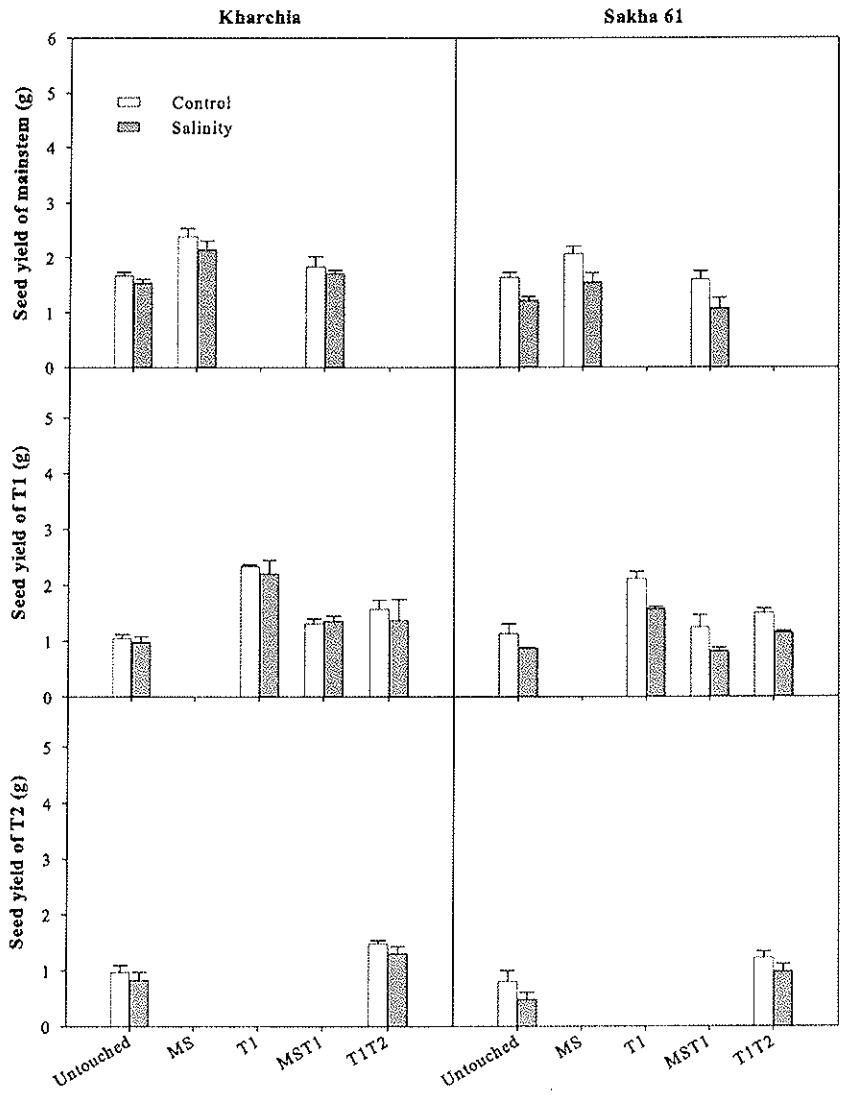

Fig. 3. Seed yields of mainstem, T1 and T2 in the different detillering treatments of the salt-tolerant (Kharchia) and salt-sensitive (Sakha 61) genotypes with or without salinity.

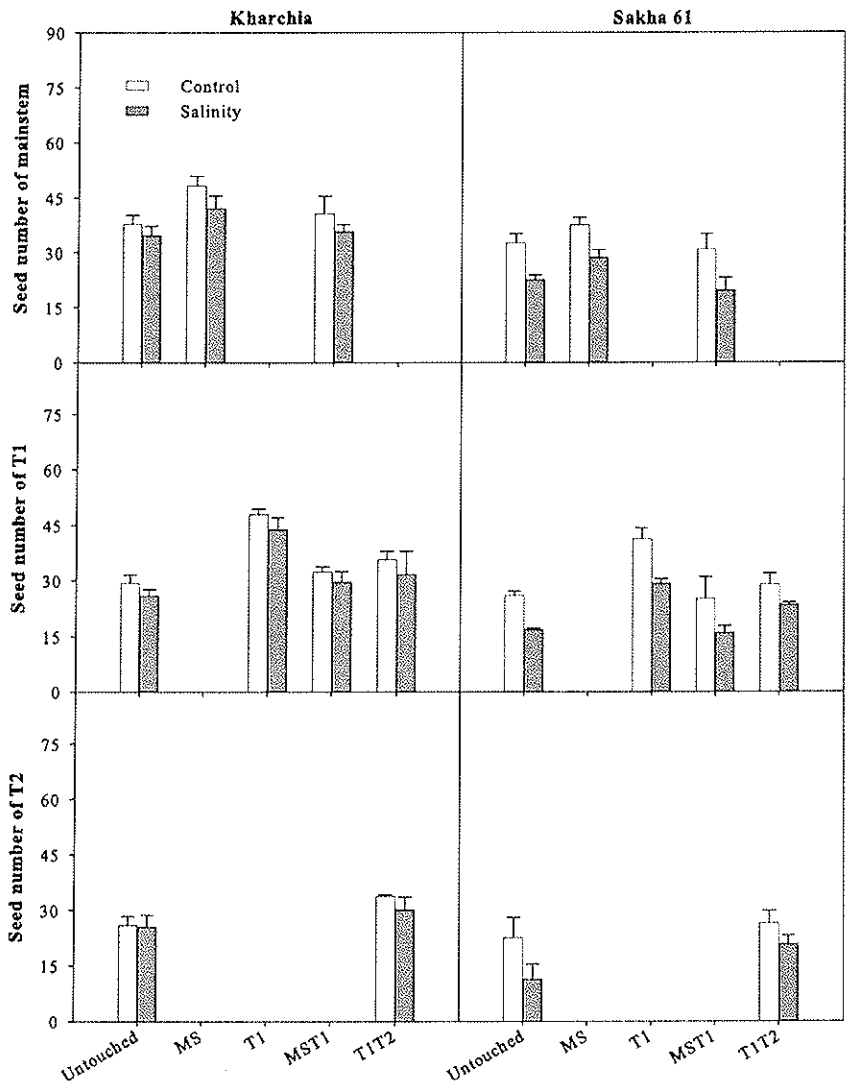

Fig. 4. Seed numbers of mainstem, T1 and T2 in the different detillering treatments of the salt-tolerant (Kharchia) and salt-sensitive (Sakha 61) genotypes with or without salinity.

3.2. Association of substem tiller growth with detillering treatments

Compared to the non-saline plants, salinity reduced leaf numbers of substem tillers T1 and T2 in the untouched treatment in Sakha 61 only (Table 1) and no reduction in the leaf number of Kharchia was observed even in the detillered treatments. Furthermore, the detillered treatments did not change the leaf number of the salt-stressed substem tillers of either genotype compared to the untouched treatment (Table 1). Interestingly, under the moderate salt level used, substem tiller T1 was able to show a smaller reduction in shoot dry weight than the mainstem during the period of growth, e.g. the vegetative growth, in the salt-tolerant, but not in the salt-sensitive genotype (Figs. 1 and 2). For example, the reduction in shoot dry weight of Kharchia due to salinity in the untouched treatment was about 11% for the mainstem, 3% for the substem tiller T1 and 12% for the substem tiller T2 at day 45 after sowing; the analogous values for Sakha 61 were 8%, 19% and 30%, respectively (Figs. 1 and 2).

With a similar pattern on the mainstem, the detillered treatments significantly increased leaf area, seed yield and shoot dry weight at maturity on the substem tillers compared to the untouched treatment in both genotypes under saline conditions, except for the MST1 treatment of Sakha 61 (Figs. 1–3; Tables 1 and 2). The increased seed yield in the detillered treatments was related more to an increase in seed number than in spikelet number (Figs. 4 and 5). Under saline conditions, salinity inhibited the substem tiller growth of both Kharchia and Sakha 61 by reducing both shoot dry weight and leaf area, which, in turn, resulted in a reduced seed yield, seed number and spikelet number on the substem tillers (Figs. 1–5; Tables 1 and 2). Compared with the untouched treatment, however, the greater reductions by salinity were observed in all detillered treatments of substem tiller T1 for Sakha 61, e.g. by 24% for leaf area, by 12% for seed yield and by 8% less for shoot dry weight at maturity, respectively; for Kharchia, the reductions tended to be smaller in the detillered treatments, the exception being the T1T2 treatment. For the substem tiller T2, the T1T2 treatment resulted in a smaller reduction in leaf area, seed

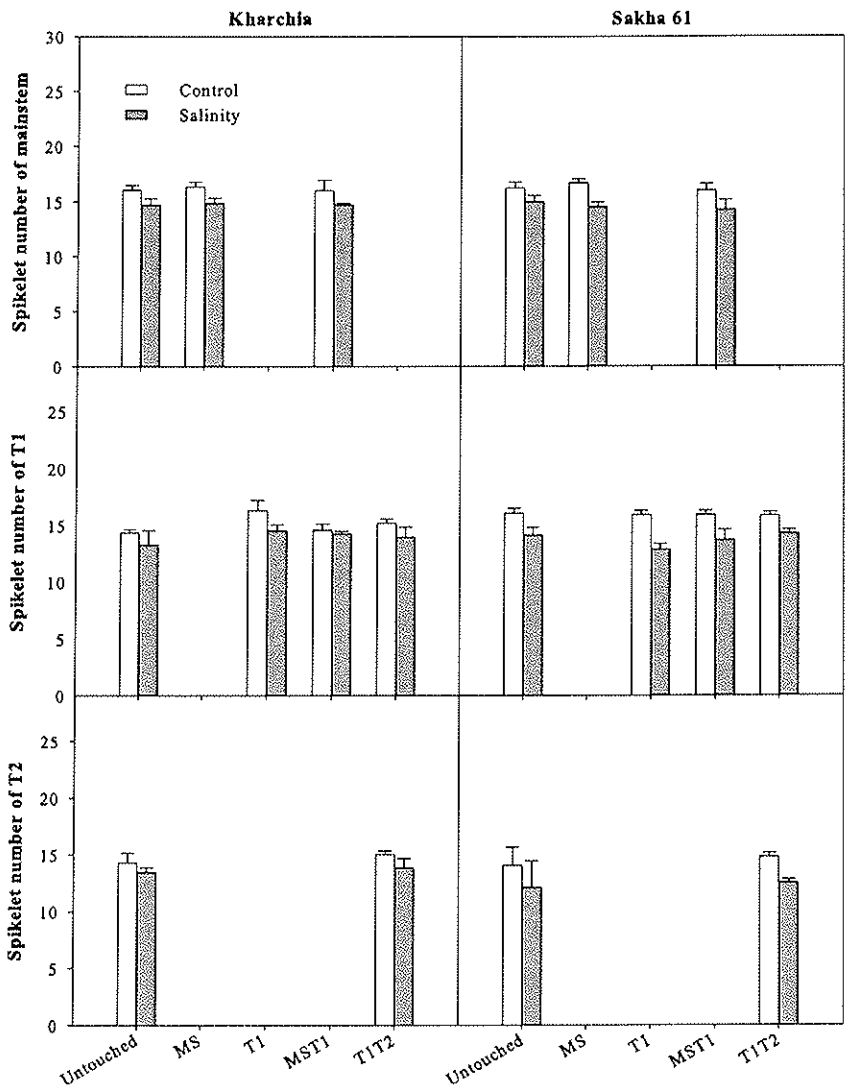

Fig. 5. Spikelet numbers of mainstem, T1 and T2 in the different detillering treatments of the salt-tolerant (Kharchia) and salt-sensitive (Sakha 61) genotypes with or without salinity.

yield and shoot dry weight at maturity for both genotypes under saline conditions, especially for the salt-sensitive genotype.

3.3. *Association of whole-plant growth with detillering*

The effects of salinity on shoot dry weight, seed yield and seed number per plant are presented in Figs. 6 and 7 and Table 2. Except for the T1 treatment at day 45 after sowing, shoot dry weight per plant was less affected by salinity in Kharchia than in Sakha 61 over all treatments at either harvest. Our results (Fig. 6) further show that the reduction in shoot dry weight per plant under saline conditions for Sakha 61 became continually greater over time until the mature stage, whereas a smaller reduction for Kharchia was found at the mature stage, a difference that might stem from their differential salt tolerance during the reproductive growth stage. For example, the reduction in shoot dry weight per plant of Sakha 61 at maturity compared to day 45 after sowing was about 10% greater in the untouched treatment, 19% in the MS treatment, 12% in the T1 treatment, 14% in the MST1 treatment and 2% in the T1T2 treatment. By contrast, the reduction in shoot dry weight per plant of Kharchia at maturity was dependent on tiller number per plant (Fig. 6, Table 1). Furthermore, the enhanced salt tolerance of Kharchia during reproductive growth may greatly reduce losses in seed yield and seed number per plant regardless of treatments compared with Sakha 61.

Compared with the untouched treatment, the detillered treatments decreased shoot dry weight of both harvests, seed yield and seed number per plant regardless of the genotype and salinity. Furthermore, this reduction with the MS and T1 treatments was greater than that with the MST1 and T1T2 treatments (Figs. 6 and 7; Table 2). Under saline conditions, however, the manipulation of tiller number could alter the apparent salt tolerance per plant in both the salt-tolerant and salt-sensitive genotypes. Overall, the reductions in shoot dry weight at maturity, seed yield and seed number per plant for Kharchia under saline conditions tended to be higher in the detillered treatments of one or two tillers per plant compared with the untouched treatment, whereas these were smaller for Sakha 61.

Table 2
Mean squares and *F*-tests of the effects of salinity (S) and detillering (D) and their interactions (S × D) for shoot dry weights at day 45 and day 95 after sowing, seed yield, seed number and spikelet number of the mainstem, substem tillers and total plant in Kharchia and Sakha 61

Variable	Kharchia			Sakha 61		
	Salinity	Detillering	S × D	Salinity	Detillering	S × D
(a) Mainstem						
Shoot dry weight at day 45 after sowing	0.032 ns	0.040*	0.005 ns	0.011 ns	0.048***	0.001 ns
Shoot dry weight at day 95 after sowing	0.82***	3.23***	0.03 ns	2.95***	1.64***	0.53*
Seed weight	0.128**	0.715***	0.005 ns	1.085***	0.281***	0.096*
Seed number	101.8**	136.8***	3.6 ns	401.1***	94.5**	60.3*
Spikelet number	8.50***	0.11 ns	0.02 ns	13.36***	0.43 ns	0.28 ns
(b) Tiller one						
Shoot dry weight at day 45 after sowing	0.035*	0.057**	0.009 ns	0.050***	0.018**	0.001 ns
Shoot dry weight at day 95 after sowing	0.43*	5.69***	0.06 ns	2.88***	3.01***	0.12*
Seed weight	0.05 ns	1.73***	0.02 ns	0.90***	0.84***	0.10*
Seed number	76.3**	378.6***	0.7 ns	407.8***	271.9***	81.4*
Spikelet number	7.43***	2.67**	0.57 ns	28.9***	0.6*	0.6*
(c) Tiller two						
Shoot dry weight at day 45 after sowing	0.0058 ns	0.0006 ns	0.0004 ns	0.055*	0.002 ns	0.007 ns
Shoot dry weight at day 95 after sowing	0.36*	2.17***	0.02 ns	0.68**	1.82***	0.01 ns
Seed weight	0.080*	0.715***	0.001 ns	0.230*	0.653**	0.034 ns
Seed number	12.9 ns	115.5**	7.0 ns	214.1*	135.7*	24.7 ns
Spikelet number	3.04*	0.99 ns	0.10 ns	13.72*	0.99 ns	0.08 ns
(d) Total plant						
Shoot dry weight at day 45 after sowing	0.12*	1.31***	0.01 ns	0.16***	0.83***	0.11*
Shoot dry weight at day 95 after sowing	2.51***	11.63***	0.05 ns	12.81***	10.65***	0.30*
Seed weight	0.29*	2.87***	0.02 ns	3.68***	1.80***	0.19*
Seed number	201*	3630***	16 ns	2101***	1211***	128**

***$P \leq 0.001$; **$P \leq 0.01$; *$P \leq 0.05$; ns, not significant at $P > 0.05$.

4. Discussion

Regardless of the genotype and salt stress, a reduction in tiller number is associated with increases in leaf area, shoot dry weight, seed yield and seed number per tiller on both the mainstem and substem tillers in spring wheat (Table 1), which is in agreement with the observation of Kirby and Jones (1977) in barley. Alaoui et al. (1988) pointed out that the enhanced leaf area may increase

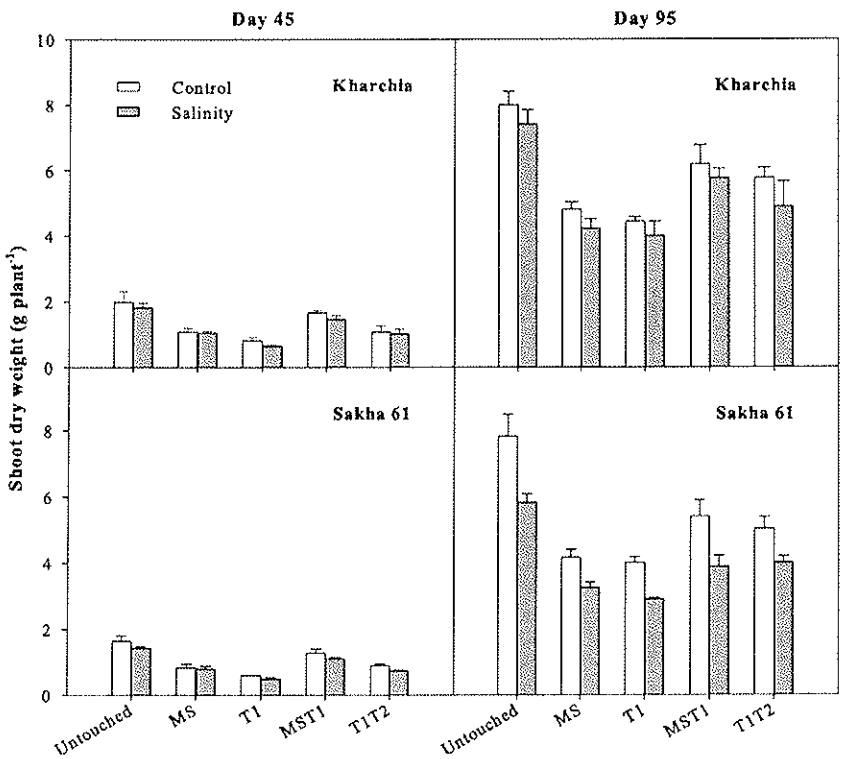

Fig. 6. Shoot dry weight of the whole-plant in the different detillering treatments of the salt-tolerant (Kharchia) and salt-sensitive (Sakha 61) genotypes with or without salinity at two harvest times.

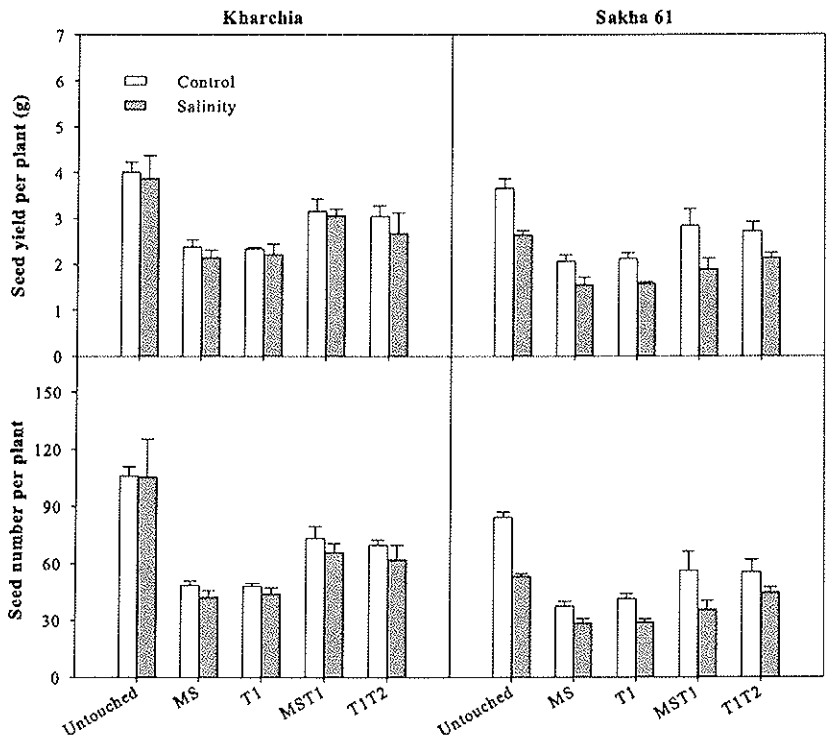

Fig. 7. Seed yield and seed number of the whole-plant in the different detillering treatments of the salt-tolerant (Kharchia) and salt-sensitive (Sakha 61) genotypes with or without salinity.

the photoassimilate supply needed for the greater tiller seed yield. For the whole-plant, however, reduced tiller numbers significantly reduces shoot dry weight, seed yield and seed number. It is apparent that tiller number is a very important contributor to the total seed yield of plant in wheat, despite seed yield being increased in the mainstems or substem tillers of the detillered treatments. It has been reported previously, that the increased seed yield on the mainstem resulting from tiller removal does not compensate for the loss of the substem tillers (Kemp and Whingwiri, 1980). The present study also suggests that the enhanced seed yield on the substem tillers due to tiller removal did not compensate for the loss of the mainstem.

Under saline conditions, knowledge about how the difference in tiller number affects the salt tolerance of the mainstem and substem tillers as well as of whole-plant could prove to be more crucial in terms of improving wheat yield under salt stress. Hu et al. (1997) have pointed out that, under moderate salinity, nutrient deficiency and salinity may equally limit plant growth, and they may not interact. The nutrient activities and ratio of salt ions in the mainstem and substem tillers could be important determinants of plant salt tolerance. Mainstem-to-substem tiller relationships are naturally complex, but they can be summarized in cereal plants (e.g. wheat and barley) as follows: (1) under adequate nutrient supply, the mainstem translocates nutrients to the substem tiller to support its growth and development, and the substem tiller also translocates nutrients to the mainstem (Kemp and Whingwiri, 1980; Lauer and Simmons, 1985; Lauer and Simmons, 1988); (2) under poor nutrient supply, the mainstem monopolises the available nutrients, greatly decreasing their translocation to the substem tiller, which may also decrease or stop the nutrient translocation to the mainstem (Gu and Marshall, 1988; Sticksel et al., 1999); and (3) the translocation of nutrients from the mainstem to the substem tiller is great in early plant development and decreases subsequently, with the nutrient translocation from the substem tiller to the mainstem only occurring before the later reproductive growth stage (Lupton, 1966; Lauer and Simmons, 1988). Therefore, under low nutrient availability and high toxic-ion ratios, the respective capacities of the mainstem and substem tillers to obtain nutrients or exclude toxic ions contribute to their own salt tolerance, thereby affecting that of the whole-plant in turn.

In this experiment, one tiller per plant (i.e. the MS or T1 treatments) greatly increased the shoot dry weight, leaf area, seed yield and seed number on the mainstem or substem tiller T1, respectively, compared with the corresponding values in the untouched treatment regardless of the genotype and salt stress, indicating the high potential of both mainstem and substem tiller to take up nutrients under saline conditions. By contrast, the mainstem and substem tillers could have the different responses to salinity due to the competition for nutrients and the accumulation of toxic ions, for which both tiller number and genotype could play a key role. For example, the salt tolerance of the mainstem was decreased in two tillers per plant (i.e. the MST1 treatment) compared with one tiller per plant (i.e. the MS treatment) in the salt-sensitive, but not in the salt-tolerant genotype. As nutrient competitors within the plant, the substem tillers could act as either a sink or a source of nutrients associated with the mainstem, which have been reported by Lauer and Simmons (1985,1988) in barley. The translocation of nutrients between substem tillers and mainstem, which may affect the specific effects of toxic ions within the mainstem, likely depends on the wheat genotype. For example, the movement of nutrients from substem tiller one to the mainstem in the saline environment may have operated more effectively in the MST1 treatment to limit the average mainstem seed reduction within Kharchia than within Sakha 61.

This study showed the smaller inhibition of growth on the substem tiller T1 than on the mainstem in the salt-tolerant genotype under moderate salinity in the untouched plant. This indicates that the substem tillers (or at least for the primary tillers) may be by either receiving more assimilates and minerals from the mainstem and growth medium or translocating less photoassimilate to the mainstem, which has been observed in barley (Kirby and Jones, 1977; Lauer and Simmons, 1988). Here, the manipulation of tiller number with or without mainstem provides the evidence to support that the export and import of nutrients from the mainstem to the substem tillers could be of importance with respect to salt tolerance. Our results showed that the shoot dry weight of substem tiller T1 at maturity in two tillers per plant with the mainstem (i.e. the MST1 treatment) in the salt-tolerant genotype Kharchia was less reduced compared to that of two tillers per plant without mainstem (i.e. the T1T2 treatment). For the salt-sensitive genotype Sakha 61, by contrast, this reduction was higher in two tillers per plant with the mainstem than without mainstem (Figs. 1 and 2, Table 2).

Differences in nutrient transport from the mainstem to the substem tillers or vice versa in the salt-tolerant and salt-sensitive genotypes could be associated with their different mechanisms of salt tolerance. El-Hendawy et al. (2005b) confirmed that salt-tolerant and salt-sensitive wheat genotypes use ion exclusion and high accumulation, respectively, in response to saline conditions. Kirby and Faris (1972) pointed out the possibility in barley that the adjustment of resources between the mainstem and substem tillers could help the plant to recover from poor environmental conditions. Therefore, we considered that the exclusion of toxic ions in the salt-tolerant genotype in combination with the relatively weak competition to balance nutrient distribution between the mainstem and substem tillers under saline conditions might diminish the negative effects of toxic ions on the growth of mainstem and substem tillers. By contrast, the high accumulation of toxic ions in the salt-sensitive genotype in combination with an increased competition for nutrients between the mainstem and substem tillers may enhance the inhibition of growth of both the mainstem and substem tillers. Our results show that the substem tillers (or at least for the primary tillers) of the salt-tolerant genotype express superior genetic traits in relation to the exclusion of harmful ion during the reproductive growth stage compared to that of the salt-sensitive genotype. At the whole-plant level, the substem tillers could play an important role in improving the salt tolerance.

5. Conclusion

In the treatments with one or two tillers per plant, shoot dry weight, seed yield and seed number per plant were significantly decreased in both the salt-tolerant and salt-sensitive genotypes compared with the untouched plant (more than three tillers) regardless of salinity, while these same variables tended to be increased in the treatments with one tiller (mainstem or substem tiller). The increased seed yield per tiller apparent upon tiller reduction could be due to the increased seed number within the spikelet of tillers under such conditions. Our manipulations of tillers could not alter the inherent genotypic effects on the differential salt tolerances between the genotypes. The salt-tolerant genotype remained more tolerant to salinity in shoot dry weight than did the salt-sensitive genotype under all the detillered treatments performed. This could be the reason why the mainstem and substem tillers of the salt-tolerant genotype are more tolerant to salinity than those of the salt-sensitive genotype. The role of substem tillers is likely important in plant salt tolerance in relation to tiller number and accumulative effects within the plant among the different wheat genotypes.

Acknowledgements

The authors thank Dr. P.A. Hollington (CAZS, University of Wales, United Kingdom) for providing seeds of Kharchia. This work was supported through the German Research Foundation (DFG, Project number 862/2-1). The authors thank the anonymous reviewer for the outstanding and dedicated work.

References

Alaoui, A.C.E., Simmons, S.R., Crookston, R.K., 1988. Effects of tiller removal on spring barley. Crop Sci. 28, 305–307.
Benbelkacem, A., Mekni, M.S., Rasmusson, D.C., 1984. Breeding for high tiller number and yield in barley. Crop Sci. 24, 968–972.
Christen, O., Lovett, J.V., 1993. Effects of a short-term *p*-hydroxybenzoic acid application on grain yield and yield components in different tiller categories of spring barley. Plant Soil 151, 279–286.
El-Hendawy, S.E., Hu, Y., Yakout, G.M., Awad, A.M., Hafiz, S.E., Schmidhalter, U., 2005a. Evaluating salt tolerance of wheat genotypes using multiple parameters. Eur. J. Agron. 22, 243–253.
El-Hendawy, S.E., Hu, Y., Schmidhalter, U., 2005b. Growth, ion content, gas exchange, and water relations of wheat genotypes differing in salt tolerances. Aust. J. Agric. Res. 56, 123–134.
Grieve, C.M., Lesch, S.M., Francois, L.E., Maas, E.V., 1992. Analysis of main-stem yield components in salt-stressed wheat. Crop Sci. 32, 697–703.
Gu, J., Marshall, C., 1988. The effect of tiller removal and tiller defoliation on competition between the main shoot and tillers of spring barley. Ann. Appl. Biol. 112, 597–608.
Hu, Y., Oertli, J.J., Schmidhalter, U., 1997. Interactive effects of salinity and macronutrient level on wheat. I. Growth. J. Plant Nutr. 20, 1155–1167.
Huel, P., Baker, R.J., 1991. Performance of oligoculm spring wheats grown in a semi-arid environment. Can. J. Plant Sci. 71, 199–203.
Jones, H.G., Kirby, E.J.M., 1977. Effects of manipulation of number of tillers and water supply on seed yield in barley. J. Agric. Sci. (Cambridge) 88, 391–397.
Kemp, D.R., Whingwiri, E.E., 1980. Effect of tiller removal and shading on spikelet development and yield components of the main shoot of wheat and on the sugar concentration of the ear and flag Leaf. Aust. J. Plant Physiol. 7, 501–510.
Kirby, E.J.M., 1973. Effect of temperature on ear abnormalities in uniculm barley. J. Exp. Bot. 24, 935–947.
Kirby, E.J.M., Faris, D.G., 1972. The effect of plant density on tiller growth and morphology in barley. J. Agric. Sci. (Cambridge) 78, 281–287.
Kirby, E.J.M., Jones, H.G., 1977. The relations between the main shoot and tillers in barley plants. J. Agric. Sci. (Cambridge) 88, 381–389.
Kirby, E.J.M., Appleyard, M., Fellowes, G., 1985. Leaf emergence and tillering in barley and wheat. Agronomie 5, 193–200.
Lauer, J.G., Simmons, S.R., 1985. Photoassimilate partitioning of main shoot leaves in field-grown spring barley. Crop Sci. 25, 851–855.
Lauer, J.G., Simmons, S.R., 1988. Photoassimilate partitioning by tillers and individual tiller leaves in field-grown spring barley. Crop Sci. 28, 279–285.
Lupton, F.G.H., 1966. Translocation of photosynthetic assimilates in wheat. Ann. Appl. Biol. 57, 355–364.
Maas, E.V., Grieve, C.M., 1990. Spike and leaf development in salt-stressed wheat. Crop Sci. 30, 1309–1313.
Maas, E.V., Lesch, S.M., Francois, L.E., Grieve, C.M., 1994. Tiller development in salt-stressed wheat. Crop Sci. 34, 1594–1603.
MacKown, C.T., Van Sanford, D.A., Ma, Y.Z., 1989. Main stem sink manipulation in wheat. Plant Physiol. 89, 597–601.
Martinez-Carrasco, R., Thorne, G.N., 1979. Physiological factors limiting grain size in wheat. J. Exp. Bot. 30, 669–679.
Mitchell, K.J., 1954. Influence of light and temperature on growth of ryegrass (*Lolium* spp.). III. Pattern and rate of tissue formation. Physiol. Plant. 7, 51–65.
Mohamed, G.E.S., Marshall, C., 1979. Physiological aspects of tiller removal in spring wheat. J. Agric. Sci. (Cambridge) 93, 457–463.
Papadakis, J.S., 1940. The relation of the number of tillers per unit area to the yield of wheat and its bearing on fertilizing and breeding this plant—the space factor. Soil Sci. 50, 369–388.
Sticksel, E., Maidl, F.X., Retzer, F., Fischbeck, G., 1999. Nitrogen uptake and utilization in winter wheat under different fertilization regimes, with particular reference to main stems and tillers. J. Agron. Crop Sci. 183, 47–52.
Thorne, G.N., 1982. Distribution between parts of the main shoot and the tillers of photosynthate produced before and after anthesis in the top three leaves of main shoots of Hobbit and Maris Huntsman winter wheat. Ann. Appl. Biol. 101, 553–559.
Thorne, G.N., Wood, D.W., 1987. The fate of carbon in dying tillers of winter wheat. J. Agric. Sci. (Cambridge) 108, 515–522.
Zeng, L., Shannon, M.C., Grieve, C.M., 2002. Evaluation of salt tolerance in rice genotypes by multiple agronomic parameters. Euphytica 127, 235–245.