The root growth strategies of three wheatgrass in early seedlings

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Abstract

Research was conducted on crested, slender and northern wheatgrasses, commonly available wheatgrasses for the Canadian prairies, under 6% and 12% of gravimetric water content, to determine the effect of water stress on root growth for seedling growth. The results indicate that Root growth rate varies across early seedling phase for these grasses. Rapid root biomass accumulation occurred in the early phase of seedlings. Reducing water supplement increased biomass allocated to roots earlier for plant growth. Reduced water treatments demonstrated a non-linear changed root biomass growth rate for crested wheatgrasses and northern wheatgrasses.

Key words: root; wheatgrass; water stress; seedling

1. Introduction

Germination and early seedling growth are the most critical phase of a plant's life (Johnson 1986; Waddington and Snoop 1994), as both processes are highly sensitive to environmental variability, and need reliable water supply (Waddington and Snoop 1994; Fay and Schultz 2009). Once the primary root emerges through the seed coat, a lack of water is fatal (Frasier, Cox et al. 1987), so just-emerged seedlings have higher mortality than other subsequent life history stages (Fenner 1987). Growth strategies adopted by seedlings will decide the winner of the competition for limited resources. Delaying drought stress is identified as one of the two major strategies of species' adaptation to drought, each strategy having its specific suite of function traits (Markesteijn and Poorter 2009). Traits in morphology often associated with drought-delay such as high biomass investment to roots and high specific root lengths(Miquelajauregui and Valverde 2010). Growth analysis is a widely used analytical tool for characterizing plant growth. Of the parameters typically calculated, the most important is relative growth rate (RGR) (Hoffmann and Poorter 2002), this parameter was considered in root growth under drought as well (Padilla, Miranda et al. 2009; Woods, Archer et al. 2011), but most of previous research considered root grew as a constant rate, especially for biomass RGR because of the difficulties in measuring biomass on the same plant over time. Thus, there are few studies that examine what kind of process root biomass accumulation is followed in the seedling stage. If root growth is a dynamic process, then root biomass parameters measured at the end of seedling growth can't be used for analyses of root

growth during whole seedling phase. A detailed description of seedling morphological development could improve our understanding of the establishment process of species(Cornaglia, Schrauf et al. 2005). Three commonly available wheatgrasses, for the Canadian prairies, were chosen for this study to show how root growth rate varies as seedlings develop, and how water stress influences certain phases of seedling growth.

2. Materials and methods

2.1Experiment design

The experiment was conducted in greenhouse at SPARC from May to July, 2011. Experimental design was a full factorial randomized block with 4 replications. Species, soil moisture and harvest time were as main factors. The experiment was repeated twice. Seeds of three wheatgrass species, *Agropyron cristatum* (L.) Gaertn. ssp. *pectinatum*, *Agropyron trachycaulum* (Link) Malte ex H.F.Lewis *Elymus trachycaulus* and *Agropyron dasystachyum* （Hook.）Vasey. *Elyms lanceolatus* ssp. *lanceolatus*）cultivars used and year of harvest were planted (n=5) separately into each tubes , heavy-wall polyvinylchloride plastic, 154 cm deep, 2.7 cm in diameter, sealed bottom with caps and filled with sand at two specific moisture contents. Water and sand mixed by mixer base on 6% (reduced) and 12% (control) of gravimetric water content (WC, Equation1) which was calculated following:

$$WC = \frac{(W_{wet} - W_{dry})}{W_{dry}} \times 100\% \qquad [1]$$

where W_{wet} *and* W_{dry} were weight of soil before and after dring at 105℃ for 48h. About 0.5cm sand was placed over the seeds, leaving a void of about 1cm about the sand. After that, the top of each tube was covered with a double thickness of monolayer plastic film held on by elastic band (John Waddington 1994). The tubes were weighed and arranged in four blocks. The covers were removed after the first seedling emerged, and seedlings were removed to maintain one plant per tube. Tubes were weighed and watered daily to attain the initial weight. The mean daily temperature in greenhouse was 21±2℃. One seedling of each species under different treatments in each block was harvested at an interval of 4 days after first seedling emerged (Seedlings were harvested 5 times in each experiment). Shoot height, root length and the number of root branches and leaves of the seedlings harvested were recorded. Shoots and roots were dried at 70℃ for 48h, and weighted separately. Root to shoot biomass ratio (R:S ratio, Equation2), relative growth rate (RGR, 10^{-1}mg $g^{-1}day^{-1}$, Equation3), relative elongation rate（RER, $mm^{-1}day^{-1}$, Equation4）, relative growth rate of leaves and branches(No. day^{-1}) of each seedling at each sample were calculated. The formulation as follows:

$$R:S = \frac{Rmass}{Smass} \qquad [2]$$

where *R* and *S* were root and shoot respectively.

$$RGR = \frac{(\log W_j - \log W_i)}{t_j - t_i} \qquad [3]$$

Where W_i and W_j ($j>i$) were the weight of seedling in ith and jth harvests respectively.

$$RER = \frac{L_j - L_i}{t_j - t_i} \quad [4]$$

Where L_i and L_j ($j>i$) were the length root in ith and jth harvests respectively. Same formulation was used for relative growth rate of root branches, where L_i and L_j ($j>i$) were the number of leaves or root branches in ith and jth harvests respectively.

2.3 Statistical analysis

The experiment design was a randomized complete block with three species, two water treatments and five harvests (harvest every 4 days). A mixed-model analysis of variance was performed on the data. Experiment runs were set as random effects, and Proc Mix results indicated no significant difference between runs ($P>0.05$), therefore, results were pooled. Differences in the number of root branches, length, R: S biomass ratio, biomass of shootings, roots and total biomass were tested using two-way analysis of variance (ANOVA). One-way ANOVA was used to examine the variance in branches growth rate, R: S ratio, RER and RGR. All tests were conducted with SAS 9.2 (SAS Institute Inc., Cary, North Carolina, USA). The significance level of $\alpha=0.05$ was used for all analyses, and data are presented as means ± one standard error of means (SEM).

3. Results

3.1 Cumulative growth of three wheatgrass

Species Effect

No significance was detected between root growth parameters at first harvest. Only one growth index, root branches, significantly differed among species, for second and last harvests ($P<0.05$, and $P<0.001$, respectively, Table1). More growth parameters significantly differed among species at the third and fourth harvests (5 and 3 parameters separately, Table 1) than at other harvests. All of growth parameters for NWG, were lower than the other species regardless of water treatments (Table 2).

Water treatments effect and interaction effect between species and water treatments

At the first harvest, all of seedling growth indices except for root biomass and total biomass were significantly different between water treatments ($P<0.05$, Table 1). Effect of water treatments on R: S biomass ratio significantly depended on species ($P<0.05$, Table 1, Table 4). At second harvest, water treatments had a significant effect on the number of root branches ($P<0.01$, Table 1). At the third and five harvests, all of seedling growth indices, except for root biomass and R:S biomass ratio differed between water treatments($P<0.01$, Table 1). The response of the number of branches to water treatments significantly depended on species, at the third and fifth harvests ($P<0.05$ and $P<0.01$, respectively, Table 1, Table 4). At the fourth harvest, water treatments had a significant effect in the number of root branches, shoot biomass and total biomass (Table 3). Effect of water treatments on total biomass depended on species at fourth harvest ($P<0.05$, Table 1, Table 4). The different water treatments had a significant impact on root biomass ($P<0.05$, Table 1, table 4).

Seedlings subjected to control water with higher value in growth parameters had significant response to water treatments at each harvest than that under reduced water treatment ($P<0.05$, Table 3). Root branching was more influenced by water treatments for all wheatgrasses across all phase (Table1). SWG was more affected by water shortage than other species (Table 4).

Total biomass increased with days after emergence under both water treatments, but increased more quickly under control water than reduced water treatment (Fig.1). Effect of water treatments on total biomass was significant at last two harvests for SWG, whereas no significant difference was detected across all phases for other species (Fig.1). R:S biomass ratio for plants either subjected to control water or reduced water tended to increase with days after emergence (Table 5, Fig.1), although this trend is not significant for crested wheatgrass under reduced water treatment and northern wheatgrass under control water treatment (Fig.1). This trend was more rapid under control water than reduced water treatment for CWG and SWG (Fig.1)，while contrary for NWG (Fig.1). However, plants subjected to reduced water treatment allocated more biomass to root at an earlier phase than those under control water treatment (Table 5, Fig.1). Under control water treatment, CWG and SWG allocated more biomass to root at fourth harvest (Table5). Under reduced water treatment, CWG, SWG and NWG allocated more biomass at the second, third and fifth harvests (Table5), separately. Water treatments had a significant effect on R:T biomass ratio, but these occurred at different phases, for CWG at second harvest ($P<0.01$,Fig.1), for SWG at first harvest ($P<0.01$,Fig.1) and for NWG at last harvest ($P<0.01$,Fig.1).

3.2 Relative growth rate for seedling

All of species showed higher growth rate (except for root branches appearance rate) in initial days after emergency. Root branches appearance rate increased with days after emergence, but reduced water treatment slowed down the rate for SWG (Fig.2). Root RGR subjected to control water showed a decreasing trend across harvests, and reduced water treatment changed this trend (Fig.2, Table 7).

One way ANOVA was performed on growth rate across all of harvests under control and reduced water respectively (Table 6, Fig.2). The results indicated that under control water treatment, almost all of growth rate parameters (except for root RER of SWG) were significantly differ among harvests (Table 6, Fig.2). Under reduced water, no difference was detected in root branches growth rate across the harvests (Table6). Other parameters of growth rate for plant subjected to reduced water were significantly different among harvests (Table 6). Water treatments influenced seedling growth rate, but significant difference occurred at different phases. For root branches growth rate, these different detected during first, second and fourth harvests for CWG, whole phases for SWG, third and fourth harvests for NWG (Fig.2). For root elongation, differences were found almost of whole phase (except for fourth harvest) of CWG, during second harvest for SWG and during first and fourth harvest for NWG (Fig.2). The effect of water treatments were found in root RGR. The differences were detected during second to last harvests for CWG (Fig.2), during first to fourth harvests for SWG (Fig.2), and during third and last harvest for NWG(Fig.2). Reduced

water treatment slowed seedling RER, and shoot RGR, while increasing root RGR 4 days after emergence (Fig.2).

4. Discussion and Conclusion

Strategies of wheatgrass

CWG and SWG adopt similar strategies such as promoting more root length, accumulating more biomass for whole plant than NWG. SWG performed better than CWG, and accumulated more branches, and gained more root biomass under well water treatment (Table 3). However SWG dramatically reduced the total plant biomass under drought (Table5). Drought reduced total plant biomass in all of three species (Table4), results that are consistent with other studies on different plant species (Fotelli, Geßler et al. 2001; Villagra and Cavagnaro 2006; Wu, Bao et al. 2008). Plant seedlings can adopt to water stress by a number of mechanisms (Xu, Deng et al. 2010), adaptive responses in morphology may be a primary mechanism by which these species can cope with delaying drought stress (Markesteijn and Poorter 2009) and the environmental characteristics of their respective habitats (Patterson, Guy et al. 1997). This kind of morphological plasticity enables a plant to change its growth pattern as it encounters different soil conditions (Hutchings 1988).

Biomass allocation

Alterations in biomass partitioning between above and belowground components, e.g. expressed by the root to shoot ratio, have been reported frequently (Schall, Lödige et al. 2012), and drought drove more biomass to be allocated to root is well documented. In this study, reducing water supplement increased biomass allocated to roots earlier for plant growth, although R:S ratio was increasing with days after emergence as well as under higher water treatment. Our results support previous studies. Partitioning more biomass to below ground and maintaining higher R:S ratio may be beneficial to enhanced water absorption (Wu, Bao et al. 2008), while water deficit increase was due to the asymmetrical reduction in shoot and root biomass thus increasing the R:S ratio (Xu, Deng et al. 2010).

Growth rate

Root growth rate varies across seedling phase for species (Fig.2). Rapid root elongation and biomass accumulation occurred in the early phase of seedlings. Reduced water treatments mainly effect growth rate in early phase of seedling for CWG and SWG, and demonstrate a non-linear changed root biomass growth rate for CWG and NWG, but mainly effect growth rate in middle and end phases of seedling for NWG. There is no doubt that reduced water availability will reduce turgor and therefore growth rate, if no physiological or biochemical adaptations occur to the growth process (Davies and Bacon 2003). While resources such as water, carbon and nutrients are hardly consumed, they certainly have the potential to influence the growth rate of a plant (Robinson 1991). At a whole organ level, growth rate slows when the root is exposed to a low water potential. Many plants show this slowing in growth rate when water supply is limited (Davies and Bacon 2003). Plant species vary considerably in the RGR that they can achieve under favourable growing conditions (Lambers and Poorter 1992). Slow potential RGR is thought to be part of a nexus of

adaptations to unfavourable growing conditions (Iii, Autumn et al. 1993; Van Der, Poorter et al. 1994). In this study, SWG slowed root growth rate and expressed trends more significantly than other species under reduced water treatment (Fig.2).

There are a number of methods for seedling elongation in dynamic measurement rather than root biomass (Mackie-dawson and Atkinson 1991), although Root Biomass RGR is one of important parameter to measure plant growth (Hoffmann and Poorter 2002). From our experiment, root RGR was not consistent, and comparing root RGR between treatments at different phases could result in different conclusions. Biomass parameter in multi-phases should be used for analysis of root growth, and further approaches for monitoring root biomass dynamic need to be developed.

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Table 1 P-value of Mixed model Analysis for each harvest

Days after emergence	*Treatment*	*Root Branches*	*Root length*	*Root biomass*	*Total biomass*	*R:S ratio*
4	**Species**	0.3881	0.8555	0.0892	0.0717	0.3486
	Water	0.0011	0.0098	0.124	0.3347	0.0169
	Species*water	0.2048	0.6712	0.208	0.6710	0.0368
8	**Species**	0.0369	0.1626	0.0591	0.2482	0.2328
	Water	0.0001	0.0682	0.0836	0.4821	0.1669
	Species*water	0.1412	0.1637	0.1566	0.1714	0.1242
12	**Species**	0.0021	0.0252	0.002	0.0258	0.0069
	Water	<.0001	0.0106	0.1316	0.0154	0.2529
	Species*water	0.0396	0.9113	0.764	0.7976	0.9741
16	**Species**	0.0009	0.1443	0.0014	0.1216	0.0003
	Water	<.0001	0.0656	0.0903	0.0158	0.3106
	Species*water	0.2335	0.6492	0.0376	0.0450	0.5472
20	**Species**	<.0001	0.5999	0.0715	0.0992	0.7842
	Water	<.0001	0.007	0.0974	0.0203	0.4319
	Species*water	0.003	0.6767	0.0463	0.0892	0.0861

Table 2 Seedling growth traits which were significant different among species. Lowercase letters in a row show significant difference among species. Seedling growth traits with significant species effect and interaction between species and water treatments were not listed in this table. All significance were declared at P<0.05, according to Tukey test. Values are means± 1SEM. n=7-8

Days after Emergence (day)	*Growth indices*	*Crested Wheatgrass*	*Slender Wheatgrass*	*Northern Wheatgrass*	*SEM*
8	root branches	13.9498a	13.8125a	7.6494b	2.5589
12	root length	133.94a	122.06ab	95.5943b	15.2058
	root biomass	3.194a	3.619a	2.264b	0.317
	total biomass	6.694ab	7.469a	5.523b	0.688
	R:T biomass ratio	0.9396a	0.9756a	0.7323b	0.074
16	root branches	38.875ab	55.8938a	25.875b	7.0736
	R:T biomass ratio	1.2278a	1.031ab	0.7892b	6.1174

Table 3 Seedling growth traits which were significant different between water treatments. Lowercase letters in a row show significant difference between water treatments. Seedling growth traits with significant species effect and interaction between species and water treatments were not listed in this table. All significance were declared at P<0.05, according to Tukey test. Values are means± 1SEM. n=7-8

Days after Emergence (day)	*Growth indices*	*Control*	*Reduced*	*SEM*
4	root branches	4.25a	1.5833b	0.5398
	root length (mm)	58.7083a	47.0417b	4.9907
8	root branches	16.508a	7.0998b	2.3142
12	root length (mm)	131.9600a	102.4400b	14.2585
	total biobiomass(mg)	7.2630a	5.8610b	0.6340
16	root branches	57.2917a	23.1375b	6.4927
20	root length (mm)	202.7900a	160.3200b	22.9918
	total biobiomass(mg)	13.900a	10.8400b	1.4620

Table 4 Seedling growth indices with significant interaction between species and water treatments at each harvest. Lowercase letters in a row show significant difference between water treatments for each species. All significance were declared at P<0.05, according to Tukey test. Values are means± 1SEM. n=7-8

	Days after Emergence	*Crested Wheatgrass*		*Slender Wheatgrass*		*Northern Wheatgrass*		
		Control	Reduced	Control	Reduced	Control	Reduced	SEM
The number of root branches	**12**	28.500b	20.750b	51.250a	19.750b	24.875b	9.789b	6.682
	20	64.250b	37.500b	126.000a	45.625b	54.375b	30.631b	13.093
Root length (mm)	**12**	148.370a	119.500ab	139.870ab	104.250ab	107.630ab	83.564b	17.747
Root biomass (mg)	**16**	5.050a	6.075a	6.213a	4.225ab	4.137ab	2.425b	0.673
	20	7.013ab	5.238b	9.063a	5.825ab	4.688b	6.001ab	1.006
Total biomass (mg)	**16**	9.725ab	10.69ab	12.69a	7.887ab	9.825ab	6.378b	1.436
R:T biomass ratio	**4**	0.4259b	0.5404ab	0.3921b	0.7840a	0.5898ab	0.5661ab	0.0985

Table 5 Root to Shoot biomass ratio of three wheatgrass at each harvest. Lowercase letters in a column show significant difference among harvests for each species. All significance were declared at P<0.05, according to Tukey test. Values are means± 1SEM. n=7-8

Days after	*Crested Wheatgrass*		*Slender Wheatgrass*		*Northern Wheatgrass*	
Emergence	Control	Reduced	Control	Reduced	Control	Reduced
4	0.426c	0.540b	0.392b	0.784a	0.590a	0.566b
8	0.696bc	1.136a	0.820a	0.909a	0.751a	0.702b
12	0.906ab	0.973ab	0.948a	1.004a	0.687a	0.734b
16	1.126a	1.330a	2.162a	1.085a	0.784a	0.758b
20	1.252a	1.059ab	1.111a	1.117a	0.813a	1.257a
SEM	0.101	0.137	0.524	0.105	0.107	0.145
P value	<.0001	0.0026	<.0001	0.0945	0.3608	0.0021

Table 6 P value of one way ANOVA to harvests

Growth rate	*Crested Wheatgrass*		*Sledner Wheatgrass*		*Northern Wheatgrass*	
	Control	Reduced	Control	Reduced	Control	Reduced
Root branches (No. day^{-1})	0.0287	0.0644	<.0001	0.0561	<.0001	0.1205
Root RER (mm day^{-1})	0.0003	0.0002	0.0817	0.0146	0.0001	0.0002
Root RGR (10^{-1}mg g^{-1}day^{-1})	<.0001	<.0001	<.0001	<.0001	<.0001	0.0004

Table 7 Equations and coefficients of determination (R^2) for the regression of growth rate on days after emergence for three wheatgrass.

Growth indies	*Control*		*Reduced*	
	Equation	R^2	Equation	R^2
Root branches appearance rate (No.day^{-1})				
CWG	y=-1.2+0.689x-0.022x^2 ns	0.617	y=-6.09+2.25x-0.183x^2+0.005x^3 ns	0.835
SWG	y=-0.769+0.589x **	0.937	y=-0.656+0.259x *	0.785
NWG	y=-2.452+0.799x-0.025x^2 ns	0.862	y=2.805-0.594x+0.032x^2 ns	0.822
Root elongation (mm day^{-1})				
CWG	y=-12.317+(688.245/x)-(6156.619/x^2)+(15391.411/x^3) ns	0.413	y=20.899-3.165x+0.291x^2-0.009x^3 ns	0.781
SWG	y=10.506+1.626x-0.251x^2+0.009x^3 ns	0.831	y=11.578+(-80.412/x)+(332.732/x^2) *	0.990
NWG	y=32.788-5.955x+0.440x^2-0.010x^3 ns	0.634	y=0.699+4.885x-0.64x^2+0.022x^3 ns	0.981
Root biomass GRG(10^{-1} mg g^{-1} day^{-1})				
CWG	y=0.189-0.008x **	0.97	y=-0.107+(2.90/x)-(7.37/x^2) ns	0.742
SWG	y=0.192-0.008x **	0.947	y=-0.008+(0.860/x) **	0.923
NWG	y=0.172-0.008x **	0.99	y=0.274-0.034x+0.001x^2 ns	0.935

Asterisks indicate significant differences (*P<0.05; P<0.01), 'ns' represented no significance. Number of each comparison is 5; each comparison is the mean of eight replications.**

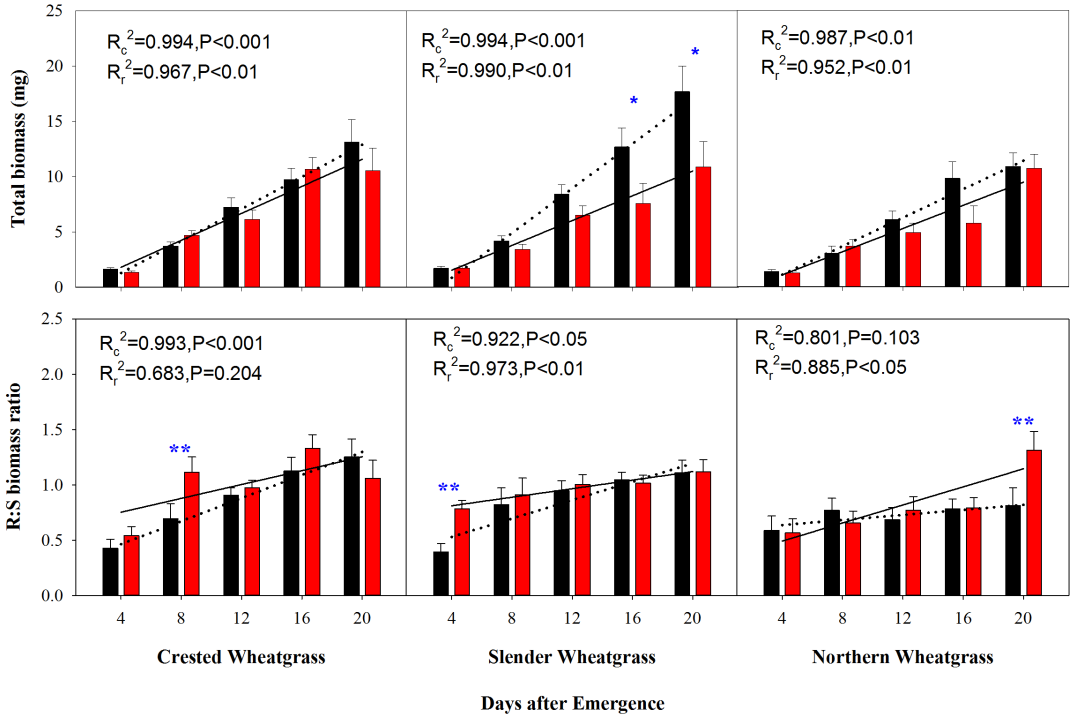

Fig.1 Mean (+SEM) seedling total biomass and R:S biomass ratio at each harvest. *=P<0.05; ** =P<0.01 for mean comparisons of control (Dark bar) and reduced (Red bar) water treatment. Fitted linear functions with R^2 (dotted line and R_c^2 : control water treatment; continuous line and R_r^2: reduced water treatment) are provided .

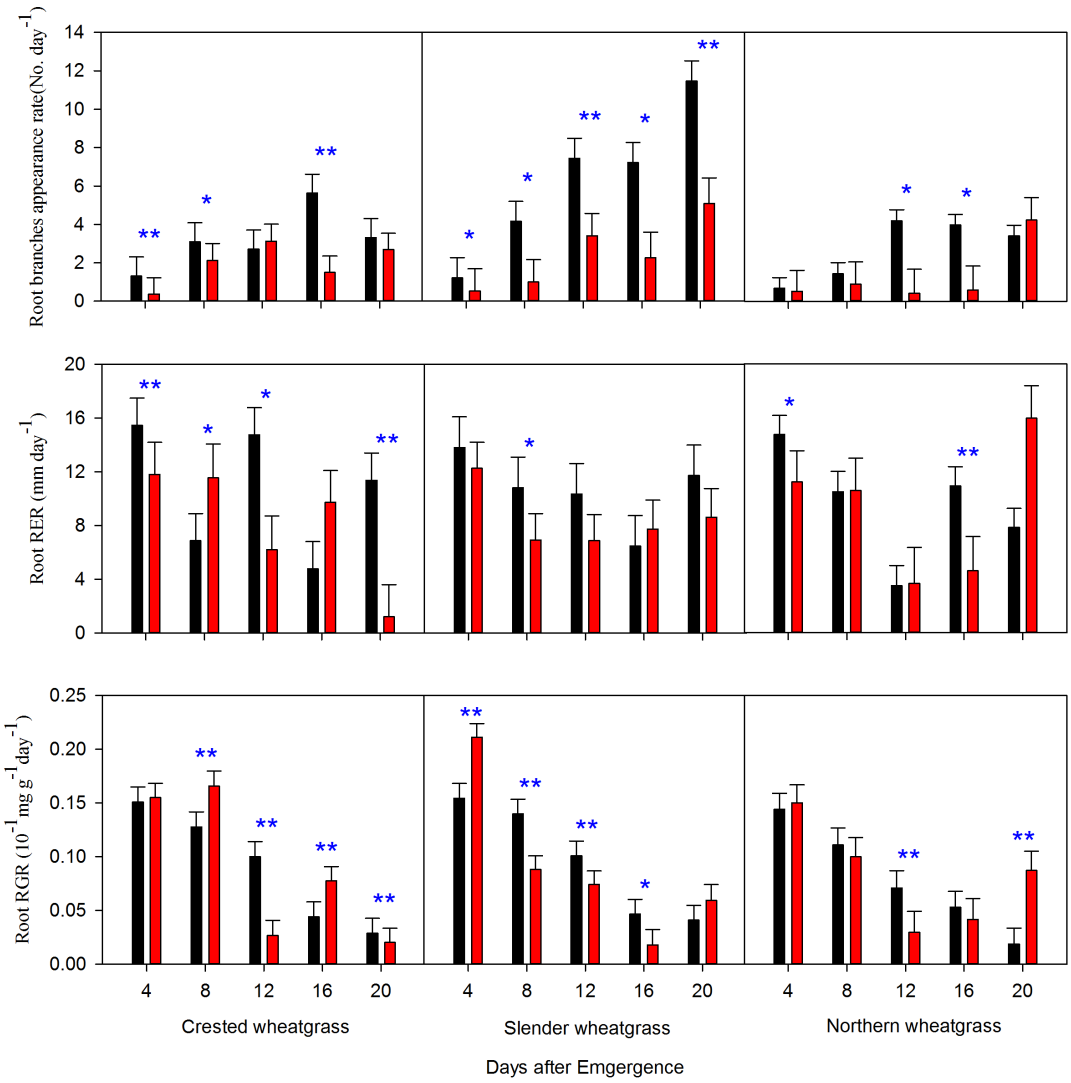

Fig.2 Mean (+SEM) growth rate at each harvest. *=P<0.05; =P<0.01 for mean comparisons of control (Dark bar) and reduced (Red bar) water treatment.**