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Effect of Local Shading and Drought Both Singly and Combined on Tiller Ramets of Agrostis stolonifera L.

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Abstract: In this study, to examine the effect of single and multiple stresses applied to a single group of tiller ramet on their growth and development. The response of these treatments was measured at the level of the treated ramet and the entire clone. Ramet number, branch production and elongation, and biomass were recorded for the treated ramet and the extending main stolon. Overall the results showed that there was a very large effect of both stresses either drought with or without shade on both tiller production as well as dry weight of the localized tiller ramet and some how the other parts of the stolon.

Key words: Multiple stresses, ramet, main stolon, A. stolonifera L.

Introduction

Agrostis stolonifera (Creeping Bent grass), a member of the Gramineae, is a fast-growing, stoloniferous, patch-forming perennial grass, which is common in a wide range of fertile habitats. It is found in aquatic habitats and mire, woodland margins, maritime habitats, most types of spoiled heaps, moist grassland and arable land (Grime et al., 1990). Ramets are vegetatively produced from growth modules with root and shoot components that are capable of independent existence, if they are separated from the main plant (Harper, 1977). Clonal growth may be defined as the horizontal extension of a plant by the addition of ramets that develop their own roots as well as the shoot (Silvertown, 1987). The established clonal plant is thus a population of interconnected ramets of various ages and origins where different groups of ramet by their spatial separation may experience different edaphic and climatic conditions. Alternatively, apart from newly developing ramets and the extending apical region of the rhizome or stolon, the clone may function as a series of interconnected but physiologically independent ramets. Resources acquired by individual ramets are therefore not widely distributed within the clonal system but are utilized locally by ramets (Marshall, 1990). However intermediate patterns of physiological organization may occur, as a shortfall in the supply of carbohydrate following shading or defoliation

of one part of a clonal plant and may be buffered by the transport of current assimilate from other parts of the clone, allowing previously the independent units to become physiologically integrated (Forde, 1966; Nyahoza et al., 1973; & Alpert and Mooney, 1986). There have been several studies on the physiological organization of stoloniferous plants to determine weather the plant operates as a fully integrated system (in which carbon and mineral nutrients such as phosphate move freely within entire plant) or it operates as a series of physiological independent ramets. One way of studying physiological organization is to place a ramet in resource-rich or resource-poor conditions. If the growth response is local, then it can be concluded that the ramet is physiologically independent. But if there is a more widespread growth response, this indicates that the plant is physiologically integrated.

Materials and Methods

The experiment was conducted in the Pen-y-ffridd field station at University of Wales Bangor, (UK) during February 1996. In greenhouse No.1 having a minimum temperature of 14°C under natural lighting but with a minimum photoperiod of 14h, provided with 400W high-pressure sodium lamps. Twenty main stolons (MS) were selected from a population of A. stolonifera L. which had been maintained under glasshouse

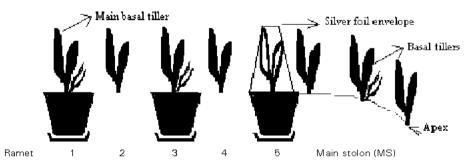


Fig. 1: Experimental treatments (T1-T4); R1, R3 and R5 are rooted ramets of the main stolon, and R2 and R4 are unrooted. R1 is the oldest ramet of the main stolon.

Tre atments	Ramet 1	Ramet 3	Ramet 5
T1 (control)	: 100 ml H₂O	+ 100 ml H _z O	+ 100 ml H _z O
T2	: 100 ml H , 0	+ 100 ml H , 0	+ SHADING + 100 ml H,0
T3	: 100 ml H ,O	+ 100 ml H,O	+ SHADING + DROUGHŤ
T4	: 100 ml H ₂ O	+ 100 ml H ₂ O	+ DROUGHT

conditions for one year by regular vegetative propagation. The second youngest node from the apex was rooted by pinning to the surface of 3.5 cm diameter pots containing John Innes No.1 compost. This unit was classed as ramet1 (R1). Three weeks later, when the MS had produced six fully extended nodes, ramet 3 (R3) and ramet 5 (R5) were rooted in the same way as for R1 but R2 and R4 left unrooted. The stolon was disconnected from the mother plant after one week. When nodel roots had been produced by these nodes (after about 10 days) four localized drought and shading treatments were established on R5 with five replicates of each treatment. The set-up of the treatments T1-T4 is described in (Fig. 1).

Hundred ml water was supplied every other day to the rooted ramets 1, 3 and 5 throughout the experiment. Saucers were placed under all pots to retain the applied water. In drought treatment no water was supplied to R5 from the start of the treatments; in the shading treatment the entire tiller arising from the ramet 5 (R5) was darkened by enclosing in a silver foil envelope.

For R1-R5 the longest main basal tiller and the number of basal tillers were measured together with MS length (R5-apex) and number of MS tillers at four-days intervals throughout a 12 days period. A final harvest was then made and each plant was separated into its component parts: main basal tillers and tillers of each ramet and MS (R1-R5, R5-apex), MS tillers and the root system of ramets 1,3 and 5. These components were dried at 70 $^{\circ}\text{C}$ for biomass determination. The statistical analysis was made using ANOVA (Anonymous, 1993), the comparison of means was performed by Tukey's honestly significance difference (HSD) test. The result described as significant are statistically different at the P < 0.05 critical level of probability.

Results and Discussion

The length of main basal tillers (MBT) of rooted ramet 1 was observed to be significantly affected by the treatments. Although there was no difference in relation to the control (T1), T2 (shading only) was significantly greater than T4 (drought only) (Table 1). The production of tillers by R1 was however not significantly affected by the treatments (Table 2). For ramet 2 no significant effects were observed on the length of the MBT and tillers production (Tables 1 & 2). For ramet 3 there was a significant effect on the length of MBT between T1 control and the T3 treatment (shading with drought) where it was reduced in the later (Table 1). However no significant effect was observed for tiller production in R3 (Table 2). The

length of the main basal tillers of R4 was significantly affected by the treatments but there was no effect on tillers number; the significant difference was again between T1 control treatment and T3 (shading with water stress) (Table 1 & 2). However on R5 where the localized treatments were applied, highly significant effects were observed on both the length of MBT as well as the tillers production (Tables 1 & 2). All treatments reduced MBT length and tillers number in relation to the control T1. In terms of the length of the main stolon, T3 and T4 resulted in a significant reduction but there was no effect on tiller production along the axis (Table 1 & 2). The biomass of the main basal tiller (MBT) and basal tillers produced by R1 were observed to be significantly decreased by the localized water stress treatment to ramet 5 compared to the control T1 and T2 treatment (Table 3a). No significant effects were found in relation to the dry weight of ramet R2, R3 and R4. However the biomass of the MBT and basal tillers of R5 was significantly decreased by all the treatments (T2. T3 and T4) a reduction of around 75% (Table 3a). A highly significant effect was also observed on main stolon biomass (including tillers) which was reduced by the two water-stress treatments (T3 and T4). The local treatments to ramet 5 had a highly significant effect on root production of R1 where all treatments reduced dry weight by more than 50% (Table 3b). Similarly all these treatments also significantly decreased the root weight of R3, but to a lesser degree. All treatments significantly reduced the root production of R5 by around 50% with no significant differences between them. A large effect was observed on total plant dry weight by all the localized treatments to R5 (Table 4a). The shoot: root dry weight ratio of R1 was increased by all the localized treatments but there was no effect for R3. But for R5 both shading treatments had a value of about half that of the control whereas the combined shading and drought treatment resulted in a large increase as compared to control T1 (Table 4b).

Overall the results of present experiment showed that there was a very large effect of water stress with and without shade on both tiller production and dry weight of the treated ramet (Gardner, 1965). In addition the water balance of plants depends on the rate of transpiration. Thus a small water deficit may have a large effect on plant development if it has a poorly developed root system. However there was relatively little effect of the treatments on the length of the main stolon or its tiller production. This suggests that growth was maintained by the utilization of carbohydrate reserves, located in the shaded tillers or adjacent to main stolon

Table 1: The Effect of the localized drought and shading on the main basal tiller length of R1-R5 and MS after 12 days (± S.E).

Length of main basal tiller of R1-R5 and main stolon (cm) Ramet 1 Ramet 2 Ramet 3 Ramet 5 Ramet 4 Main stolon T1: control 14.86±2.18 12.36±2.64 21.68±1.18 14.90±1.02 26.42 ± 1.72 0 65.42 ± 2.97 33.46±1.37 46.16±1.73 4 22 44 + 2 64 19 02 + 2 81 27 22 + 1 99 24 68 + 1 88 75 02 +3 52 8 36.90±3.25 29.92 ± 2.49 39.88±1.29 36.10±1.63 86.38±2.16 12 51.49±1.93 47.20±2.70 98.84±2.99 48.20±4.35 38.30±3.69 60.82 ± 2.31 T2: shading 15.30±1.56 13.20±1.44 16.94±0.69 12.72 ± 1.10 25.02 ± 2.13 61.42±2.46 25.46±1.89 19.22±0.92 27.70±1.02 21.76±1.28 25.36±2.13 74.60±1.65 34.84 ± 3.39 30.10±2.75 33.80±1.26 32.88 ± 3.70 25.42 ± 2.09 82.62 ± 2.20 49.48±2.77 41.88±2.19 49.80±2.61 43.88 ± 2.45 $25.52 \pm 2.02*$ 92.54 ± 2.46 12 T3: vvater stress and shading 0 11.88 ± 1.99 10.46±1.76 15 28 + 1 24 12 24 + 2 34 21 87 + 2 25 61.34 ± 2.79 4 18 84 + 2 29 15.28 ± 1.48 24 90 + 1 22 17.54 + 2.9425 18 + 1 81 69 03 + 1 88 8 75.78±1.84 19.20±2.67 30.72 ± 0.91 25.84 ± 3.32 26.38±1.27 27.00±0.75 36 82 + 2 78 41.14±0.72* 33.22 ± 3.83* 27.76 + 1.65* 12 29 92 +3 55 86 26 + 2 81 T4: water stress 11.16±2.87 10.24 ± 3.10 17.02 ± 1.66 14.90±2.52 25.68±1.46 52.54 ± 4.55 16.02 ± 4.35 15.48 ± 4.29 27.82 ± 2.48 20.70±2.73 33.02 ± 1.89 67.02 ± 2.05 8 23.08±6.33 20.26 ± 4.27 35.74±1.43 30.82 ± 3.94 40.20 ± 2.02 73.88 ± 2.01 47.16±2.04* 83.66±2.79 27.92 ± 6.09

 $[^]st$ indicates that the value in the row is significantly different from T1 control value (P < 0.05)

Table 2: Effect of localized drought and shading on tiller production of R1-R5 and MS after 12 days (±S.E).

	No. of basal t	No. of basal tillers of R1- R5 and main stolon					
Days	Ramet 1	Ramet 2	Ramet 3	Ramet 4	Ramet 5	Main stolon	
T1: control							
0	2.00 ± 0.55	1.20 ± 0.58	3.20 ± 0.20	1.20 ± 0.49	3.00 ± 0.32	8.20±1.39	
4	3.20±0.37	1.80±0.80	5.00 ± 0.32	2.20 ± 0.37	6.40 ± 0.60	13.00±0.95	
8	6.00±0.95	3.00 ± 0.63	7.20 ± 0.37	3.20 ± 0.20	8.60±0.40	16.40±1.08	
12	6.40±1.03	3.80 ± 0.37	7.60 ± 0.51	3.20 ± 0.20	8.60±0.40	17.40±0.87	
T2: shading							
0	1.80±0.58	0.60 ± 0.25	3.40 ± 0.25	2.20 ± 0.58	3.40 ± 0.25	7.60±0.68	
4	3.60±0.25	1.60±0.25	4.40 ± 0.60	2.40 ± 0.40	4.80±0.58	12.80±0.86	
8	5.60±0.87	2.40 ± 0.25	6.80±0.86	2.60 ± 0.25	5.20±0.58	16.40±0.86	
12	7.40±1.12	3.20 ± 0.37	8.80±0.86	3.20 ± 0.37	6.00 ± 0.45	19.40±0.81	
T3: vvater stress	s + shading						
0	1.40±0.68	0.20 ± 0.20	2.80 ± 0.20	1.00 ± 0.32	2.60 ± 0.40	8.00±0.45	
4	2.20±0.37	1.60±0.40	4.00 ± 0.32	1.40±0.51	4.40 ± 0.75	11.80±1.16	
8	3.40 ± 0.25	2.00 ± 0.45	5.40 ± 0.75	2.20 ± 0.49	4.80±0.66	14.20±0.86	
12	4.80±0.49	2.40 ± 0.40	7.60 ± 0.81	2.20 ± 0.49	$4.80 \pm 0.37 *$	17.00±0.63	
T4: water stres:	S						
0	2.00 ± 0.71	0.20 ± 0.20	3.00 ± 0.00	1.00 ± 0.32	2.60 ± 0.40	8.00±0.63	
4	2.80±0.74	1.00 ± 0.45	4.70 ± 0.20	1.80±0.58	5.00 ± 0.00	10.00±0.84	
8	3.40 ± 0.93	1.80±0.58	5.80±0.37	2.20 ± 0.37	6.00 ± 0.32	13.80±1.07	

^{*} indicates that the value in the row is significantly different to the T1 control value (P < 0.05).

Table 3: Effect of localized drought & shading on (a) total shoot dry weight of R1-R5 and main stolon and (b) root dry weight of R1, R3 & R5

after 12 days.				
(a)	T1 Control	T2	T3	T4
Ramet 1	0.322	0.368	0.192	0.17*
Ramet 2	0.137	0.156	0.261	0.065
Ramet 3	0.426	0.448	0.287	0.367
Ramet 4	0.181	0.175	0.104	0.126
Ramet 5	0.748	0.202*	0.163*	0.55*
Main stolon	1.687	1.562	1.252	1.006
(b)				
Ramet 1	0.85	0.067	0.037	0.03
Ramet 3	0.109	0.099	0.073	0.08
Ramet 5	0.18	0.104*	0.073*	0.078*

⁽a) Total shoot (main basal tiller+ramet tillers) dry weight (g)

Table 4: Effect of localized drought & shading on (a) total plant dry weight (g) and (b) total shoot & root dry weight ratio of ramet 1, 3 and 5 after 12 days.

	and dianter 12 days.				
(a)	T1 Control	T2	T3	T4	
	3.875±0.247	3.181 ±0.215	3.100±0.199	2.477 ±0.147	
(b)					
Ramet 1	3.788	5.493	5.189	5.667	
Ramet 3	3.908	4.525	3.932	4.588	
Ramet 5	4.156	1.942	2.233	7.115	

internodes (Moran et al., 1953; Milthrope and Davidson, 1966) and, by the import of current assimilates from unshaded tillers (Forde, 1966; Ong and Marshall, 1979).

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⁽b) Total root dry weight (g)

 $[^]st$ indicates that the value in the row is significantly different to the T1 control value (P < 0.05).