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STOLON FORMATION AND SIGNIFICANCE FOR SWARD TILLER DYNAMICS IN PERENNIAL RYEGRASS

C. Matthew[1], S.J. Quilter[1], C.J. Korte[2], A.C.P. Chu[1] and AD. Mackay[3]
[1]Deparmtent of Agronomy, Massey University, Palmerston North
[2]MAFTech, Gisborne. [3]Grasslands Division, DSIR, Palmerston North

Abstract

In a pot trial to investigate stolon formation in perennial ryegrass (*Lolium perenne* L.), 4 genotypes of ryegrass tested all formed stolons. After burial with approximately 30 mm soil in August, cutting and burial, or cutting alone, stolon numbers in November were 18, 8 and 3 (SED 3) per plant, respectively. In a grazed ryegrass sward stolon lengths were measured at intervals between May 1987 and April 1988, and for hard and lax grazed plots respectively, were 58 and 96 m/m^2 in May, increased to 137 and 164 m/m^2 in December, then declined to 47 and 74 m/m^2 in April 1988. Active stolon formation in the field began when tillers were buried by earthworm activity and stock trampling in winter. It appears that stolon formation in ryegrass is a response to a seasonal cycle of burial similar to that for white clover.

Studies of tagged tillers indicated a pattern of sward renewal in early summer by rapid production of large numbers of tillers from stolons at the base of dying flowering tillers. Other research results suggest that this pattern of sward renewal in perennial ryegrass may be widespread. Implications for grazing management are briefly discussed.

Keywords: tiller appearnace rate, perennation, carbohydrate, perennial ryegrass. stolon formation

INTRODUCTION

It has long been known that ryegrass plants (*Lolium perenne* L.) sometimes adopt a stoloniferous growth habit, but only two New Zealand papers describe this phenomenon. Using gel-electrophoresis Harris et al. (1979) demonstrated that individual genotypes of ryegrass in a lawn had spread by means of stolons to cover patches up to 0.8 m in diameter. Korte & Harris (1987) recorded stolon numbers up to 2100/m^2 in a ryegrass-white clover sward. They concluded that the occurrence of stolons in perennial ryegrass has been underestimated and suggested that stolon formation follows tiller burial by earthworm casting and animal treading during winter.

This paper reports results from a pot experiment on factors influencing the number of stolons formed, and from a field experiment on the occurrence of stolons in a grazed pasture and on the relationship between stolon formation and sward tiller dynamics.

EXPERIMENTAL

Pot experiment

Ryegrass tillers of 4 genotypes ('Grasslands Nui' control; Whatawhata hill country collection; old pasture, Manutuke research station; lawn at DSIR) were transplanted into pots at Manutuke Horticultural Research Station in April 1987 and grown on until December 1987. Numbers of stolons and internodes per plant were counted in October, November and December for(i) plants cut, (ii) for plants cut and covered with approximately 3 cm soil In August, and (iii) for plants uncut and covered with soil. No stolons had been found when plants were examined prior to application of Soil.

Field experiment

When a study of root mass and root replacement rates for ryegrass was begun at Massey University in December 1986, quantities of dead stolon were found among the root samples. When active stolon formation was observed in the field in May 1987 it was decided to measure stolon length during the experiment. The experiment comprised 100 m^2 plots of Ellett ryegrass hard and frequently (H: target herbage mass 800 to 1600 kg DM/ha) or laxly and infrequently (L: target 1800 to 3000 kg DM/ha). During root harvests (carried out as described by Matthew et *al.* (1986) at about 7-week intervals from 26 May 1987 to 10 April 1988) stolons were separated out from root samples and measured. In March 1987 about 2000 tillers in 24 fixed quadrats (100 mm diameter plastic rings) were tagged and left to become buried by earthworm casting and stock trampling. The fixed quadrats were dug up in December 1987, and the fate of tagged tilers and the origin of existing tillers determined.

RESULTS

Pot experiment

Covering cut plants with soil more than doubled the number of stolons and uncut plants covered with soil had highest stolon numbers (Table 1). Cutting reduced plant size, reducing tiller and stolon numbers per plant (Table 1). All genotypes formed stolons and differences among genotypes in numbers of stolons per plant were not significant ($P>0.05$). The number of stolons increased with time (Table 1).

Table 1: Number of tillers, stolons, and rooted internodes per plant in pot experiment

	Management				Month			
	cut	cut + soil	Uncut + soil	SED[1]	Oct	Nov	Dec	SED
Tillers	80	79	89	9 NS	72	59	117	7***
Stolons	3	8	18	3***	8	9	13	2*
Internodes	5	12	29	5***	11	14	21	3'

1. For tables 1 - 3: SED -standard error of difference, NS — not significant. * p < 0.05, ** p < 0.01, *** p < 0.001.

Field experiment

Stolons were found to comprise vascularisation (V) segments formed by series of nodes laid down below the growing point at the formation of each new leaf (A Fig. 1), and internode (I) segments formed by internode elongation (B, Fig. 1). The V sections were distinctive because their closely spaced nodes gave a knobbly appearance to the naked eye and rafts of roots were attached. The V and I segments were counted separately after the first harvest in May.

Total stolon length was 58 and 96 m stolon/m^2 ground for H and L plots respectively on 26 May, increased steadily until December, and then declined again (Table 2). L plots consistently had more total stolon than H plots and this was due to increased length of I segments on these plots (Table 2). When tillers per m^2 were counted in September, I formation had restored growing points to ground level on L plots whereas they were still buried on H plots. This latter point was confirmed by measurements of growing point height in relation to ground level on 21 October (H = -14 mm, L = +80 mm, $P<0.01$).

The average burial between March and December as judged by the distance from the base of the fixed quadrats to the soil surface was 15 and 18 mm ($P<0.1$) for H and L plots respectively. The average length of stolon on surviving tagged tillers

Table 2: Stolon lengths (m stolon/m^2 ground) in ryegrass swards at Massey University from 8 July 1987 to 10 April 1988

Stolon category	Grazing treatment	8 Jul	20 Aug	20 Oct	20 Dec	21 Jan	8 April[2]	SED[3]
				Date				
V	Hard	48	31	45	49	50	36	12 NS
	Lax	36	35	50	44	46	25	
I	Hard	41	31	70	88	86	9	24 • ☒
	Lax	88	80	118	120	127	49	
Total	Hard	90	61	114	137	118	45	32 • ☒
	Lax	102	115	165	164	173	74	

1. V - vascularisation segments, I - internode segments.
2. Live stolon only, measured.
3. SED - standard error of difference for comparing treatment values of a particular date, significance levels apply to experiment grand means.

Table 3: Tiller classification (% total live tillers) by category of origin for a post-flowering ryegrass sward (December 10)

Grazing treatment	Tagged tillers		Tillers emerged post tagging		
	Reproductive	Vegetative	Derived from vegetative	Derived from reproductive	Origin uncertain
Hard	3	12	19	52	14
Lax	7	11	21	48	12
SED	2.2 NS	5.1 NS	6.0 NS	12.7 NS	9.6 NS

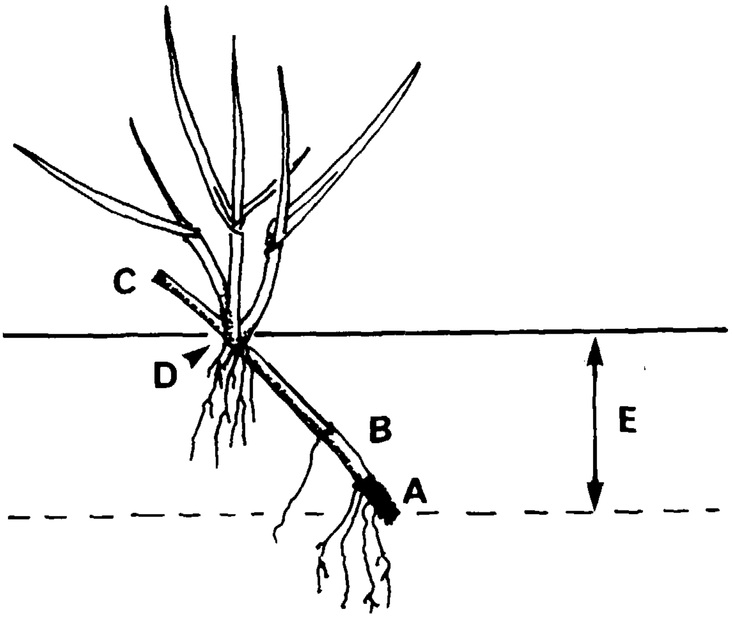

Figure 1: Stolon and daughter tillers in perennial ryegrass, illustrating pattern of perennation.
(A: V segment with nodes close spaced: B: I segment formed by internode elongation: C: Dying flowering tiller; D: I" daughter tiller and two 2" tillers; E: movement of soil surface relative to tiller during winter, typically 15 to 20 mm).

was 19mm (H) and 26 mm (L) (P<O.l) and the proportions of tillers tagged in March surviving at least until flowering were 39% (H) and 27% (L) (P<0.05). Analysis of tillers present on 10 December (Table 3) showed very similar patterns for both H and L treatments and a majority of tillers present were primary or secondary daughter tillers arising from stolohs of tillers which had flowered (Table 3). Tags were by this time about 15 mm below the soil surface, but all tagged tillers still alive had formed stolon so that their growing points were no longer buried.

DISCUSSION

The term "stolon" in this paper refers to segments of vascular tissue formed below the growing point of a ryegrass tiller. The definition of the term is discussed by Harris et al. (1979). In both pot and field experiments stolon formation was reduced with increased intensity of defoliation. A possible explanation for this could be that carbohydrate levels within the plant influence the degree of internode elongation. In the pot experiment burial appeared to be the major factor inducing stolon formation. In the field experiment active stolon formation began after burial of tillers by earthworm casting after autumn rain. The greatest increase in stolon lengths occurred between August and October, shortly after tillers had been buried by stock trampling in soft soil and just before the onset of reproductive growth. This confirms the findings of Korte & Harris (1987) and indicates that ryegrass tillers undergo a seasonal cycle of burial and replacement parallel to that previously documented for white clover (Hay *et al.* 1987). Total length of ryegrass stolon in these swards (Table 1) was of the same order as that recorded for white clover (48 - 150 m/m^2) if stolon mass figures of Hay & Chapman (1984) are divided by weight per unit lenth.

At the time of tiller production by underground stolons sward daily tiller appearance rates (TAR) were 100-150 $tillers/m^2$, 2-3 times higher than at other times of the year (Matthew 1988). Korte (1986) and L'Hullier (1987) also reported a high peak of TAR in early summer. Thus their results probably reflect a period of tiller production from underground stolons too. Aerial tillers (L'Hullier 1987) were also observed in our experiment and differ from daughter tillers of underground stolons only in that the node from which the tiller originates is above rather than below the soil surface.

In Britain Colvill 8 Marshall (1984) showed that tillers appearing after flowering may live a full 12 months, longer than tillers appearing at other times of the year. Data from this study (Matthew et *al.* in prep.) show that December-tagged tillers produce 2-3 times more daughters from their stolons the following summer than March-tagged tillers. In this study vegetative proliferation of early-spring tillers accounted for only 20% of tillers in the sward in early December (Table 3) and natural reseeding (L'Huillier & Aislabie, 1988) did not appear to be important in sward rejuvenation. This indicates a tendency for perennation in perennial ryegrass to follow a pattern illustrated in Figure 1. From December to April vascularisation of new tillers occurs (A) until the growing point is overtaken by winter burial (E). On burial (May - October) internode elongation occurs (B). Survivors flower and die or are decapitated (C). New daughter tillers are formed and rapidly proliferate to form new tiller hierarchies (D). These new tillers repeat the cycle while the previous season's stolons (A) begin to die. Colvill & Marshall (1984) also recognised that the post-flowering tillers ensure the perenniality of the plant, although they did not mention the presence of stolons.

Management that encourages daughter tiller formation from stolons in early summer is likely to improve persistence, and autumn pasture growth rates Poor resistence of ryegrass in summer dry districts may be due to a failure of daughter tillers formed in December to establish and survive. Management that encourages internode formation may also be useful to effect spread between rows after direct drilling. Further research in these areas should be very rewarding.

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