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The potential of seed-shedding and seedling development to contribute to the persistence of white clover (*Trifolium repens*) in grazed swards in Uruguay

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SUMMARY

The present study was conducted to investigate whether white clover (*Trifolium repens* L.) in grazed swards in Uruguay can produce and shed sufficient seed, and whether sufficient seedlings can develop and survive, to make an important contribution to the long-term persistence of the species. Five sites, on which survival of white clover had been better than is usual in Uruguay, were studied in 1995–97. The sites had been sown with white clover 11–15 years previously and were managed mainly by cattle grazing. The number of white clover inflorescences/m^2 was at least 18 at nearly half the counts in the study and the number of viable seeds in the top 5 cm of soil was at least 1500 at half the counts. The results for both the above variables suggest that all five sites had a supply of seed greater than a commercial seed rate at some times of the year. However, the number of seedlings/m^2 was >100, a possible target in these conditions, at only one fifth of the counts, and the proportion of seedlings that survived from one recording date to the next (a period of 4–5 weeks) varied from >0·7 to zero. It seems, therefore, that, in these conditions, the failure of seeds to convert to established plants is likely to be a greater constraint than the production and shedding of seeds. There was considerable variability with time, and between and within sites at each stage of the reproductive cycle. On one site, competition from Bermudagrass (*Cynodon dactylon*) greatly reduced the number of white clover seedlings/m^2. Overall, the results suggest that white clover in grazed swards in Uruguay can produce and shed sufficient seed, and that sufficient seedlings can develop and survive, to make a significant contribution to the long-term persistence of the species. However, each year there is a risk of seedlings being killed in dry, hot weather.

INTRODUCTION

In moist, temperate environments, such as most parts of the UK, white clover (*Trifolium repens* L.), if well established and appropriately managed, can often survive difficult periods such as harsh winters and dry summers. In drier or less temperate environments, however, white clover may not survive difficult conditions, such as severe droughts. In Australia, for example, summer moisture stress has been identified as the primary environmental constraint limiting the agronomic performance and persistence of white clover (Jahufer *et al.* 2002). The same is true in Uruguay, where hot, dry summers make it difficult for white clover to persist (Olmos 1997). In the Northern Tablelands of New South Wales, Australia, at a similar latitude to Uruguay, Archer & Robinson (1989) noted that the probability of white clover survival was very greatly reduced by a combination of low soil moisture and temperatures around 30 °C, similar to daytime summer temperatures in Uruguay. Because of the risk that white clover plants may be killed when conditions are very dry and hot, long-term persistence of the species in a sward may depend on having accumulated a reserve of seed in the soil and on the subsequent, successful establishment of

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seedlings at a wetter, cooler time of year. Jahufer *et al.* (2002) referred to selection based partly on intensive flowering and high seed production in an attempt to produce a cultivar adapted to persist in this type of environment. Jones (1982) noted the need for white clover in the subtropical coastal regions of south-east Queensland, Australia, to be able to regenerate from a reserve of seed in the soil, but also for the species to be able to spread and persist by stolons when there is sufficient moisture.

Uruguay is primarily a pastoral country, with >0·9 of the agricultural area in permanent pasture (FAO 2004). White clover has been quite widely used there, both for oversowing into native pastures and for sowing on bare ground after ploughing and cultivating. However, the climate (Corsi 1982) is marginal for the species and more information is needed about the effectiveness of seed production and seedling development as an aid to persistence, so that management can be more soundly based and better-adapted cultivars introduced.

The aim of the present study was to investigate whether white clover in grazed swards in Uruguayan conditions can produce and shed sufficient seed, and whether sufficient seedlings can develop and survive, to make an important contribution to the long-term persistence of the species.

MATERIALS AND METHODS

Study sites

The study was conducted on five sites (Berrutti, De Brum, Engels, López and Sanz) in different parts of Uruguay (Fig. 1) with swards that had been sown with white clover. The sites ranged in latitude from 30° 56′ S to 33° 10′ S and in longitude from 54° 07′ W to 56° 51′ W. They were all <200 m a.s.l. and on flat or slightly sloping (<5°) ground. The cultivars of white clover that had been sown were Zapicán on three sites, Yi on one and Bayucuá on one (Table 1). Zapicán (also known as Estanzuela Zapicán) was selected at La Estanzuela, Colonia, southern Uruguay, from a population introduced from Santa Fé, northern Argentina; it is early-flowering, with medium to large leaves and good seed yields (Caradus & Woodfield 1997). Yi is an early-flowering type, based on Ladino introductions to Uruguay. Bayucuá is a medium-large-leaved type, selected in Salto, north-west Uruguay, from a population introduced from Santa Fé (Caradus & Woodfield 1997); this population survived a very dry summer initially, in 1959. Commonly, white clover was the only species sown, but in some cases another legume or *Festuca* was also sown. The study began in 1995 on swards which had been sown 11 to 15 years previously (Table 1). All five sites had been well managed, to the extent that the combination of management and environment had allowed white clover to persist. Four sites were used for cattle grazing and one (Sanz) for both cattle grazing and seed production.

The sites chosen were ones where survival of white clover had been better than is usual in Uruguayan conditions. They had had a sufficient period (at least 11 years) to allow poorly adapted genotypes to die out. The populations studied, therefore, would be expected to show characteristics well suited to survival in these conditions. It was beyond the authors' resources at the time to compare these populations with 'control' populations or to compare closely controlled management strategies with the existing commercial management.

In the top 20 cm of soil on the sites, soil pH (in water) varied from 5·0–6·0 and available P (De Zamuz & Castro 1974) from 5 to 64 mg/kg (Table 1). Exchangeable K varied from 2·2 to 4·9 mmol(+)/kg and exchangeable Al from 0·8 to 3·3 mmol(+)/kg. Clay content varied from 180–350 g/kg, silt from 250–590 g/kg and sand from 60–510 g/kg (Table 1). Field capacity varied from 230–409 g/kg, permanent wilting point from 104–200 g/kg and water availability in the top 20 cm from 31–43 mm (Table 2).

Typical mean air temperatures ranged from 12 °C in July to 24 °C in January. The northern sites (De Brum and Berrutti) were slightly warmer than the southern ones (Engels and Sanz), with López intermediate. The variation between sites in mean annual pan evaporation (from an open water surface) was from 868–983 mm. The site in the north east (Berrutti) had about 10% higher mean annual rainfall than the other sites (1247 mm compared with 1134 mm), greater mean winter water excess than the others (388 mm compared with 302 mm) and a lower mean summer water deficit than the others (35 mm compared with 63 mm).

Soil moisture

Soil moisture was determined by oven-drying five samples per site from the top 18 cm for 4–5 days at 65 °C in open trays. Samples were taken at approximately monthly intervals (Table 2).

Inflorescences and their seeds

On each site a permanent 5×20 m grid, containing one hundred 1×1 m squares, was laid out in October 1995, before the beginning of the flowering period. Within this grid, white clover inflorescences were counted (but not removed) in one 20×50 cm quadrat per 1×1 m square in each of 50 randomly selected squares in the period 23–31 October 1995. At Berrutti, De Brum, Engels and Sanz, white clover inflorescences were also counted in all 100 squares in the periods 12–15 November 1996 and 11 December 1996–3 January 1997. At least 300 mature

Table 1. *Soil analysis, soil pH, available soil P, sown cultivar of white clover and age of sward on five study sites in Uruguay*

Site	Soil analysis (g/kg)			Soil pH	Available soil P (mg/kg)	Sown cultivar	Age of sward (years)
	Sand	Silt	Clay				
Berrutti	350	390	260	5·0	5	Yi	11
De Brum	60	590	350	5·5	7	Bayucuá	12
Engels	420	370	200	5·1	64	Zapicán	15
López	510	250	240	6·0	10	Zapicán	12
Sanz	350	470	180	5·4	5	Zapicán	11

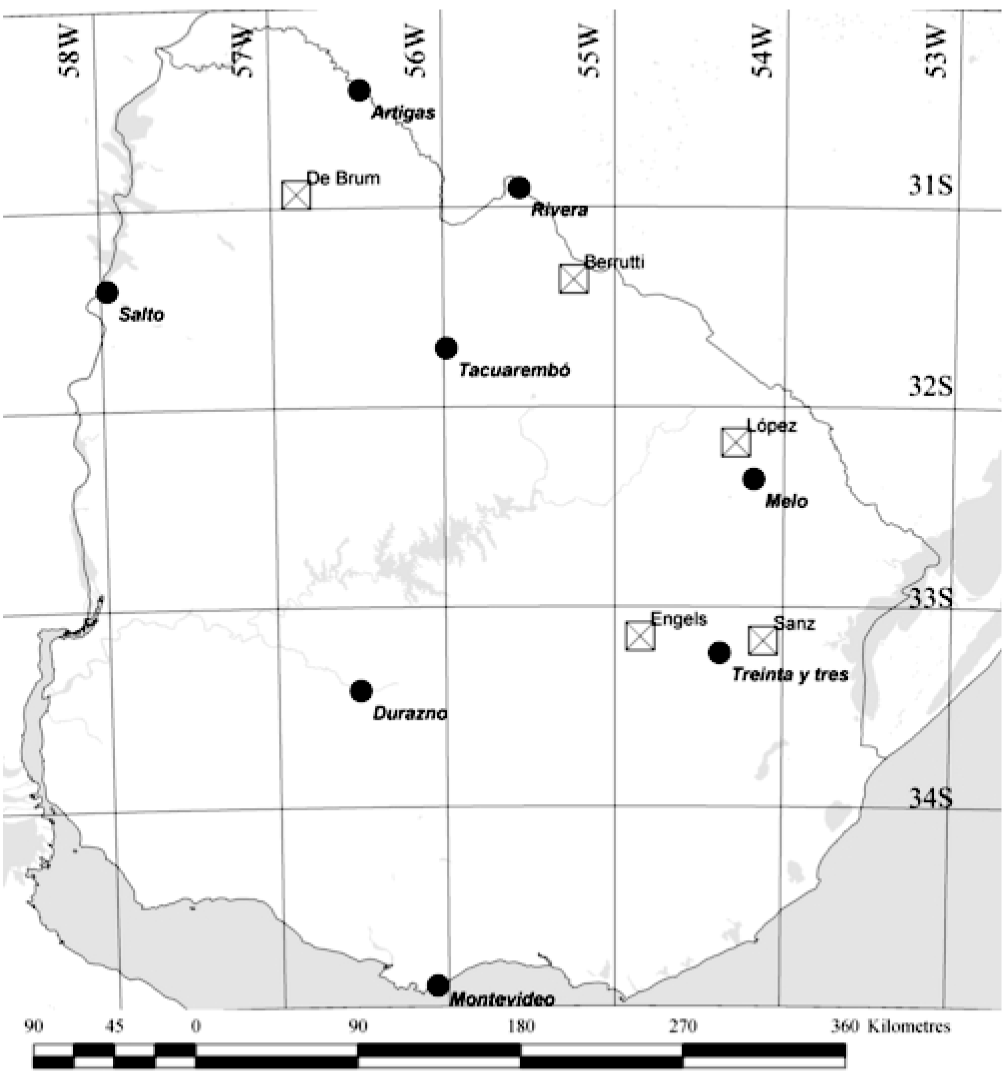

Fig. 1. Location of experimental sites (⊠) and selected towns (●) in Uruguay. Transverse Mercator projection. Map reproduced with permission of ESRI (UK).

Table 2. *Soil moisture content in different periods, field capacity, permanent wilting point, and available water on five study sites in Uruguay*

	Site					
Sampling period	Berrutti	De Brum	Engels	López	Sanz	Mean*
			Soil moisture content (g/kg)			
23–31 Oct 1995	179	243	289	184	208	230
1–9 Dec	128	192	85	83	82	122
28 Dec–11 Jan	183	155	77	127	79	124
9–10 Feb 1996	151	288	183	229	222	211
6–8 Mar	191	210	56	162	73	133
29 Apr–7 May	201	456	289	†	272	305
4–6 Jun	157	242	179	†	167	186
9–15 Jul	268	226	257	†	268	255
3–4 Sep	287	224	270	†	284	266
9–17 Oct	255	275	225	†	205	240
12–15 Nov	283	447	263	†	238	308
11 Dec–9 Jan	181	246	61	†	67	139
11–24 Feb 1997	279	317	191	†	222	252
27 Mar–3 Apr	120	154	93	†	112	120
25 Apr–2 May	252	344	210	†	216	256
11–18 Jun	295	418	246	†	277	309
11–22 Aug	278	328	280	†	296	296
Mean	217	280	191	†	193	220
			Field capacity (g/kg)			
	265	409	255	230	240	292
			Permanent wilting point (g/kg)			
	134	200	104	115	105	136
			Available water (mm) in the top 20 cm of soil when the soil is at field capacity			
	33·8	42·9	39·2	30·7	35·8	37·9

* Excluding López.
† Not recorded.

inflorescences per site were collected from the area adjacent to the grid in each of two periods, 23 October 1995–11 January 1996 and 12 November 1996–9 January 1997. 'Hard' seeds in these inflorescences were defined as those that did not absorb water, due to an impermeable seed coat, during incubation on moist filter paper at 20 °C for 10 days.

Soil seed bank

Within the permanent grid on each site, soil was sampled from each of 50 randomly selected squares in late October 1995 and late March 1996 and from all 100 squares in mid November 1996 and late April 1997. Each soil sample was approximately 320 ml, made up of three cores per square, each 5·2 cm diameter × 5 cm deep. The soil from each sample was spread in a layer *c.* 1·3 cm deep in a plastic tray 18 × 14 × 4 cm, with small holes in the bottom for drainage. The trays were kept in a building with a transparent plastic roof, with netting to exclude 0·5 of the light; they were watered daily. Seedlings other than those of white clover were removed and those of white clover were counted and removed when the first trifoliate leaf was visible.

Seedlings of white clover from the October 1995 batch of soil samples were counted eight times in the period 15 November 1995–7 February 1996; those from the March 1996 batch were counted eight times in the period 29 April–18 July; those from the November 1996 batch were counted 11 times in the period 3 January–17 September; those from the April 1997 batch were counted five times in the period 12 July–17 November. Various procedures were followed to enhance germination. The October 1995 trays were kept in a refrigerator at 5 °C from 7–28 December and the soil was turned over on 28 December and again on 22 January. The soil in the November 1996 trays was allowed to dry out between 2 February and 2 March; watering was resumed thereafter. The soil in the April 1997 trays was allowed to dry out between 17 September and 18 October, followed by a resumption of watering.

Table 3. *Numbers of inflorescences, viable seeds and seedlings of white clover on five study sites in Uruguay in different periods. Data are presented as means ± S.E.*

	Site						
Sampling period	Berrutti	De Brum	Engels	López	Sanz	Mean	*P*
			Numbers of inflorescences/m²				
23–31 Oct 1995†	18·6 ± 2·07	17·8 ± 3·28	32·8 ± 3·55	33·0 ± 3·70	0·6 ± 0·21	20·6	0·001
12–15 Nov 1996‡	21·8 ± 1·12	0·0	0·1 ± 0·08	*	3·4 ± 0·36	6·3	0·001
11 Dec 1996–3 Jan 1997‡	7·5 ± 0·58	0·0	0·2 ± 0·05	*	31·4 ± 2·45	9·8	0·001
			Numbers of viable seeds/m² in soil seed bank				
Late Oct 1995†	1500 ± 141	320 ± 34	670 ± 60	1270 ± 175	1650 ± 142	1080	0·001
Late Mar 1996†	5610 ± 381	1710 ± 154	3090 ± 210	9980 ± 817	7150 ± 486	5510	0·001
Mid Nov 1996‡	90 ± 13	140 ± 18	150 ± 20	170 ± 23	380 ± 37	180	0·001
Late Apr 1997‡	3180 ± 206	470 ± 40	1170 ± 78	3130 ± 228	3530 ± 193	2290	0·001
			Proportion of viable seed in the October 1995 batch that germinated before cold treatment†				
	0·186 ± 0·0216	0·194 ± 0·0403	0·038 ± 0·0115	0·047 ± 0·0108	0·045 ± 0·0101	0·102	*
			Numbers of seedlings/m²				
29 Apr–7 May 1996§	24 ± 5·9	6 ± 2·9	18 ± 5·0	*	20 ± 5·4	17	0·048
4–6 Jun 1996§	25 ± 5·4	6 ± 2·6	15 ± 4·3	*	27 ± 5·7	18	0·002
9–15 Jul 1996§	368 ± 55·3	34 ± 17·3	91 ± 27·8	422 ± 59·1	160 ± 36·6	215	0·001
20–30 Aug 1996§	34 ± 11·2	19 ± 8·5	29 ± 10·3	216 ± 27·6	104 ± 17·2	80	0·001
21–23 Feb 1997§	181 ± 20·1	2 ± 2·4	3 ± 3·0	15 ± 6·0	22 ± 7·2	45	0·001
25 Apr–2 May 1997§	590 ± 50·0	2 ± 3·9	15 ± 8·4	48 ± 14·5	54 ± 15·4	142	0·001
10–18 Jun 1997§	402 ± 33·8	2 ± 3·2	9 ± 5·3	58 ± 12·9	45 ± 11·4	103	0·001
11–22 Aug 1997§	8 ± 3·0	0	10 ± 3·4	39 ± 6·5	14 ± 4·0	14	0·001

* Not recorded.
† 49 D.F. for each site.
‡ 99 D.F. for each site.
§ 24 D.F. for each site.

Numbers of seedlings

White clover seedlings were counted in each of 25 quadrats (20 × 25 cm) on each site in each of eight periods: 29 April–7 May, 4–6 June, 9–15 July and 20–23 August 1996 and 21–23 February, 25 April–2 May, 10–18 June and 11–22 August 1997. Recording at López, however, did not begin until July 1996. The quadrats were placed at random within the area surrounding the permanent grid, within 5 m of the grid. However, at Sanz approximately half the surrounding area within 5 m of the permanent grid was dominated by Bermudagrass (*Cynodon dactylon* (L.) Pers.), therefore the positioning of the quadrats was restricted: on each date 12 were placed at random in parts of the sward where Bermudagrass was present and 13 in parts where it was absent.

Seedling survival

At Berrutti, De Brum, Engels and Sanz, white clover seedlings were counted and their position mapped in each of six (in 1996) or eight (in 1997) 50 × 50 cm quadrats, placed within the area surrounding the permanent grid, within 5 m of the grid. Each of these quadrats remained in a fixed position for the full recording period of each year. On each date of recording, apart from the first date of each year, the survival or non-survival of each plant mapped on the previous recording date was noted. Some of the seedlings mapped on a particular date may have emerged after the previous recording date, while others had survived since at least the previous date. The dates of recording were the same as the dates on which seedlings were counted in the randomly placed quadrats, plus one additional record in the period 25 March–3 April 1997.

Statistical analysis

Statistical analysis was carried out by GLM (generalized linear models) (McCullagh & Nelder 1989) using Genstat (Genstat 5 Committee 1997) to test for differences between sites (Table 3). Because of very large differences between sites in means and variances for all variables, a separate S.E. was calculated for each site for each set of data (Tables 3 and 5). A *t*-test was used to see if the presence or absence of Bermudagrass affected the number of clover seedlings (Table 4).

Table 4. *Numbers of seedlings/m² of white clover on different dates at Sanz, Uruguay, in the presence and absence of Bermudagrass* (Cynodon dactylon)

Date	Bermudagrass Present (11 D.F. on each date)	Bermudagrass Absent (12 D.F. on each date)	*P*
7 May 1996	0	38	
4 Jun 1996	12	42	0·05
12 Jul 1996	53	258	0·001
23 Aug 1996	23	178	0·001
21 Feb 1997	0	43	
2 May 1997	2	103	0·001
18 Jun 1997	7	80	0·001
22 Aug 1997	0	28	

Table 5. *Proportions of white clover seedlings that survived from one recording date to the next at four study sites in Uruguay in 2 years*

Period of survival, mean of four sites (Berrutti, De Brum, Engels and Sanz)	Mean	S.E.	D.F.
Apr/May to Jun 1996	0·560	0·0995	74
Jun to Jul 1996	0·724	0·1015	57
Jul to Aug 1996	0·649	0·0320	675
Feb to Mar/Apr 1997	0·054	0·0280	298
Mar/Apr to Apr/May 1997	0·000	–	–
Apr/May to Jun 1997	0·634	0·0905	177
Jun to Aug 1997	0·312	0·0405	563
Site and year, mean of periods within a year	Mean	S.E.	D.F.
Berrutti 1996	0·586	0·0365	405
De Brum 1996	0·588	0·0790	84
Engels 1996	0·510	0·0755	95
Sanz 1996	0·838	0·0370	221
Berrutti 1997	0·132	0·0250	673
De Brum 1997	0·000	–	–
Engels 1997	0·511	0·1390	44
Sanz 1997	0·603	0·0575	261

RESULTS

Soil moisture

At the first sampling (in October 1995) the soils contained some plant-available moisture in the top 18 cm, but by the second and third samplings (December 1995 to early January 1996) the soils in this layer had dried to around the permanent wilting point (Table 2). By the fourth sampling (February 1996) the soils had gained some moisture, but they were very dry again by the fifth sampling (early March 1996). By late April/early May 1996 the soils were generally near field capacity. They were drier in June 1996 and very dry in December 1996/early January 1997 and again in late March/early April 1997.

Inflorescences and their seeds

In late October 1995, white clover was flowering at Berrutti, De Brum, Engels and López, with the largest number of inflorescences/m² at Engels and López, but there were almost no inflorescences at Sanz (Table 3). In contrast, in late 1996, white clover was flowering at Berrutti and Sanz, but there were almost no inflorescences at De Brum and Engels.

The proportion of the seeds collected in 1995/96 that were 'hard' was 0·34 (S.E. 0·039, D.F. 7). The equivalent proportion in 1996/97 was 0·80 (S.E. 0·025, D.F. 13). In neither year was there a statistically significant difference between collection sites in the proportion of 'hard' seeds.

Soil seed bank

When the soil was sampled in March or April, at the end of the summer, soon after the main flowering period of white clover, the number of viable white clover seeds present was large ($3900/m^2$ on average, equivalent to a seed rate of 25 kg/ha, if the 1000-seed weight was 0·65 g) (Table 3). There were considerable differences between sites and, to a lesser extent, between years. The largest number of viable seeds at this time, averaged over 2 years, was at López ($6560/m^2$) and the smallest number was at De Brum (1090).

When the soil was sampled in late October or mid November, before the main flowering period, the number of viable white clover seeds present was much lower than in March or April ($630/m^2$ on average, equivalent to *c*. 4 kg/ha) (Table 3). Again there were some differences between sites, with Sanz having the largest number of viable seeds, on average (1020) and De Brum the smallest number (230). Only a low proportion of the white clover seeds that germinated from the soil sampled in October 1995 did so before the cold treatment in the refrigerator; this applied particularly at Engels, López and Sanz (Table 3). The soil sampled in November 1996 did not have a period in a refrigerator and the number of seeds that germinated was lower than the number from the October 1995 sampling.

Numbers of seedlings

At Berrutti, large numbers of white clover seedlings/m^2 were recorded in July 1996 and in February, April and June 1997 (Table 3); the numbers were very much lower in August 1996 than in June 1996 and very much lower in August 1997 than in April and June 1997. At López (Table 3) and at Sanz in the absence of Bermudagrass (Table 4), large numbers of white clover seedlings/m^2 were recorded in July 1996, and the numbers had not declined as abruptly as at Berrutti by the following month. The numbers of white clover seedlings were lower at De Brum and Engels than at the other three sites, but again there appeared to be an increase to July 1996 and a decline to the following month. At De Brum, Engels, López and Sanz, there were generally fewer white clover seedlings/m^2 in 1997 than in 1996. At Sanz the numbers of white clover seedlings/m^2 in the parts of the sward containing Bermudagrass were very low, particularly in 1997 (Table 4).

Seedling survival

The proportion of white clover seedlings mapped on one recording date that survived to the next recording date was very low between February and March/April 1997 and zero from March/April to April/May 1997 (Table 5); the proportion that survived was lower between June and August 1997 than between July and August 1996. The proportion that survived was particularly high at Sanz in 1996 and particularly low at De Brum and Berrutti in 1997. The proportion that survived was generally lower in 1997 than in 1996.

DISCUSSION

The results suggest that white clover in grazed swards in Uruguay can produce and shed sufficient seed, and that sufficient seedlings can develop and survive, to make a significant contribution to the long-term persistence of the species. The number of white clover inflorescences/m^2 was at least 18 at nearly half the counts in the study; if half the 18 inflorescences survived grazing long enough to shed 100 viable seeds each, they would provide a seed rate of >5 kg/ha, i.e. above a commercial seed rate. The number of viable seeds/m^2 in the soil seed bank was at least 1500 at half the counts; this equates to a seed rate of >9 kg/ha, well above commercial rates. However, the number of seedlings/m^2 was >100, a possible target in these conditions, at only one fifth of the counts, suggesting that much of the available seed either does not germinate or produces seedlings that do not survive long. The seedling survival results show that, at the moister, cooler times of year, more than half the seedlings can survive at least the 4–5 week period between recording dates, but that in dry, hot conditions all seedlings may die.

There was considerable variability with time, and between and within sites. The variability was apparent at each stage of the reproductive cycle – in the numbers of inflorescences, the numbers of viable seeds in the soil seed bank, the numbers of seedlings and the proportions of seedlings that survived. Some of the low values can be explained by soil dryness at critical times. Dryness can restrict the ground cover of white clover (Hutchinson *et al*. 1995) and hence the numbers of nodes/m^2. Weather conditions, particularly temperature, influence the proportion of nodes that produce inflorescences (Thomas 1987). Grazing animals may remove a large proportion of the inflorescences produced, before seed is shed (Chapman & Anderson 1987). An example of this was at Engels, where a high stocking rate during the 1996 flowering period seemed to be a major reason for the lack of inflorescences on that site at the November and December counts. Dryness (Archer & Robinson 1989) and insufficient soil disturbance (Barrett &

Silander 1992) may restrict the proportion of seeds that germinate. Dryness may also restrict the proportion of seedlings that survive (Jones 1980; Archer & Robinson 1989). A striking instance in the present study was the almost complete failure of white clover seedlings mapped on one recording date to survive to the next recording date in autumn 1997. By late March 1997 the upper layer of the soils was close to the permanent wilting point.

Competition from established grasses, such as at Sanz with Bermudagrass, can also restrict the emergence and survival of white clover seedlings, as noted by Archer & Robinson (1989). The negative effect of Bermudagrass at Sanz on the number of white clover seedlings could have been due to a shortage of white clover seed, to restricted germination of the seed present, or to early death of the seedlings produced. However, it was not possible to determine the contribution of each possibility from the data collected in the present study.

To a limited extent the relative abundance of white clover inflorescences could be traced through to the subsequent relative abundance of seedlings. Thus, the relatively large number of inflorescences in October 1995 at López was followed by a relatively large number of seeds in the soil the following March and a relatively large number of seedlings in July. In contrast, at De Brum, the numbers of inflorescences, seeds and seedlings were all low. Not surprisingly, the numbers of seedlings recorded in the swards were much lower than the numbers of viable seeds recorded earlier. The numbers of white clover seeds/m^2 recorded in the present study were comparable with numbers recorded in south-east Queensland (Jones & Evans 1977; Jones 1982) and New South Wales (Archer & Rochester 1982; Archer & Robinson 1989).

The white clover populations in the present study were ones that had survived, probably by a combination of vegetative and sexual reproduction, for 11–15 years. The combination of genotype, environment and management had evidently allowed survival for this period. However, the zero and near-zero values in Tables 3–5, e.g. the failure of seedlings to survive at De Brum in 1997, suggest that it is difficult to ensure long-term survival without reseeding, and confirm the marginal nature of the Uruguayan environment for this species. However, the survival of white clover can be made a priority in sward management. This might involve supplying additional P (Singh *et al.* 1999), controlling competing species such as Bermudagrass, and sufficiently protecting the sward from grazing to allow inflorescences to develop and produce seeds. In Uruguay it will also be worthwhile to produce or import cultivars better adapted to persist in this environment and to test management techniques that have proved useful elsewhere.

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REFERENCES

Archer, K. A. & Robinson, G. G. (1989). The role of stolons and seedlings in the persistence and production of white clover (*Trifolium repens* L. cv. Huia) in temperate pastures on the Northern Tablelands, New South Wales. *Australian Journal of Agricultural Research* **40**, 605–616.

Archer, K. A. & Rochester, I. J. (1982). Numbers and germination characteristics of white clover seed recovered from soils on the Northern Tablelands of New South Wales after drought. *Journal of Australian Institute of Agricultural Science* **48**, 99–101.

Barrett, J. P. & Silander, J. A. (1992). Seedling recruitment limitation in white clover (*Trifolium repens*; Leguminosae). *American Journal of Botany* **79**, 643–649.

Caradus, J. R. & Woodfield, D. R. (1997). World checklist of white clover varieties II. *New Zealand Journal of Agricultural Research* **40**, 115–206.

Chapman, D. F. & Anderson, C. B. (1987). Natural re-seeding and *Trifolium repens* demography in grazed hill pastures. I. Flowerhead appearance and fate, and seed dynamics. *Journal of Applied Ecology* **24**, 1025–1035.

Corsi, W. (1982). *Regionalización agroclimática de Uruguay para cultivos. Estación Experimental La Estanzuela Miscelánea No. 40*. Colonia, Uruguay: Estación Experimental La Estanzuela.

De Zamuz, E. M. & Castro, J. L. (1974). *Evaluación de métodos de análisis de suelo para determinar fósforo asimilable. Estación Experimental La Estanzuela Boletín Técnico No. 15*. Colonia, Uruguay: Estación Experimental La Estanzuela.

FAO (2004). Food and Agriculture Organization of the United Nations, FAOSTAT. URL http://faostat.fao.org/, verified 23/8/05.

GENSTAT 5 COMMITTEE (1997). *Genstat 5 Release 4.1: Reference Manual Supplement to Genstat 5 Committee (1993) Genstat 5 Reference Manual Release 3*. Oxford, UK: Numerical Algorithms Group.

Hutchinson, K. J., King, K. L. & Wilkinson, D. R. (1995). Effects of rainfall, moisture stress, and stocking rate on the persistence of white clover over 30 years. *Australian Journal of Experimental Agriculture* **35**, 1039–1047.

Jahufer, M. Z. Z., Cooper, M., Ayres, J. F. & Bray, R. A. (2002). Identification of research to improve the efficiency of breeding strategies for white clover in Australia – a review. *Australian Journal of Agricultural Research* **53**, 239–257.

Jones, R. M. (1980). Survival of seedlings and primary taproots of white clover (*Trifolium repens*) in subtropical pastures in south-east Queensland. *Tropical Grasslands* **14**, 19–22.

Jones, R. M. (1982). White clover (*Trifolium repens*) in subtropical south-east Queensland. I. Some effects of site, season and management practices on the population dynamics of white clover. *Tropical Grasslands* **16**, 118–127.

JONES, R. M. & EVANS, T. R. (1977). Soil seed levels of *Lotononis bainesii*, *Desmodium intortum* and *Trifolium repens* in subtropical pastures. *Journal of Australian Institute of Agricultural Science* **43**, 164–166.

MCCULLAGH, P. & NELDER, J. A. (1989). *Generalized Linear Models, 2nd edition*. London: Chapman and Hall.

OLMOS, F. (1997). Efecto del estrés hídrico estival en la composición botánica de pasturas convencionales. In *Efectos climáticos sobre la productividad de pasturas en la región noreste*. *Boletín Divulgación No. 64*, pp. 13–20. Tacuarembó, Uruguay: INIA Tacuarembó.

SINGH, D. K., SALE, P. W. G., GOURLEY, C. J. P. & HASTHORPE, C. (1999). High phosphorus supply increases persistence and growth of white clover in grazed dairy pastures during dry summer conditions. *Australian Journal of Experimental Agriculture* **39**, 579–585.

THOMAS, R. G. (1987). Reproductive development. In *White Clover* (Eds M. J. Baker & W. M. Williams), pp. 63–123. Wallingford, UK: CAB International.