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Patterns of seed softening and seedling emergence of nineteen annual medics during three years after a single seed crop in southern Queensland

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Summary. To produce seed to determine the rates of seed softening of annual medics in the subtropics, 8 lines of barrel medic (*Medicago truncatula*), 3 lines of burr medic (*M. polymorpha*), 4 lines of snail medic (*M. scutellata*), and 1 line of each of button medic (*M. orbicularis*), strand medic (*M. littoralis*) and gama medic (*M. rugosa*) were grown at Warra in southern inland Queensland, in 1993. Seed of a fourth line of burr medic, a naturalised line, was harvested from Hermitage Research Station at that time. Pods were placed on the soil surface and buried at a depth of 7 cm, both in flywire envelopes and as free pods. Residual hard seed numbers were determined each year for 3 years from the envelopes, and seedlings were counted and removed from the free pods after each germination event. Patterns of softening of seeds from the same seed populations were also determined after placing them in a laboratory oven with a diurnal temperature fluctuation of 60/15ºC for periods of 16, 40 and 64 weeks followed, after each time period, by 4 diurnal cycles of 35/10ºC.

More than 90% of the original seeds were hard. Seed softening at the soil surface ranged from 26% after 3 years in button medic to almost complete softening in the gama medic after only 2 years. Burial had little effect on the rate of softening of the button medic but about halved the rate of softening of the other lines. The barrel medics were vulnerable to losses of large numbers of seedlings which softened and germinated in January–February and the snail medics from seedlings emerging in August–December. The proportion of soft seeds recovered as seedlings in the buried compared with the surface pods was higher in the larger-seeded medics, snail and gama, and lower in the other, smaller-seeded medics. Laboratory techniques effectively ranked the medic lines for their rate of seed softening in the field and provided some insight into their seasonal patterns of seed softening.

A wide range of seed softening patterns is available for fitting the requirements of various farming systems. The most appropriate pattern of softening will depend on the variability of medic seed production between years and the need for self regeneration of the medic after a cereal crop.

Introduction

Ley pastures based on annual medics, pasture legumes which ripen their seeds in the spring, are an option for improving soil fertility, and hence wheat yields and protein content, in the southern Queensland and northern New South Wales components of the northern grain belt of Australia (Dalal *et al.* 1991; Lloyd *et al.* 1991). To be successful in this environment the medics should produce sufficient seed with appropriate germination regulating mechanisms for the accumulation of seed reserves that will enable the legume to persist through years of poor seed production. The loss of germinable seeds following summer rains is a handicap for annual mediterranean legumes in summer rainfall environments (Hagon 1974). Hardseededness (seed coat impermeability) is the main mechanism regulating germination of annual medics between- and within-years (Taylor 1996*a*).

The importance of seed softening (the change to seed coat permeability) patterns between years on long-term persistence in annual medics has been demonstrated by Taylor and Downes (1995) using a simulation model. Few detailed studies have been made of patterns of medic seed softening beyond the first summer in Australia, and these have all been made in mediterranean environments in southern Australia (Taylor and Ewing 1988, 1992; Taylor 1996*a*). These studies have shown marked differences between species and lines within species, as well as marked effects of the seasons in which seeds are

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grown, on patterns of seed softening. One of these studies (Taylor and Ewing 1988, 1996) also described a reduced rate of seed softening that occurred as a result of burial of residual hard seeds present at the end of the first summer, as may occur in years of cropping.

Different patterns of seed softening within-years in a number of medics have been described in south-western Australia by Taylor (1996*a*, 1996*b*). More than half the annual softening of some, but not all, lines of *Medicago polymorpha* occurred between the first week of March and June. This higher proportion of seeds softening in the autumn rather than the summer can be important in the reduction of seed losses from false breaks of season in this mediterranean environment. Such patterns of softening could be of even greater benefit in the summer-dominant rainfall environment of southern Queensland.

In order to understand how changes in seed reserves of annual medics may influence their adaptation to different farming systems in the subtropics, we investigated patterns of seed softening and seedling emergence in 19 lines from 6 species in a field experiment over 3 years. Fourteen of the 19 medics chosen were commercial cultivars. Of these, Sava snail and all barrel medics except Mogul, have been or are now widely used in farming and grazing systems in the southern subtropics. The snail medic lines, SA 1868 and SA 3110, were included in this study because of their impending release as cultivars (E. J. Weston pers. comm.), the button medic, SA 8460, because of its demonstrated potential in marginal environments (Clem and Jones 1996), and the barrel medic, Z 914, because it was bred from cv. Jemalong as an aphid-resistant replacement.

We also attempted the simulation of this seed softening pattern in the laboratory by subjecting hard seeds to various temperature fluctuations that have been used successfully for some lines of annual medics by Taylor (1996*a*).

Materials and methods

Pod production

Pods of 4 lines of snail medic (*Medicago scutellata* L.), 8 lines of barrel medic (*M. truncatula* Gaertn.), 3 lines of burr medic (*M. polymorpha* L.), and 1 line of each of button medic (*M. orbicularis* L.), strand medic (*M. littoralis* Loisel.) and gama medic (*M. rugosa* Desr.) were grown in 1993 at Warra, Queensland (26°47'S, 150°53'E; 686 mm average annual rainfall with 35% falling from May to October; elevation 317 m). The pods were grown in single 5 by 3.5 m plots in a grey cracking soil, alternatively classified as a Vertisol (typic Chromustert) or Ug5.2 (Northcote 1979), which originally supported a predominantly brigalow (*Acacia harpophylla*) and belah (*Casuarina cristata*) vegetation. The plots were fertilised with single superphosphate at 80 kg/ha and hand broadcast on 14 April 1993 with either 16 kg/ha of the snail medics or 8 kg/ha of the other species. All seeds were inoculated with appropriate rhizobia. The plots were not grazed.

Newly ripened pods were collected from the Warra site on 30 November 1993 when samples for estimates of seed yield were also obtained. An additional line of burr medic, 'naturalised burr medic' with spiny burrs, was collected from the Hermitage Research Station, Warwick, Queensland (28°12'S, 152°06'E; 660 mm average annual rainfall with 37% falling from May to October; elevation 475 m), in November 1993. One hundred pods of each medic line were allocated at random into 48 pod lots for placement in the field in flywire envelopes and as free pods. Supplies of snail medic cv. Kelson were only sufficient for the free pod treatments and the laboratory studies.

Initial germination tests were conducted on 200 seeds that were separated by hand from each of 3 pod lots from each of the medic lines. The proportions of viable soft seeds were determined by placing the seeds on moist blotting paper in aluminium germination trays in the laboratory for 14 days at temperatures that fluctuated diurnally between 19 and 24°C. The remaining pods were threshed using a 'Venables' medic thresher and the seeds recovered and weighed.

Field studies

The seed softening study involved 18 medic lines x 2 depths of placement x 6 times of sampling x 3 replications. Pod lots were placed in light grey, fibreglass flywire envelopes with a 1 mm mesh, similar in colour to the soil surface. A small amount of soil from the site was also placed in each envelope to simulate the surface conditions that pods would encounter at the site. Two envelope sizes were used: 20 by 15 cm for the snail medic pods and 16 by 12.5 cm for the pods of the other medics. This enabled the pods to be placed in a single layer. The envelopes were fastened with stainless steel staples and placed at either the soil surface or buried at a depth of 7–10 cm. The surface envelopes were placed in a shallow depression equal in depth to the thickness of the pods, pinned to the soil surface by a galvanised wire spike 15 cm long and left uncovered. The buried envelopes were placed in a 10 cm deep trench, and covered with soil. The tops of these envelopes were about 7 cm below the soil surface. Medic lines, depths of placement and sampling times were all randomised within each replicate. The envelopes were placed at Warra (the site at which the pods, except the naturalised burr medic, were produced) on 21 March 1994. This was much later than intended owing to wet conditions. As medic seedlings appeared in these treatments they were killed by spraying with glyphosate.

Samples were removed on 7 July 1994, 24 November 1995 and 13 June 1996. The samples taken in July 1994 were stored in a coldroom at 1°C for 6 months before they could be processed. The later samples were processed immediately. A subsample of 100 seeds was carefully removed by hand from the pods in each sample. These were weighed and tested for permeability, as described previously for the initial germination tests. The remaining pods were mechanically threshed and the seeds recovered and weighed. The total number of residual seeds was calculated from the mean weight per seed obtained from the subsample.

The seedling emergence study involved the placement of pod lots of 19 medic lines as free pods at 2 depths (soil surface and 7 cm) with 3 replications on 21 March 1994. The pods at the soil surface were anchored by pressing them into the soil to a depth of about one half of their thickness. Medic seedlings which emerged were counted and removed after each rain. Twenty seedling counts were made between (and including) 20 June 1994 and 13 June 1996. In July 1996, seed of 6 lines (SA 3110 snail, cvv. Cyprus and Jemalong barrel, naturalised and cv. Serena burr and SA 8460 button) was recovered from both the soil surface and depth treatments to compare the numbers of residual seeds with those placed in the flywire envelopes. Soil to a depth of 4 cm was recovered from the surface treatments and to 12 cm from the buried treatments, from which the pods and seed were carefully washed. Seedling emergence counts of the remaining lines were continued into spring 1996, prompted by the observation of a large number of snail medic seedlings in September.

Rainfall and temperature at the soil surface and at a depth of 7 cm, were measured using an ‘Environdata’ automatic weather recording station.

Laboratory studies

Residual hard seeds from the initial tests for viable soft seeds in the original seed populations were subjected to 16 weeks of gradual diurnal temperature fluctuations of 60/15ºC (as described by Taylor 1981) beginning in mid April 1994. Three replicates of a minimum of 175 seeds were placed in manila envelopes in the 60/15ºC chamber. The proportions of soft seeds and of viable soft seeds were then determined by placing the seeds on moist filter paper in petri dishes for 14 days at 20ºC. Latent soft seeds were identified by subjecting the residual hard seeds to 4 diurnal cycles of 35/10ºC (involving linear 8 h rises and 16 h falls in temperature) and re-testing for permeability, as above. Residual hard seeds were subjected to 2 further periods of 24 weeks at 60/15ºC followed, in each instance, by 4 diurnal cycles of 35/10ºC with further testing for permeability after each temperature treatment.

Data analyses

The number of seeds that had softened in the field at each sampling occasion was calculated by subtracting the number of residual hard seeds from estimates of the original number of hard seeds present in each cultivar at the start of the experiment. The number of soft seeds was then expressed as a percentage of the original hard seed number. These data were analysed using split plot analyses of variance, with and without arcsine transformation [arcsine$\sqrt{(p/100)}$ where p is percentage seed softened]. Since the non-transformed data did not deviate markedly from normality, and since the arcsine transformation did not improve that, the differences presented in Figures 2 and 4, and Tables 3 and 4 are based on the analysis of non-transformed data.

Results

Original seed populations

Rainfall at Warra during the growing season in the seed production year (1993) was sporadic and below average (Table 1). There was excellent plant establishment after rain in May, and above-average rainfall in July and September maintained good plant growth during winter and early spring. Despite less than average rainfall in October and November seed yield was high in all lines except Kelson snail and Paraponto gama medics (Table 2). Flowering times were not recorded but some indication of the relative flowering times can be obtained for some of the lines that were grown at Roma (26º33'S, 148º46'E; 596 mm average annual rainfall with 36% falling between May and October; elevation 315 m) from a 20 May planting in 1994 (B. A. Robertson unpublished data) (Table 2). There is no obvious explanation for the relatively poor seed production from cv. Kelson, when compared with SA 3110 which is also a late flowering snail medic.

Numbers of seeds per pod ranged from 1.5 in Paraponto gama medic (which goes some way towards explaining its relatively poor seed production) to 12.6 in the button medic (Table 2). Mean weight per seed ranged from 2.24 mg in the strand medic to 17.66 mg in SA 1868 snail medic. The initial proportion of soft viable seeds ranged from 0.5% in naturalised burr medic to 7.4% in Cyprus barrel medic, and averaged 3.0% for all lines.

Table 1. Monthly and long-term (102 years) average monthly rainfall (mm) at Warra during the growing season

Month	1993	Average
April	0	41
May	25.8	37
June	14.2	40
July	93.4	41
August	0.2	30
September	53.5	34
October	35.8	57
November	26.6	67
Total	249.5	347

Table 2. Details of relative flowering times and seeds used in the experiment

Days to flowering is the number of days to flowering from a 20 May sowing at Roma in 1994 (mean of 8 replicates) (B. A. Robertson unpublished data)

Line	Days to flowering	Seed yield (kg/ha)	No. of seeds per pod	Seed weight (mg/seed)	No. of hard seeds per pod lot	Initial soft seeds (%)
Snail medic						
Sava	74 ± 1.6	1326	5.02	15.14	502	1.2
SA 1868	84 ± 1.7	979	4.85	17.66	485	1.7
Kelson	103 ± 1.9[A]	158	5.10	15.02	510	2.2
SA 3110	109 ± 1.9[A]	1238	5.37	16.63	537	5.3
Barrel medic						
Caliph	75 ± 1.6	868	6.12	3.95	612	1.3
Cyprus	81 ± 1.7	972	6.60	3.97	660	7.4
Parabinga	94 ± 1.8	1065	7.95	4.03	795	3.8
Jemalong	103 ± 1.9	569	8.85	2.89	885	3.8
Z 914	n.a.	818	9.05	3.28	905	1.2
Sephi	123 ± 1.9	997	7.03	4.47	703	4.7
Mogul	n.a.	826	6.22	3.54	622	4.2
Paraggio	128 ± 1.9	925	7.11	3.81	711	1.5
Burr medic						
Naturalised	n.a.	n.a.	4.82	2.32	482	0.5
Serena	n.a.	864	4.32	2.70	432	3.2
Santiago	82 ± 1.7	1011	5.08	2.98	508	2.3
Circle Valley	94 ± 1.8	612	4.32	2.77	432	1.8
Button medic						
SA 8460	81 ± 1.7	1288	12.60	3.91	1260	4.7
Strand medic						
Harbinger AR	n.a.	785	4.92	2.24	492	1.8
Gama medic						
Paraponto	n.a.	305	1.54	7.62	154	4.0
s.e.m.	n.a.	n.a.	0.20	0.16	20.2	0.04

[A] SA 3110 flowered earlier than Kelson when sown in March (140/177 days), July (75/85 days) and slightly later when sown in September (97/94 days), but always much later than SA 1868 (80, 63 and 51 days respectively) and Sava (73, 63 and 41 days respectively) at Roma in 1994 (B. A. Robertson unpublished data). n.a., not available.

Seed softening in the field

Rainfall and temperatures recorded at the soil surface and at 7 cm depth during the experimental period are presented in Figure 1. The winters of 1994 and 1995 were much drier than average and the mean soil surface minimum temperatures were low, reflecting the occurrence of frequent frosts. At the same time the mean monthly winter maximum temperatures were rarely below 30°C, reflecting warm sunny days, conditions that characterise the subtropical winter environment. Mean monthly summer surface temperatures were not exceptionally high and, in each of 1994, 1995 and 1996, were in inverse proportion to rainfall and the radiation levels experienced in cloudy conditions. These are conditions that characterise the subtropical summer environment.

Patterns of annual seed softening for each of the medic lines, calculated from the July 1994, November 1995 and June 1996 sampling times are shown in Figure 2. For the first sampling time, seed softening was calculated from the total residual seed numbers rather than from the numbers of residual hard seeds, as the storage of these samples at 1ºC before processing appeared, in itself, to cause substantial seed softening. Seed softening from the last 2 sampling times was based on the proportions of hard seeds present in the residual seeds, of which up to about 10% were found to be soft in some lines. The proportion varied according to the timing of the most recent germinating rain.

Relatively few seeds of any of the medics softened during the first year, which was not surprising in view of the lateness of the pod placement in the field (21 March 1994). Most seed softening in that year occurred in the burr medics. The proportion of seeds that softened increased considerably in all lines in the second year, with large differences in softening both between and within species. The total soft seeds after 2 years ranged from 15% in the button medic to 99.5%

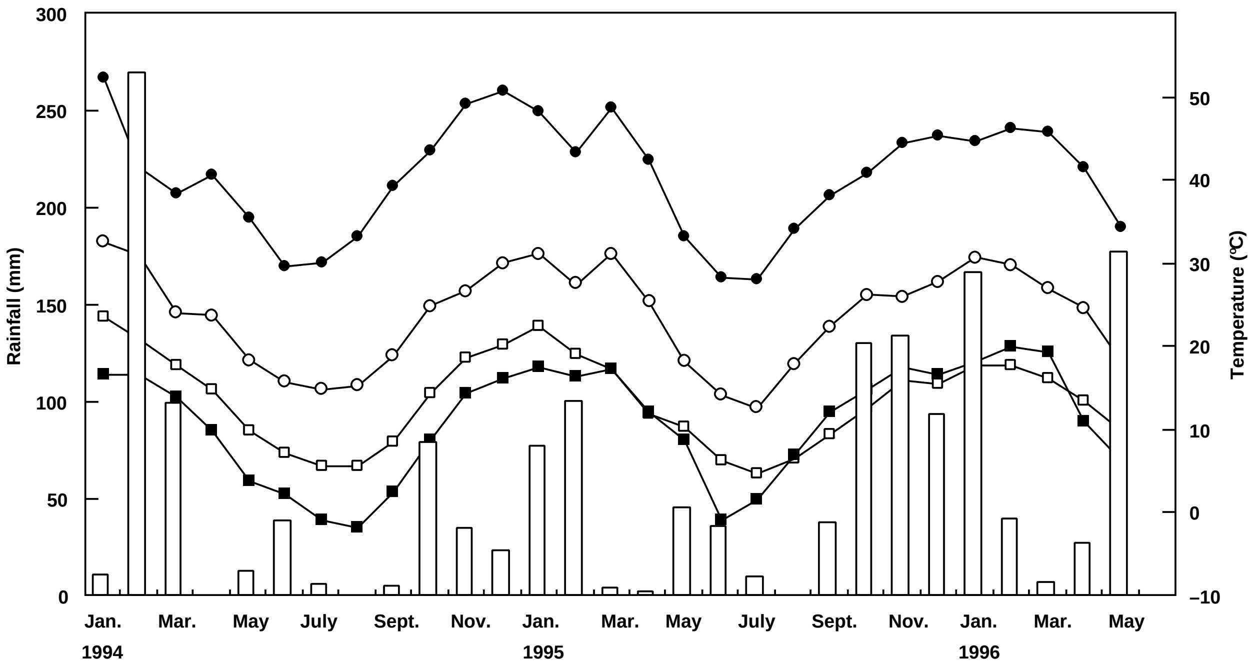

Figure 1. Mean monthly maximum (○, ●) and minimum (□, ■) soil temperatures at the soil surface (solid symbols) and at a depth of 7 cm (open symbols), together with monthly rainfall (bars) at Warra.

in Paraponto. With only a few exceptions, the ranking of lines for the proportions of seeds that softened was maintained into the third year. The proportion of seeds that had softened by the third year was only 26% in the button medic.

The rate of seed softening was reduced by burial in all lines, except for the button medic which was unaffected by burial (Fig. 2). The rate of softening of the buried seeds was generally about half to two-thirds that of seeds which remained at the soil surface.

Seedling emergence

The proportions of the original numbers of hard seeds that produced seedlings between January and February, April and July, and August and December in each year are presented in Figure 3. No summer emergence was possible in 1994 as the pods were not placed in the field until March. Likewise, in 1996, when the numbers counted were low, the experiment was formally terminated before any seedlings emerged in spring. However, further counts, prompted by the observation of a large number of snail medic seedlings in September 1996, accounted for an additional 2.7% of Sava, 4.7% of SA 1868 and 6.5% of Kelson placed at the soil surface, and 18.7, 13.6 and 14.6%, respectively, of those lines placed at depth. There were no data for SA 3110 as seed of that line had been excavated in July as described previously.

Emergence from surface pods. All seedlings that emerged in 1994 did so in June, with the exception of a small number of seedlings from all the snail medics which emerged following rain in October. In 1995, rains in January (Fig. 1) produced considerable numbers of barrel medic seedlings, some snail medics and relatively few of the other species (Fig. 3). Further seedlings of all lines emerged in June and July. Two lots of seedlings emerged in November, most noticeably from the snail medics and, to a lesser extent, from some of the barrel medics. Fewer seedlings of all lines emerged in the summer and autumn of 1996 than in 1995. While a few barrel medic seedlings emerged in January most seedlings of all lines emerged in May. The total recovery of seedlings to June 1996 averaged 25% of the seed of all lines which softened in the flywire envelopes, and ranged from 11% in Harbinger AR, through 14% in the button medic, 20% in the burr medics, 23% in the gama medic, 28% in the snail medics to 29% in the barrel medics.

Emergence from buried pods. Seedling emergence in 1994 was virtually confined to the snail medics, which all produced higher seedling numbers than were obtained from the surface pods. Again, some of these seedlings emerged following rain in October. In 1995, Paraponto and most of the snail medics produced more seedlings from the buried pods than were obtained from the surface pods. A high proportion of these seedlings

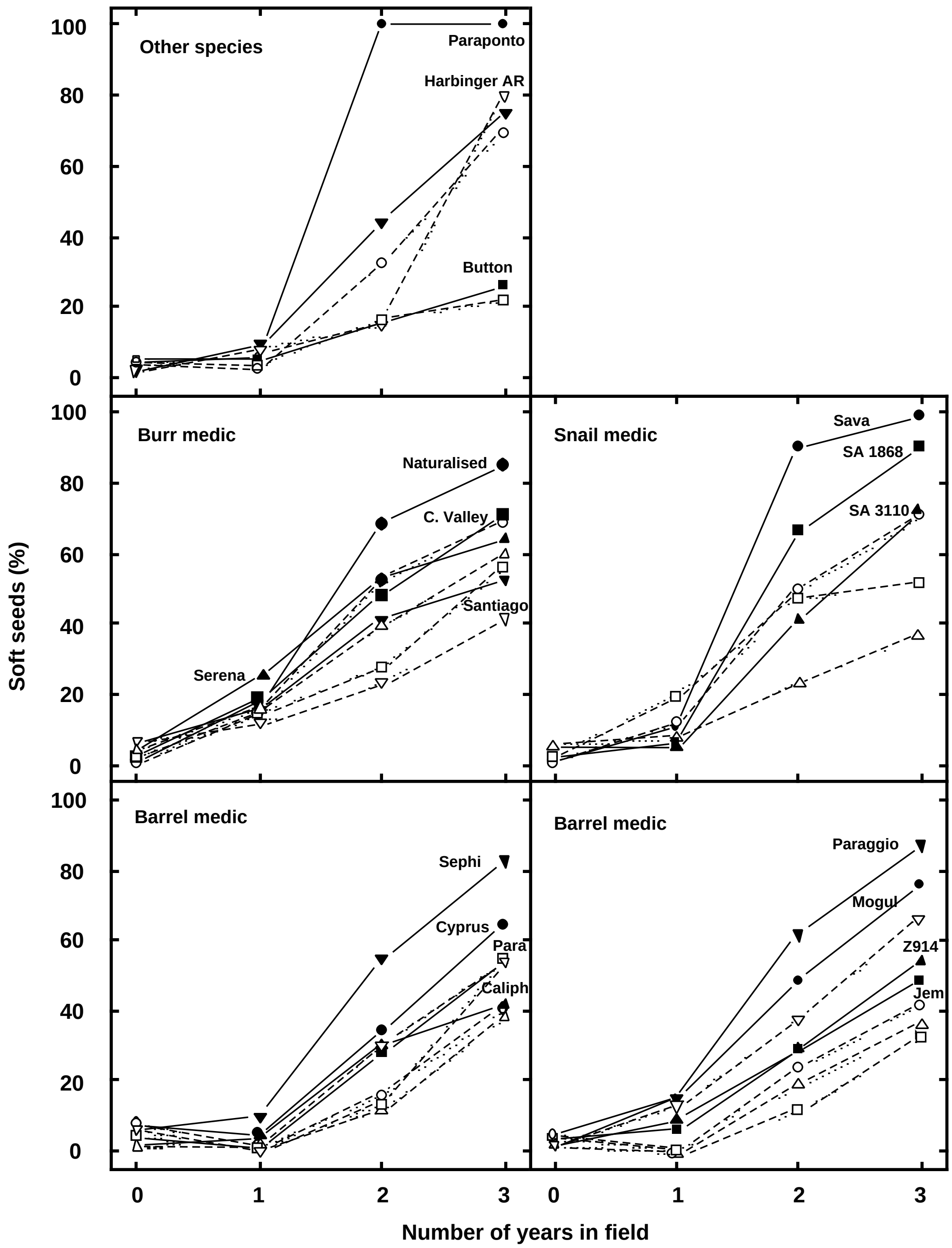

Figure 2. Seed softening in 18 lines of annual medics over 3 years at the soil surface (●, ■, ▲, ▼) and at a depth of 7 cm (○, □, △, ∇). l.s.d. (P = 0.05) between lines: year 1, 7.1; year 2, 12.4; year 3, 11.9. l.s.d. (P = 0.05) between depths: year 1, 8.1; year 2, 12.8; year 3, 19.3.

emerged in autumn, with fewer seedlings emerging in summer. Seedling numbers from all other lines that emerged from depth in 1995 were generally less than those obtained from the surface pods and there were far fewer summer seedlings. Few seedlings of any of the medic lines emerged in 1996. The total recovery of soft seeds as seedlings to June 1996 averaged 22% for all lines, and ranged from 3% in Harbinger AR through 4%

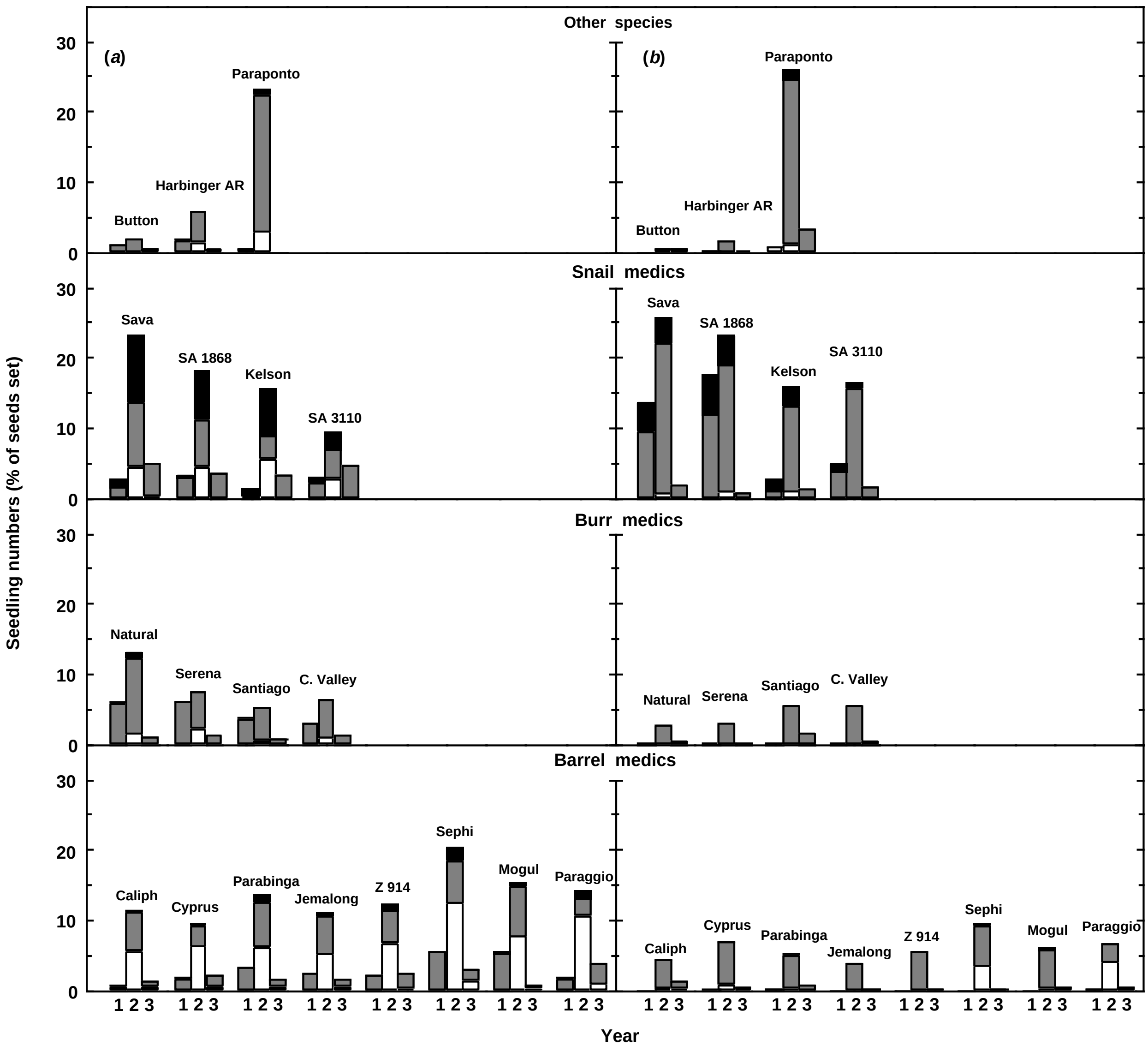

Figure 3. Seasonal patterns of seedling emergence of 19 medic lines over 3 years (1, 1994; 2, 1995; 3, 1996) at Warra. (*a*) Soil surface pods; (*b*) buried pods. Open bars, January–February; shaded bars, March–July; solid bars, August–December.

in the button medic, 10% in the burr medics, 15% in the barrel medics, 43% in the gama medic to 68% in the snail medics.

The number of residual seeds recovered from the soil surface at the end of the experiment was much lower from the free pods than from the pods enclosed within the envelopes ($P<0.01$ for all lines except SA 3110 where $P<0.05$) (Table 3). Residual seeds recovered from free pods that were buried were not significantly different from those recovered following placement in envelopes at that depth, except for SA 8460 and Cyprus which were lower ($P<0.01$).

Seed softening in the laboratory

The progress of seed softening in the laboratory is shown in Figure 4, both before and after the treatment with 4 cycles of 35/10°C at each treatment interval at 60/15°C. The 35/10°C treatment had a marked effect on seed softening in all the snail and burr medics, but produced little or no further softening in any of the other medics.

More seeds of all medics softened during the first 16 weeks of laboratory treatment than did so during the first year in the field (which did not commence until March in that year). Although a trend was beginning to

Table 3. Seed recovery from free pods and envelopes, expressed as a percentage of original seed numbers, in selected lines at the end of the experiment

Treatment	Pods in flywire envelopes		Free pods	
	Surface	Buried	Surface	Buried
Snail medic				
SA 3110	40.1	64.1	31.2	58.6
Burr medic				
Naturalised	16.8	31.9	2.6	30.3
Serena	37.3	41.0	7.6	37.3
Barrel medic				
Cyprus	37.2	64.4	17.8	50.1
Jemalong	53.0	69.3	23.8	62.0
Button medic				
SA 8460	74.5	78.5	22.2	65.5
For all comparisons:				
l.s.d. (P = 0.05) = 8.68				
l.s.d. (P = 0.01) = 11.58				

emerge, there was no correlation between the field and laboratory treatments in this instance (Fig. 5*a*). On the other hand seed softening in the second and third years in the field was highly correlated (P<0.001) with the second and third treatment intervals in the laboratory (Fig. 5*b* and *c*). Laboratory softening overestimated field softening in most of the barrel medics in the second and third years and underestimated field softening in the other medics. It has since been shown that these underestimations in the snail and burr medics have been overcome by subjecting the seeds to additional cycles of the 35/10°C treatment. This occurred after the residual hard seeds were subjected to another 24 weeks at 60/15°C (making a total of 88 weeks) followed by 4 diurnal cycles at 35/10°C, then 2 additional periods, each of 4 cycles, of the 35/10°C treatment (Table 4). The results of this additional laboratory treatment are not shown in Figure 4 as there are no comparable field data. The 2 additional treatments at 35/10°C more than doubled the numbers of soft seeds of the snail and burr medics that were obtained at this time after the standard 4 cycle treatment at 35/10°C, except for cv. Sava in which a large proportion of seed had already softened.

Discussion

Extrapolation from the present data to other environments and other growing seasons in the same environment should be approached with caution. There is ample evidence that other patterns of seed softening and seedling emergence may be obtained from seeds of specified lines produced in other seasons, either at other sites or in other years at the same site (e.g. Taylor and Ewing 1992; Taylor 1996*a*). Additionally, the late placement of seed in the field in March 1994 owing to rain, after laboratory storage in diurnally fluctuating temperatures of 24/19°C, would have affected the proportion of soft seeds measured in July 1994 (Fig. 2). However, the close correlations of field and laboratory soft seeds after 2 and 3 years in the field (Fig. 5) give credibility to the ranking of lines for patterns of seed softening over time. Thus, the results provide some indication of what may be expected in this summer rainfall environment, and of the ranking between lines.

Seed softening between years

A high level of initial protection against germination, an essential attribute for the persistence of winter annual legumes in a summer rainfall environment, was afforded the original seed populations with >90% of the original seeds of all lines sampled in November 1993 being hard. The subsequent rates of softening of these seeds in the first year of the field experiment were unrealistically low as the high temperatures of summer, which cause the preconditioning stage of seed softening (if not the complete softening process), were not experienced due to the late placement of the medic pods. The rates of seed softening in subsequent years were similar to those described in mediterranean environments in southern Australia for those barrel and burr medic lines (cvv. Cyprus, Serena, Santiago and Circle Valley) for which long-term field softening data have been described (Taylor and Ewing 1988, 1992, 1996; Taylor 1996*a*). Likewise, the effect of burial in reducing the rate of seed softening was similar in magnitude to that described by Taylor and Ewing (1988) for cvv. Cyprus and Serena. This similar seed softening behaviour in these 2 contrasting environments occurred despite summer soil temperatures averaging about 10°C lower in the summer rainfall environment, presumably as a consequence of the combined effects of soil that was more frequently moist and a greater cloud cover. Soil temperatures in winter, on the other hand, averaged about 5°C higher in the Queensland environment.

It is noteworthy that seed softening in the earliest flowering snail medics, Sava and SA 1868, was more rapid than in the later flowering lines, SA 3110 and Kelson. This contrasts with the barrel and burr medic cultivars in which seed softening in the later flowering lines, for example Paraggio and Sephi barrel medics, occurred more readily. Similarly, Caliph barrel medic, which was derived from Cyprus, was earlier to flower and slower to soften than Cyprus.

Our results indicate that there is a wide range of seed softening patterns in the medic cultivars that are used successfully in farming systems in the subtropics. The desirability of the pattern of softening depends to a large extent on the farming system used and the reliability of seed production between years. The rotation system most commonly used in southern Queensland is flexible and involves 4–10 years of grass–medic pasture followed by

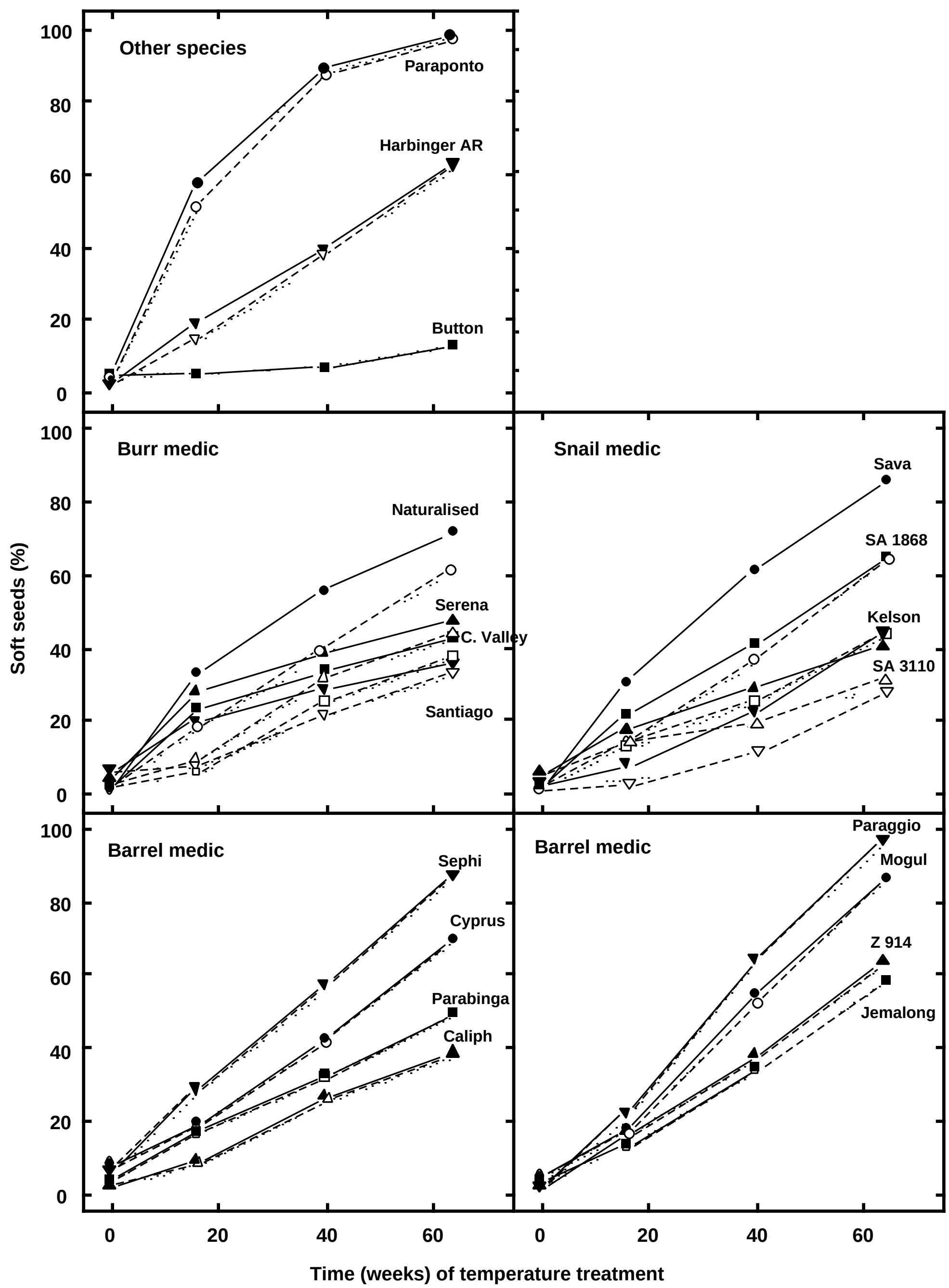

Figure 4. Softening of seeds of 19 medic lines over 16, 40 and 64 weeks of laboratory treatment at 60/15ºC (open symbols) followed, after each treatment interval, by 4 diurnal cycles of 35/10ºC (solid symbols). l.s.d. (P = 0.05): between lines, 7.5; between times, 6.0.

an extended period of cropping, usually at least 6 years, with the medic being resown after the cropping phase. The main requirement for hard seed longevity (i.e. pasture persistence) in such a system is for the development of a sufficient seed bank to enable the medic to re-establish within the pasture after years in which few, if any, seeds are produced. In the subtropics, as in southern Australia, early flowering lines are more

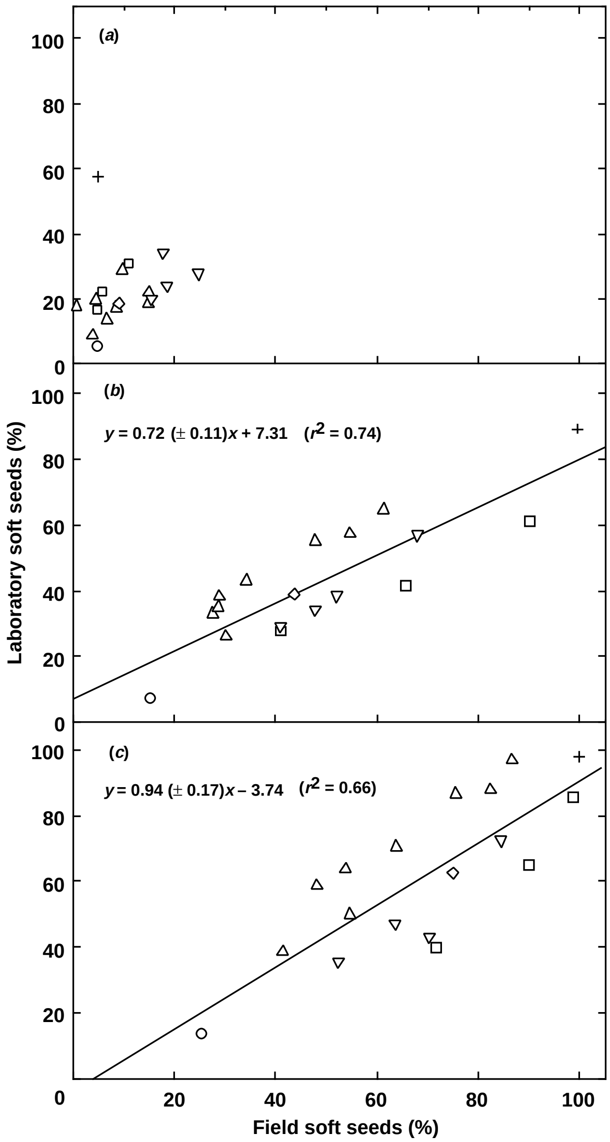

Figure 5. Relationship between percentage seed softening at the soil surface in the field after (*a*) 1, (*b*) 2 and (*c*) 3 years, and seed softening in the corresponding laboratory treatments. Standard deviations of the regression coefficients are shown in parentheses. □, snail medic; △, barrel medic; ▽, burr medic; ○, button medic; ◇, strand medic; +, gama medic.

Table 4. Total seed softened (percentage of original seed numbers) after three separate treatments, each of four cycles of 35/10ºC, of seeds that had been subjected to an additional 24 weeks at 60/15ºC (making a total of 88 weeks)

Line	Additional 24 weeks at 60/15ºC	Number of cycles at 35/10ºC 4	8	12
Snail medic				
Sava	87.8	94.5	97.8	98.5
SA 1868	66.0	79.2	85.5	91.3
Kelson	48.3	55.5	64.0	74.5
SA 3110	42.0	49.2	56.8	64.7
Barrel medic				
Caliph	53.5	53.8	53.8	53.8
Cyprus	88.0	88.0	88.2	88.2
Parabinga	67.6	67.8	67.8	68.0
Jemalong	73.7	73.8	74.0	74.2
Z 914	77.8	78.0	78.0	78.0
Sephi	97.3	97.3	97.3	97.3
Mogul	97.9	97.8	97.8	97.8
Paraggio	100.0	100.0	100.0	100.0
Burr medic				
Naturalised	75.0	81.5	85.0	86.2
Serena	52.5	55.2	57.3	58.3
Santiago	40.3	42.5	43.3	44.3
Circle Valley	47.5	51.0	55.0	57.0
Button medic				
SA 8460	17.5	17.5	17.5	17.5
Strand medic				
Harbinger AR	75.8	76.5	77.3	77.7
Gama medic				
Paraponto	99.0	99.0	99.2	99.2

Between field and laboratory treatments for any medic:
l.s.d. ($P = 0.05$) = 4.4
l.s.d. ($P = 0.01$) = 5.9
Between medics for any field and laboratory treatment:
l.s.d. ($P = 0.05$) = 5.7
l.s.d. ($P = 0.01$) = 7.6

likely to produce seed on a year-by-year basis in marginal environments (N. M. Clarkson and D. L. Lloyd unpublished data). Thus, early flowering lines with slower patterns of seed softening, such as Cyprus barrel medic, have been successful in mixed pastures in such environments. On the other hand, the early flowering Sava snail medic has rarely been successful in mixed pastures. Although adaptation is complex, it is possible that the rapid seed softening characteristic of this line, coupled with its late regeneration after autumn softening, could contribute to its relative lack of success. Lines that regenerate late into mixed grass–medic pasture are likely to encounter a dry soil profile and a lower probability of substantial follow-up rain (Clewett *et al.* 1994). Similarly, the seed softening pattern in Paraponto expressed in the present experiment may be too rapid, and its seed production capacity too low, for its long-term persistence in the subtropics. However, the rate of softening in button medic may be excessively slow from the point of view of a rapid build up of sward density in the early years of the pasture phase, although this may be compensated by its ability to produce very large numbers of seed (Table 2). The fate of medic seeds that are buried by tillage in crop years is largely irrelevant in such long-term cropping systems as few seeds of most of the medic lines would survive the cropping phase.

In those farming systems in southern Queensland which involve shorter pasture and cropping phases, self-regeneration of medic after the cropping phase is desirable. In these systems hard seed longevity becomes more important, as is the case in southern Australia. Nevertheless, the relatively soft-seeded Sava snail medic is successfully used as a mono-specific pasture in systems in which soil water is conserved by fallowing, by implementing a pasture phase frequency of 1 in 3 (for example, as outlined by Lloyd *et al*. 1992). The longevity of seed banks in these situations depends on patterns of seed softening between years, which are influenced by the interaction between a number of management and environmental factors. Some of these interactions have been explored in simulations involving burr medic in Western Australia using the seed dynamics model of Taylor and Downes (1995).

Seedling emergence patterns within years

The timing of seedling emergence presents a useful indication of the patterns of seed softening that can be obtained within years, providing that rainfall has been conducive to germination and seedling emergence.

There is no clearly defined optimum time of year for seeds of winter growing annuals to soften and germinate in summer rainfall environments. Seasonal conditions can promote useful seedling emergence any time between January and July. However, germination before March is likely to result in seed wastage as there are relatively few years in which these seedlings survive to produce productive plants. Although seed losses in January and February are likely to be highest from the barrel medics (Fig. 3), the apparent disadvantage to that species is offset by further seeds softening and germinating after February. In summer rainfall environments where medic is used successfully, there is a high probability of significant rainfall events occurring in March and April (Clewett *et al*. 1994) which can promote the development of seedlings from these early germinations, even in competitive grass–medic pastures where competition for water and light requires careful control by grazing. The ‘summer’ seedling emergence pattern of barrel medics, associated with the high probability of early autumn rainfall, helps explain the success of barrel medics in mixed pastures in the subtropics. Snail medics, which soften their seed and regenerate later than the barrel medics, are successful in short-phase farming systems as noted previously. However, germination that occurs between August and December, which was particularly marked in the snail medics (as has also been reported by Crawford and Nankivell 1989), is a source of loss to their seed reserve.

The much lower numbers of seedlings (Fig. 3) obtained in all treatments in the third year (1996), compared with the second year (1995), are not readily explained. Similar numbers of seeds softened in most lines in both years and rainfall appears to have been more favourable for seedling establishment in 1996. It is likely that the heavy rains in January and May 1996 (Fig. 1) would have washed some of the surface pods away, but this explanation does not hold for the buried pods which also produced fewer seedlings. It is possible that the very wet conditions experienced in 1996 may have resulted in losses of germinated seeds from damping-off, a common occurrence during very wet conditions in the subtropics and a factor that may have reduced the recovery of soft seed as seedlings from all germinations, particularly during the warmer months. It is unlikely that the death of seeds would have contributed significantly to the lower seedling emergence as there is ample evidence that hard seeds that have been in the field for more than 3 years remain viable (Taylor and Ewing 1996).

The higher proportions of soft seeds of the snail and gama medics that produced seedlings from the buried compared with the surface pods probably reflect the more favourable moisture conditions experienced by seeds that germinate at depth, despite their slower rate of seed softening. This apparent advantage appears to have been offset in the smaller-seeded medics by the limitations imposed by seed size on their lesser physical ability to emerge from depth.

The lower recovery of seeds at the end of the experiment from the free pods compared with those in envelopes, at the soil surface (Table 3), was attributable to observed wash, and perhaps to an unmeasurable loss of small-podded species down cracks which developed in the soil in dry times.

Laboratory simulation of seed softening

The seed softening behaviour in the laboratory treatments is consistent with the 2-stage conceptual model used by Taylor (1981, 1996*a*) to describe the seed softening process in subterranean clover and annual medics. While the first or preconditioning stage of softening (which results in latent soft seeds) takes place with either constant or alternating temperatures, the final stage of softening can occur within a few appropriate diurnal temperature fluctuations having parameters which may be specific for particular genotypes (Taylor 1996*b*). Further evidence for this specificity has been obtained in the present study. While the requirements for the final stage of seed softening in the barrel, button, strand and gama medic lines were largely satisfied by the 60/15°C laboratory treatment, the additional 35/10°C treatment was necessary for the snail and burr medic lines (Fig. 4). This requirement for lower temperatures for the final stage of softening was reflected in the relatively greater number of seedlings of the snail and burr medic lines which emerged in the autumn and, in the case of snail medic, in the spring (Fig. 3).

It is notable that seed softening took place in the field even though soil temperatures of 60ºC were rarely attained at the soil surface and were never attained at a depth of 7 cm. This behaviour is consistent with the data of Quinlivan (1968) which showed that seed softening in some medics did not increase in laboratory treatments at temperatures >50ºC.

Although the laboratory simulation was effective in ranking the medic lines for field softening in the second and third summers (Fig. 5), the technique cannot be advocated for general use in medic evaluation programs involving previously untested lines as it has been shown by Taylor (1996*b*) that some lines of burr medic do not respond to this treatment. Until this limitation can be overcome the evaluation of the seed softening characteristics of medic genotypes can only be made with any confidence in the field.

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