Ecological and agronomic studies on *Chamaecrista rotundifolia* cv. Wynn related to modelling of persistence

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Abstract

This paper reports the results of a series of studies on aspects of the persistence of the tropical pasture legume *Chamaecrista rotundifolia* (round-leafed cassia) cv. Wynn. The results are contributing to formulating a quantitative model of cassia persistence.

The main study, at Samford in coastal south-east Queensland, was on the fate of cassia seed broadcast into cassia-free pastures in 1990 and 1991 to simulate seed set in an established cassia pasture. The study was carried out on a heavily defoliated and a lightly defoliated site. Seedling emergence and soil seed reserves were monitored for 3 (1991 sowing) or 4 (1990 sowing) years. There was a much higher recovery of viable oversown seed as seedlings or soil seed in the second (50%) than in the first (13%) sowing. Approximately 40% of the second sowing was recovered as soil seed after 3 years compared with 6% from the first sowing. The difference is attributed to poorer quality of the 1990 seed sample. The run-down of seed banks was similar under both defoliation intensities, but there was greater loss of seed and fewer seeds recovered as seedlings on the lightly defoliated site.

Other studies showed that: in early autumn at Samford, a cassia flower bud could develop into a mature pod and dehisce in 39 days, but a longer time was required in late autumn; there was a linear relationship between herbage yield and seed set but, for the same cassia presentation yield, ungrazed pasture set more seed than grazed pasture; seed quality of cassia varied between sites and years of collection, with quality lower in years with wet conditions during pod set; there was little predation of cassia seed placed on the soil surface at Samford, whereas, at Narayen Research Station in subcoastal southern Queensland, there was considerable predation during the hotter months; and hard seed breakdown of cassia occurred at lower temperatures than is the case for some *Stylosanthes* spp. Equations were developed which relate rooting depth of cassia seedlings and plants, and age of plants, to taproot diameter. The implications of these measurements for management of cassia pastures and for development of a model of cassia persistence are discussed.

Further quantification of factors affecting seed set and the fate of seed will be required before a model of cassia persistence can be developed that will be reliably applicable to all time/site situations.

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Introduction

Round-leafed cassia (*Chamaecrista rotundifolia*) cv. Wynn, hereafter referred to as cassia, was released as a pasture legume in 1983. It is adapted to the 700–1200 mm rainfall zone of subtropical Australia (Strickland *et al*. 1985; Partridge and Wright 1992; Jones *et al*. 1993) and is showing promise in other countries, *e.g.* China (Michalk and Huang Zhi-kai 1994) and Nigeria (Peters *et al*. 1994).

A conceptual model of cassia persistence in relation to climate and grazing pressure (Jones *et al*. 1993) is being developed into a quantitative model. The model is sufficiently generic in structure to allow modification to describe the persistence of other herbaceous tropical legumes, such as *Stylosanthes scabra*. As cassia is a short-lived perennial, relying on seed set and seedling recruitment for long-term persistence (Jones and Bunch 1995), the model is based primarily on functions describing demographic attributes, such as emergence of seedlings from seed banks. The functions have been derived mainly from measurements made in a grazing trial in subcoastal, subtropical Queensland (Jones *et al*. 1990; Anon.

1993), and one in coastal, subtropical Queensland (Jones and Bunch 1995).

However, other data relevant to development of the model, reported in this paper, were obtained from a series of smaller field-based studies on seed set (Studies 1 and 2), seed quality (Study 3), seed predation (Study 4), hard seed breakdown and longevity in seed banks (Studies 5 and 6) and relationships between rooting depth, taproot size and plant age (Study 7). Results from laboratory studies on the effect of temperature on germination and hard seed breakdown will be reported elsewhere.

Study 1 — Time from flower opening to pod dehiscence

Cassia flowers from mid-summer (January) to late autumn (May) in coastal, southern Queensland, such as Samford Research Station (27° 22'S, 152° 53'E; average annual rainfall 1105 mm). In subcoastal, southern Queensland, such as Narayen Research Station (25° 41'S, 150° 52' E; AAR 715 mm), it can also flower in late spring-early summer (November–December), depending on rainfall.

Methods

The time taken for a cassia pod to develop from a green bud was observed during March–June 1988. The experimental site was at Samford Research Station, adjacent to the grazing trial on cassia described by Jones and Bunch (1995). Forty-nine green buds, flowers or pods were marked in late March and were monitored through to pod dehiscence, recognising some 8 developmental stages (Table 1). The main stems were identified by circling them with a pigeon ring. Individual buds, flowers or pods on that stem were identified by writing a number on a small area of white "correction fluid" on the leaf arising from the same node as the peduncle.

Results and discussion

The mean, minimum and maximum number of days taken to pass through each stage and the cumulative mean number of days from green bud to dehisced pod are given in Table 1. Monthly maximum and minimum temperatures during the experimental period were 25.0 and 16.2° C (April), 23.7 and 12.5° C (May) and 21.6 and 9.6° C (June). The minimum time to pass through any stage was usually recorded in the warmer conditions early in the measurement period and the maximum time in the cooler conditions at the end. Thus, the cumulative time from green buds to pod dehiscence during warm conditions could be as short as 39 days, the accumulated minimum time periods for the various stages. Although the large variation recorded in this limited dataset made it impossible to derive any realistic relationship between temperature and time to pass through each stage, it is probable that this time would be even shorter under hotter conditions than were experienced. Pods which developed to the full length and swollen green stage after mid-May usually did not form sound seed, and data from these pods were not included in Table 1. The elongation rate of developing green pods was *ca.*3 mm per day and the mean pod length was 32 mm.

Table 1. Mean, minimum and maximum time taken for cassia to pass through different flowering and seeding stages ending in pod dehiscence, with the cumulative mean number of days from green buds.

Stages of development	Mean	Range	Cumulative
		(days)	
Green bud to yellow bud	1.8	1–3	2
Yellow bud to open flower	1.6	1–2	3
Open flower to pod appearance	1.0	1	4
Pod appearance to full length green	11.0	9–14	15
Full length to swollen green pod	24.6	18–28	40
Swollen green to firm black pod	6.4	2–11	46
Firm pod to pod with loose seed	4.4	2–8	51
Pod with loose seed to dehiscence	20.0	5–61	71

Study 2 — Seed set of cassia in relation to herbage yield

Seed set of cassia is related to cassia herbage yield as the single inflorescences are borne in the leaf axils. To describe the quantitative relationship between yield and seed set, preliminary measurements of both attributes were made in grazed and ungrazed swards.

Methods

A set of 5 quadrats of 1 m^2 were set up in an ungrazed cassia-grass pasture at Samford on March 4, 1992. The set covered a wide range of cassia yields, with Quadrat 1 having the lowest yield and Quadrat 5 the highest. The same procedure was repeated on a continuously grazed cassia pasture.

From March 4 to June 16, the 10 quadrats were inspected twice a week and mature black pods were removed. These measurements were started before there had been any pod dehiscence during that growing season. The pods collected on each day were allowed to dehisce and the numbers of sound and unsound (shrivelled, malformed or prematurely germinated) seeds were counted. Sound seed was full size, but could be either hard, soft and viable, or soft and dead. Thus, there was a record of the number of pods and number of seeds produced in each quadrat over a 3.5-month period. On June 16, after seeding had ended, the quadrats were cut and sorted into species, and their dry matter yields were measured.

Results and discussion

The cumulative numbers of sound and unsound seeds collected from each quadrat over the 3.5-month period are listed in Table 2, together with the final cassia presentation yield. The peak seed yield in the ungrazed pasture was about 8000 seeds/m^2. Cassia dry matter and seed yields were lower in the grazed pasture. In the grazed pasture, 82.5% of seed was sound, similar to that in the ungrazed pasture (82.2%). The mean number of sound seeds/pod was 8.9 for the ungrazed pasture and 7.2 for the grazed pasture.

There was a highly correlated linear relationship between final herbage yield (X, kg/ha) and cumulative seed set (Y, number/m^2) for 4 of the quadrats ($Y = 236 + 1.36X$, $r^2 = 0.92$) in the grazed pasture, but in the remaining quadrat (Number 2 in Table 2) seed set was approximately 3 times higher than would be predicted from this relationship. Presumably this quadrat was not grazed during autumn — the period of seeding. Thus, its seed yield reflected that of a quadrat of similar herbage yield in the ungrazed pasture where there was also a highly correlated linear relationship between final cassia yield (X) and cumulative sound seed set (Y): $Y = 751 + 3.21X$, $r^2 = 0.96$. Seed set per unit of biomass in the ungrazed pasture was 2–3 times that in the grazed pasture.

Table 2. Seeding of cassia in grazed and ungrazed pastures: total sound and unsound seed per m^2; number of sound seeds per pod; and measured cassia herbage yields in June.

Pasture & quadrat	Sound seed	Unsound seed	Seeds/pod	Herbage yields
	(No/m^2)	(No/m^2)		(kg/ha)
Grazed				
1	333	55	5.5	202
2	1917	275	7.9	350
3	910	205	6.6	630
4	820	228	7.1	456
5	1874	500	8.8	1316
Ungrazed				
1	902	237	8.0	216
2	1659	386	8.5	415
3	5835	1189	9.5	2226
4	6183	884	9.1	1611
5	7849	1964	9.2	2811

Using these equations, a quadrat with a cassia yield of 2000 kg/ha would have a predicted seed set of 2950 seeds/m^2 in the grazed pasture, whereas in the ungrazed pasture, the same dry matter yield would be predicted to have a seed set of 7200 seeds/m^2.

The potential for seed input estimated from these measurements is within the range of increases in seed reserves from mid-autumn (pre-seeding) to winter (post-seeding) measured in the Samford grazing study described by Jones and Bunch (1995). These increases ranged from 9100 seeds/m^2 in a year with good cassia growth to 1800/m^2 in a low rainfall year with poorer growth.

Reduction of seed production with grazing is probably due to cattle grazing cassia more readily when it is flowering and seeding in autumn. This has been documented through studies on dietary selection in cassia pastures

(Clements *et al*. 1996) and through measurements of cassia seeds in the faeces of grazing cattle (Jones and Bunch 1995; Clements *et al*. 1996). Given opportunity for selective grazing, stock usually avoid cassia in summer (Clements *et al.* 1996) resulting in minimum opportunity for seed set to be reduced by grazing of axillary buds prior to the onset of flowering.

Clearly the complex interactions between herbage yield, grazing pressure and seed set need further clarification, and studies to achieve this are in progress (C.K. McDonald).

Study 3 — Characteristics of seed collected from cassia pods in pastures

Variation in the percentage of hard seed has obvious implications for longevity of seed banks. The objective of this study was to assess the quality of cassia seed in pods collected from grazed pastures. In particular, we were interested in the variation in the proportions of sound and unsound seed in the pods and in the hard seed percentage of the sound seed. This variation was then related to weekly rainfall, number of rainy days and relative humidity for each week in the 3-week period of final pod development and ripening prior to collection.

Methods

Dry and black pods of cassia were collected in autumn (March–May) at both Samford and Narayen Research Stations in 1988, 1989 and 1990. About 40 pods were collected on each occasion. Each collection represented the range of lengths of black pods in the pasture, although they were usually full size. With one exception, pods were collected from above and within the plant canopy to represent the proportion of pods in these positions. Seed was removed from the pods and classed as either sound or unsound, as defined for Study 2.

Where there was sufficient seed, a germination test was run for 21 days at 35°/20°C day/night temperature to determine the percentage germination and the percentage of hard seed in each class of seed in each seed lot. The number of sound seeds per pod was then calculated. The proportion of pods containing holes was also recorded as a measure of insect parasitism of pods.

Results and discussion

On average, 78% of the seed was full size and sound (range 48–97%), 2% (0–10%) was sound but swollen and 20% (3–42%) was unsound (Table 3). The sample with the lowest proportion of sound seed was the only sample that was deliberately collected solely within the pasture canopy rather than on or above the canopy where most pods are sited.

Table 3. Characteristics of cassia pods collected within cassia-grass pastures at Samford (S) and Narayen (N) in 1988, 1989 and 1990: percentage of apparently sound seed in seed collected; the percentage of hard and soft viable seed in this sound seed (the remaining percentage being dead); and average number of sound seeds per pod.

Site/date collected	Sound seed	Characteristics of sound seed		Sound seeds/pod
		Hard	Soft	
	(%)	(%)	(%)	
S 28.3.88	87	54	39	8.9
S 28.4.88 [1]	83	52	22	8.5
S 28.4.88 [2]	89	63	26	8.5
N 12.5.88 [1]	87	62	24	7.6
N 12.5.88 [2]	78	66	26	6.7
N 25.5.88	94	76	19	8.4
S 26.5.88	77	76	17	7.1
N 15.3.89	97	88	8	11.5
S 30.3.89	97	38	59	11.4
S 28.4.89	65	33	43	6.1
S 24.5.89	75	56	33	6.5
S 24.5.89 [3]	48	40	51	3.4
S 20.6.89	68	56	21	5.9
S 29.3.90	58	21	67	5.6
S 23.4.90	65	35	56	7.8
S 1.6.90 [4]	57	55	45	5.4
S 22.4.91 [4]	100	54	45	7.8

[1] and [2] Collections at two sites on the one day.
[3] Black pods collected solely from within the sward canopy.
[4] Seed lots used in Study 6.

On average, the sound seed was 54% hard (range 21–88%) , 34% soft and viable (8–67%) and 12% dead (3–24%). Only 1% of the seed classified as unsound seed was viable and none was hard. Only 1% of pods (range 0–9%) contained holes bored by insects.

Overall, there were higher proportions of hard and sound seed in cassia than in Siratro (*Macroptilium atropurpureum*) in a similar study, also under field conditions at Samford, where there was more soft and unsound seed (Jones and Bunch 1988a). However, the Siratro seed was collected in different years (1973–1985), and usually in June rather than April or May, so the results are not strictly comparable. As for Siratro, hard seed levels were higher when rainfall was lower during the period of seed maturation, with a significant negative relationship ($P<0.01$) between hardseededness and rainfall during the last week before seed collection. Argel and Humphreys (1983) also found that hardseededness of *Stylosanthes hamata* was higher under drier conditions.

Study 4 — Predation of cassia seed

Usually, the main seed set of cassia is in mid-late autumn (April–May) although, depending on site and season, seeding has been noted from early summer (December) through to early autumn. Seed predation is known to be a major cause of seed loss in many plant communities, so preliminary studies were carried out to see if cassia seed was removed and, if so, whether predation varied with season.

Methods

The procedure was based on that of Mott and McKeon (1977). Cassia seed was placed on thin 5 × 10 cm masonite sheets. Ten seeds were placed on each sheet and there were 10 sheets at each of 4 sites. There were 2 sites at Narayen; 1 was in a native pasture which was mown once or twice a year, but never grazed, and the other was in a grazed cassia-buffel grass (*Cenchrus ciliaris*) pasture. Sheets in the latter site were protected from cattle by a 2 × 1 m cage with 10 × 10 cm mesh openings. There were 2 sites at Samford adjacent to the sites described later in Study 6. One was heavily grazed and the other lightly grazed. The Samford sites were also protected by 10 × 10 cm mesh.

To avoid seed being washed off the sheets, it was placed out at Narayen on days when there was little likelihood of rain over the next few days. With the greater frequency of rain at Samford, the sheets were sheltered with a small sheet of galvanised iron. This would have reduced radiation and soil temperatures in a small area around the seed. In addition, slug bait was placed around the sheets in the last 2 runs at Samford as it was observed that an occasional seed was inadvertently moved through adhering to slugs and being moved on the slime trail.

Sheets were re-positioned and new lots of seed were placed out at approximately monthly intervals at Narayen from January–August 1992, and again from August 1993–January 1994. At Samford, seed was placed out on 7 occasions from March–June 1990. The seed remaining on the sheets was checked every day for 6 days at Narayen and less regularly but for a longer period at Samford.

Results and discussion

The percentage of seed that remained on the sheets at Narayen on Days 2, 4 and 6 is listed in Table 4. There was a clear difference between seasons. Seed was removed rapidly in summer and, on some occasions, all seed was removed within 2 days. Removal was much slower in winter and early spring.

At Samford, 81% of seed, on average, remained after 4 days on the heavily grazed site and 92% on the lightly grazed area. In 2 runs on the lightly grazed site, placed out in mid-March and mid-April, some two-thirds of the seed was still on the sheets after 30 days. The lower losses at Samford were despite possible losses due to slug activity before bait was placed out.

We have observed that seed fall at Samford is almost always in the March–June period. Based on the limited amount of seed removed in this study, it is unlikely that seed predation will be important at this site.

There is more potential for predation at Narayen during the main seeding period in autumn and particularly following seeding during summer. Losses during winter were much less than in the warmer months, which has been recorded in detailed studies of ant predation of seeds of *Eucalyptus regnans* (Ashton 1979). Theft could also be due to small birds or small animals that could get through the 10 × 10 cm mesh, as well as to ants. There is widespread ant activity on both sites and it is likely that ants were responsible for most, if not all, of the seed removal. However, this preliminary study has not shown whether the seed was merely moved and left on the soil surface or was taken below the soil surface — and if the latter, to what depth. Our observations on the experimental sites have not shown any clumping of cassia seedlings around the entrance to ant nests.

Table 4. The percentage of cassia seed remaining 2, 4 and 6 days (D) after being placed out into a native pasture and a cassia-buffel pasture at Narayen Research Station.

Date	Native pasture			Cassia-buffel		
	D2	D4	D6	D2	D4	D6
			(%)			
Summer						
6.12.93	78	0	0	0	0	0
22.1.92	94	67	0	nm [1]	nm	nm
4.1.94	89	79	14	78	33	0
16.2.92	0	0	0	88	15 [3]	r
Autumn						
1.3.92	0	0	0	87	0	0
6.4.92	88	0	0	87	0	0
25.5.92	98	90	86	100	92	90
Winter						
22.6.92	100	94	93	100	84	82
31.7.92	100	96	94	98	90	86
26.8.92	100	100	r [2]	93	93	r
31.8.93	96	81	77	98	64	25
Spring						
4.10.93	89	73	45	75	40	39
8.11.93	77	60	45	93	34	24

[1] No measurements made at that site on this date.
[2] Measurements ended because of rain.
[3] Measurement from Day 3, prior to rain on Day 4.

Study 5 — Hard seed breakdown of cassia seed in mesh bags

The rate of hard seed breakdown in the field has a large impact on the availability of soft seed for germination (Quinlivan 1971; Mott *et al.* 1981). There is considerable variation between species on their rate of hard seed breakdown but very little is known about the rate for seed of cassia.

Methods

Approximately 200 seeds of Wynn cassia, with a hard seed content of 46%, were placed into each of 24 nylon mesh bags and pegged to the ground on bare soil at Narayen and Samford Research Stations in August 1992. Over a 6-month period at each site, 2 bags were selected at random each month and removed. The remaining ungerminated seed in each bag was counted and tested for hardseededness.

Results and discussion

The hard seed content fell rapidly at both sites. At Narayen, the percentage hard seed remaining over successive months was 24, 20, 13, 6, 3 and 1%, while at Samford, it was 26, 13, 15, 6, 4 and 2%. Using the equation of Mott *et al.* (1981), parameters were derived relating hard seed breakdown to degree days of soil surface temperature:

$$h_1 = h_f + (h_0 - h_f)*\exp^{(-k\Sigma d)}$$

where h_f is the final hard seed content, h_0 is the initial hard seed content, k is a constant, and Σd is the cumulative degree days above a threshold temperature.

With no period without hard seed breakdown, it is not possible to predict accurately a threshold temperature for Wynn, but scrutiny of these data and data from laboratory ovens (C.K. McDonald, unpublished data) suggests that it would be a maximum of 40°C, and may be as low as 30°C. Using these threshold values in the above formula gives:

at 40°C, $h_1 = 1.5 + 44.5*\exp^{(-.00255\Sigma d)}$, $r^2=0.885$

at 30°C, $h_1 = 1.5 + 44.5*\exp^{(-.00103\Sigma d)}$, $r^2=0.930$

Although using 30°C accounted for a higher percentage of the variance, the slope of the line (fitted versus actual) was closer to unity using 40°C as a threshold temperature than the slope using 30°C.

The rapid loss of hard seed in September at Narayen, in this particular seed lot, is in contrast to that found for 4 species of *Stylosanthes* at the same location (Mott *et al*. 1981) where no appreciable hard seed breakdown occurred until November–December. This rapid breakdown can be advantageous in some years. Early (December) seed set, followed by hot dry weather in January can lead to a considerable increase in soft seed in the soil seed bank. Rain in February can then bring about a large germination event (authors, unpublished data), thus giving a sparse stand of cassia the potential to increase from seed set during the same growing season. However, the faster rate of hard seed breakdown, as compared with seed of *Stylosanthes*, means that seed banks will not last as long during prolonged dry periods when there is no seed set but loss of seedlings following isolated rainfall events.

Study 6 — The longevity of cassia seed falling on to the soil surface

In established cassia-grass pastures, most seed is set in mid-late autumn. This seed falls into the sward or on to the soil surface and may become part of the soil seed bank. This study measured the rate of run-down of a soil seed bank and the recovery of seedlings from an input of seed on to pastures that did not contain cassia. It is very difficult to measure run-down of cassia seed banks in an established cassia pasture as new seed is usually dropped on to the soil surface each year.

Methods

Experimental sites were selected within 2 pastures at Samford. Both pastures were free of cassia but had contrasting presentation yields. One was a very heavily grazed pasture on a red podzolic rise, dominated by bahia grass (*Paspalum notatum*), Queensland blue couch (*Digitaria didactyla*) and narrow leaf carpet grass (*Axonopus affinis*). This site was set-stocked from 1990–1994 at 2.0 weaners/ha. The second site, on a more fertile and well drained alluvial soil, was a more productive monospecific sward of bahia grass.

The second site was selected initially as a moderately grazed farm pasture. However, to obtain a more contrasting presentation yield with the heavily grazed site and to reduce variability in yield over the site, it was fenced off in June 1992. Thereafter, it was mown once or twice a year to 6 cm. The cut material was removed from the site. The presentation yield was estimated on each site in late autumn-early winter. Twelve plots of 1 × 0.5 m were pegged in each of the 2 pastures in May 1990. Six, selected at random, were broadcast with cassia seed on June 4, 1990 and the remaining 6 on May 7, 1991. Each seed sample had been collected from dry but undehisced pods during the 2 weeks prior to oversowing. The seed samples were given a preliminary test for viability before sowing and the plots were sown with a weight of seed equivalent to *ca*. 1000 viable seeds/m^2. The exact seeding rates were calculated after germination tests, which ran for 21 days, were completed. The rates were 984 viable seeds/m^2 (55% hard) in 1990 and 1204 viable seeds/m^2 (54% hard) in 1991. These seeding rates are equivalent to *ca*. 40 kg/ha and, being equivalent to 125 pods, each with 8 seeds, per square metre of cassia pasture, they simulated a low-moderate seed set in an established cassia pasture. To ensure even application over the whole 1 × 0.5 m quadrat, the appropriate seed weight was divided into 4 lots and each was broadcast on to one of four 25 × 50 cm sections of the quadrat.

Following the first sowing in 1990, measurements of the soil seed bank were made in July 1991, 1992, 1993 and 1994. Ten cores of 7 cm diameter were sampled to a depth of 5 cm in each quadrat in each year. Sampling in any particular year was confined to one of the four 25 × 50 cm sections and after sampling the holes made from the soil sampling were filled with soil free of cassia seeds. Seed was recovered using the method described by Jones and Bunch (1988b).

Because of the results obtained from the 1990 sowing (outlined later), more frequent measurements of seed reserves were made following the 1991 sowing. One section of 25 × 50 cm was sampled each year, but one-half of this was sampled in July (mid-winter), taking 5 cores per section, and the other half was sampled in the following February (late summer).

The oversown plots from both sowings were checked regularly for seedlings until July 1994. All seedlings were removed, but counts were limited to those 25 × 50 cm sections which had not been disturbed by soil sampling. Thus, for the first 12 months of the first sowing, seedlings from the full 100 × 50 cm were counted, whereas, in the last 12 months, counts were limited to the last 25 × 50 cm undisturbed section.

Results

Rainfall. Monthly rainfall during the experimental period is given in Table 5. There were 2 years of above average rainfall and 2 of well below average rainfall.

Table 5. Seasonal and annual rainfall at Samford for 1990–1994. Values in bold type are below the long-term average.

Year	Summer (D,J,F)	Autumn (M,A,M)	Winter (J,J,A)	Spring (S,O,N)	Total
			(mm)		
1990	447	613	**103**	**120**	1283
1991	**364**	**118**	**100**	**91**	**673**
1992	783	456	**95**	**141**	1475
1993	**196**	**110**	**80**	**205**	**591**
1994	494	365	**52**	**72**	**983**
Long-term average	445	286	150	227	1108

Rainfall during the first 3 months after oversowing (June, July and August) was similar in both years (Table 6). However, the months prior to or during seed collection (April and May) were wetter in 1990.

Table 6. Monthly rainfall for April–August 1990 and 1991, with long-term averages.

Month	1990	1991	Average
		(mm)	
April	180	17	81
May	173	68	66
June	66	74	60
July	25	26	55
August	12	0	32

Viability of oversown seed. The viability of the two seed lots, indicated by superscript [4], is listed in Table 3. Both seed lots used in oversowing had negligible amounts of full size but dead seed. However, the 1990 sample as collected had 43% of shrivelled unsound seed which was not viable. There was negligible unsound seed in the 1991 seed lot. When the seed samples were re-tested in March 1992, after storage under laboratory conditions, the May 1990 lot had 9% viable soft seed, 41% dead seed and 50% hard seed. The May 1991 lot had 26% viable soft seed, 73% hard seed and 1% dead seed. Thus, most of the seed in the 1990 sample which was soft at collection had died, indicating that this soft seed was of poor quality. In contrast, there was negligible death of soft seed in the 1991 sample and approximately half of the seed which was soft just after harvesting had become hard during storage.

Presentation yields of pasture. Averaged over 1991–94, annual pasture yields on the lightly defoliated (LD) site were at least three times those on the heavily defoliated (HD) site (3120 kg *vs* 795 kg/ha). There was negligible litter on the HD site and 3–4000 kg/ha on the LD site.

Recovery as seedlings. Seedling recovery from both sowings on both soil types has been expressed as a percentage of oversown viable seed in Table 7a. Over 94% percent of all the seedlings removed from both sowings emerged in the 6 warmer months (October–March) and less than 6% in the 6 cooler months. The highest seedling strikes within each year were recorded from November to January.

In both sowings, the highest number of seedlings was removed in the first summer after sowing. Thus, in 1991–1992, there was higher emergence from the 1991 sowing than from the 1990 sowing on both sites ($P<0.01$). This trend continued for the following 2 years on the HD site, but seedling numbers were very low on the LD site and differences between the 2 sowings were not significant. However, the percentage of seed accounted for as seedlings was similar in the 2 sowings. Seedling numbers were always higher on the HD site.

Recovery as soil seed. A far higher percentage of the seed from the second sowing was recovered in the soil seed bank ($P<0.01$) (Table 7b). There was a massive drop in seed reserves over the first year in the 1990 sowings although after that the decline was much lower with a half-life from 1992–1994 of some 21 (HD site) or 13 (LD) months. The very large drop over the first year in the 1990 sowing led to the decision to take 6-monthly samples of soil seed banks in the 1991 sowing. However, results from the second sowing were very different — losses were low on both sites over the first year and some 40% of the seed bank remained after 3 years, with a half-life of 26–30 months. There was little difference between sites in soil seed recovery.

Annual seedling recovery from the soil seed bank is given in Table 7c, in which the number of seedlings recovered during each growing season

Table 7. Annual recovery of seedlings or seed from seed of Wynn cassia broadcast on to heavily defoliated (HD) and lightly defoliated (LD) swards in autumn 1990 or 1991: (a) percentage of seed recovered as seedlings; and (b) the percentage of seed recovered in the soil seed bank. Also given is the percentage of the soil seed bank at the start of each growing season which was recovered as seedlings during that season.

Date sown	Site	1990–91	1991–92	1992–93	1993–94	Total
(a) % of broadcast seed recovered as seedlings						
6/90	HD	11.1	2.5	0.2	0.6	14.4
	LD	5.8	0.8	0.1	0.1	6.8
5/91	HD	—	8.3	4.4	7.5	20.2
	LD	—	4.6	0.1	0.0	4.7
(b) Soil seed bank as % of original broadcast seed						
6/90	HD	14	4	6	3	
	LD	14	4	6	2	
5/91	HD	—	76	72	40	
	LD	—	71	56	37	
(c) % of winter soil seed bank emerging as seedlings in the following year						
6/90	HD	11.0[1]	18.5	5.0	9.3	
	LD	5.8[1]	5.9	1.6	2.3	
5/91	HD	—	8.3	5.8	10.4	
	LD	—	4.6	0.1	0.0	

[1] The soil seed bank was not measured in this winter so seedling recovery is expressed as % of the viable seed which was oversown in autumn.

has been expressed as a percentage of the soil seed bank at the start of that season. On the HD site, some 5–20% of the seed bank was recovered as seedlings in the following season in every year. In the first season of both sowings on the LD site, *ca*. 5% of the soil seed bank was recovered as seedlings but only 1–2% in subsequent years.

Seed unaccounted for. Averaging over the two sites, we could account for only 13% of seed from the 1990 oversowing, 2.4% as 1994 soil seed and 10.6% as seedlings removed over the 4 years. In the 1991 sowing, we could account for 50.6% of seeds, 38.1% as soil seed and 12.5% as seedlings. On the HD site, we accounted for 17.6% (1990) and 59.8% (1991) of seed but only 8.4% (1990) and 41.4% (1991) on the LD site.

Discussion

Longevity of seed banks. The striking difference between the sowings in 1990 and 1991 was in the large decline in the seed bank at both sites over the first 12 months in the 1990 sowing. After this year, the rate of decline was similar in the 1990 and 1991 sowings with the half-life of the soil seed banks being 13–21 months (1990 sowing after 1991) and 26–30 months (1991 sowing). These rates are lower than can be inferred from another study at Samford where soil seed reserves were halved between winter and the following autumn (Jones and Bunch 1995). However, even if we assume a half-life for a seed bank of only 12 months, a seed bank of 5000 seeds/m^2, which can be achieved readily in one good year (Jones and Bunch 1995), could still result in a seed reserve of over 300 seeds/m^2 after four years without additional seed set.

The 1–2 year half-life of soil seed reserves implies that the breakdown rate of hard seed in this experiment was slower than was measured in litter bags in Study 5. This could be due to the fact that the litter bags were placed out on an exposed soil surface whereas seed reserves in the soil are protected by vegetation, litter and, in many cases, a shallow layer of soil. It could also reflect the seed quality of the particular seed lot used in Study 5.

Prior to the experiment, we hypothesised that the run-down of seed banks would be faster on the heavily defoliated and drier site because of greater fluctuations in soil temperature leading to greater breakdown of hardseededness. This did not occur. The run-down of cassia seed banks between winter and autumn in another experiment at Samford was also similar in lightly and heavily grazed bahia grass pastures (Jones and Bunch 1995). One explanation could be that the heavily grazed sward was a matt of rhizomatous and/or stoloniferous grasses so the large differences in yield were not associated with differences in soil temperatures. Similar differences in yield in a tussock grassland, with bare intertussock areas, may well lead to larger differences in soil temperatures and breakdown of hard seed.

Recovery of seed as seedlings. Of the seed bank present at the start of any growing season on the HD site, 5–10% was usually accounted for as seedlings during that season. Similar results were obtained in other experiments at Samford with cassia (Jones and Bunch 1995) and Siratro (Jones and Bunch 1988a). On a cumulative basis, the 14% (1990) and 20% (1991) recoveries on the HD site were very similar to the 21% recovery of oversown Siratro seed as seedlings over 6 years in a similar experiment (Jones 1981). The percentage of the seed bank recovered as seedlings was much lower in the lightly defoliated site, again as recorded by Jones and Bunch (1995).

Seed unaccounted for. As the rate of run-down of the soil seed bank was similar at the 2 sites and more seedlings were recovered at the heavily defoliated site, more seed was unaccounted for at the lightly defoliated site. Eighty seven percent of viable seed was unaccounted for as seed or seedlings in the poor quality 1990 seed lot compared with only 50% in the 1991 oversowing. This was also recorded in a similar experiment with Siratro (Jones 1981) where the proportion unaccounted for, on a viable seed basis, was greater from a poorer quality seed lot that had a higher percentage of dead seed. The 50% of seed unaccounted for in the 1991 sowing was similar to the losses in the Siratro study (Jones 1981) and to the 35–75% unaccounted for in a study on Mediterranean legumes (Taylor 1972), although only 30% of seed was unaccounted for in a study with *Trifolium subterraneum* accessions in a more reliable rainfall area of Western Australia (Taylor *et al*. 1984).

Difference between seed lots. Why was there a far greater loss of seed during the first year of the 1990 sowing than with the 1991 sowing? The reasons could lie with: (a) differences between the seed lots; (b) differences between environmental conditions before the seed actually reached the soil surface and/or became covered with soil; and (c) differences in the activity of predators between the 2 years.

The 1990 seed lot was of poorer quality than the 1991 lot and had a higher % of unsound seed than is usual (Tables 2 and 3). There was also a marked fall in viability of soft seed under laboratory storage. This seed was set under moist conditions, as April and May rainfall was about twice the long-term average (Table 6), and results from Study 3 suggest that seed quality tends to be lower under these conditions. The 1991 sample was of far higher quality and the hard seed percentage increased between testing immediately after collection and 9 months later. We have also recorded such a change with Siratro (authors, unpublished data).

In addition to the poorer quality of the 1990 seed lot, there was good rainfall in late autumn and winter and also heavy dewfalls in the 1990 winter. Consequently, the lower parts of the canopy remained moist for extended periods. Observations made after the 1990 oversowing revealed that many seeds adhering to leaves and litter had swollen but not germinated, probably due to cool temperatures, and it is likely that this accounts for much of the loss of soft oversown seed.

It is also possible that predation could have been much higher in 1990 than in 1991. However, we consider this is unlikely to be a major cause, in part because differences between the years were consistent on both the lightly and heavily grazed sites which were some 500 m apart. Furthermore, Study 4 suggested that predation of oversown seed is not a serious problem at Samford, especially in winter.

Thus, the different results from the 1990 and 1991 sowings are attributed to the poorer quality of the 1990 seed lot and possibly due to greater opportunity for this soft seed to be spoilt during wet conditions in autumn-early winter.

Study 7 — Rooting depth of cassia plants and seedlings

In order to model establishment and growth of cassia in relation to soil moisture, it was necessary to document the rooting depth of cassia plants and seedlings and relate these depths to plant age. These measurements were made within the Samford and Narayen grazing studies described by Jones and Bunch (1995) and Jones *et al.* (1990). The respective soil types were a well drained red earth (Gn 2.14, Northcote 1977) and a duplex soil with *ca.* 50 cm of coarse sandy topsoil (Dy 5.42) overlying a medium clay subsoil.

Methods and results

Depth of rooting of cassia seedlings. Forty seedlings were dug up at Samford on February 8, 1990 and their height and depth of rooting measured. The seedlings were grouped to the number of leaves, as defined in Table 8.

Table 8. Seedling height, number of seedlings in each class and rooting depth (Standard Error of Mean in brackets) for 4 size classes of cassia seedlings at Samford Research Station.

Seedling size	Seedling height	No. seedlings	Rooting depth
	(mm)		(mm)
Cotyledons	15	6	23 (4)
" + 2 leaves	27	5	42 (8)
" + 3 leaves	30	19	55 (3)
" + 4 leaves	31	10	54 (6)

The largest of these seedlings had emerged about 1 month previously, whereas the smallest had emerged less than a week previously. Similar measurements of the rooting depth of 9 seedlings at Narayen showed that seedlings with 3–6 leaves had a rooting depth of 40–70 mm. The rooting depth (and probable age of the seedlings at the time, based on rainfall events adequate for germination) suggest a root growth rate of 2–3 mm per day. This is less than the 10–20 mm per day measured by Fleming (1995) in glasshouse tests in disturbed soil and less than the 5 mm per day measured in the field at Narayen (authors, unpublished data) under optimum conditions. This slow rate of root elongation highlights the problem of 'false starts' where the soil drying front can overtake the seedling root zone, resulting in seedling death and run-down of seed reserves.

Depth of rooting of cassia plants. At Samford, the depth of rooting of 33 plants, with tap root diameters of 0.5–12 mm at the soil surface, was measured after carefully excavating a trench alongside the taproot. The relationship between taproot diameter (X, mm) and rooting depth (Y, mm) was: $Y = 73.2 + 78.2\ X - 3.6\ X^2$, $r^2 = 0.96$. The maximum rooting depth was 500 mm. At Narayen, the depth of rooting of 15 plants, with tap root diameters from 0.4–12 mm at the soil surface, was measured in the same way. The relationship between taproot diameter (X, mm) and rooting depth (Y, mm) was similar: $Y = 29.9 + 81.3X - 4.04X^2$, $r^2 = 0.90$. The maximum rooting depth was 450 mm.

Based on these regressions, estimated rooting depths for taproots of 2 mm diameter were 220 mm (Samford) and 180 mm (Narayen). Corresponding rooting depths for plants with diameters of 4, 8 and 12 mm were 330 and 290 mm, 468 and 420 mm, and 490 and 430 mm. Hence, larger cassia plants can exploit soil moisture reserves that are unavailable to smaller plants.

Taproot size and plant age. Taproot diameter at Samford and Narayen can be related to plant age as measurements of taproot diameter were made on more than 100 tagged cassia plants of known age in the experiments described by Jones and Bunch (1995) and Jones *et al.* (1990). At Samford, there was a good linear relationship between plant taproot diameter in mm (Y) and plant age (X) in months: $Y = 0.62 + 0.15X$, $r^2 = 0.88$. This is equivalent to an increase of *ca.* 2 mm in diameter for each growing season that the plant survives. At Narayen, taproot diameter increased more with plant age, with an increase of *ca.* 3 mm in diameter for each growing season: $Y = 0.5 + 0.28X$, $r^2 = 0.90$.

Discussion

Successful modelling of soil moisture is a prerequisite to modelling legume growth and persistence. The relationships between age and size of plant and rooting depth can be used to define the depth of soil exploited by cassia plants of different age or size and these depths can then be used in models of soil moisture.

General discussion

The results from the various studies have practical implications for the persistence and management of Wynn cassia and also for the modelling of its persistence.

Management

Green pods reaching full width and length after mid-May (very late autumn) failed to set sound seed in this study. For reliable seed set in south-east Queensland, with 5 weeks from flowering to swollen green pods, cassia needs to flower by late March–early April.

As cassia is a short-lived plant (Jones and Bunch 1995), adequate soil seed reserves must be maintained for seedling recruitment. Cassia seed reserves at Samford have a half-life of about 1–2 years, so given typical seed reserves of several thousand seeds per m^2, it will take several years for levels to decline to <100 seeds/m^2. However, in drier areas, the breakdown of hard seed is likely to be faster and it is also likely there will be more loss of seed through "false starts" with seedling emergence and death following isolated rainfall events without adequate follow-up rain for seedling survival.

The rate of breakdown in hard seed of cassia under field conditions is faster than the equivalent rate in 4 *Stylosanthes* species (Mott *et al.* 1981). Rapid hard seed breakdown can be beneficial if climatic conditions are suitable for subsequent seedling establishment (Mott *et al.* 1981), but can be detrimental for long-term persistence of a seed bank through dry conditions (Jones *et al.* 1993).

If soil seed reserves are depleted and a heavy seed set is considered desirable to enhance persistence, decreasing grazing pressure towards the end of the growing season, or removal of stock altogether, could increase seed set 2–3 fold. Removal of stock early in the growing season would have less impact as cattle at this time strongly select the associated grass and graze little cassia (Clements *et al.* 1996).

Modelling

Relationships between rooting depth and rate of root growth of seedlings (Study 7) have been incorporated in the model of cassia persistence and are of critical importance in determining whether cassia seedlings and plants survive through dry periods as calculated from a soil moisture sub-model. The information on the time taken for cassia seed pods to mature (Study 1) will be incorporated into the model as it will be used to limit predicted seed set of cassia in relation to short periods of favourable moisture and to declining temperatures in autumn. Information on proportions of viable and hard seed set (Study 3) have been included in the model but more detailed studies relating these attributes to temperature and rainfall may be required.

The preliminary data presented for Study 2 showed the importance of being able to predict how seed set of cassia was related to cassia herbage yield under different grazing pressures. This relationship is currently being examined in more detailed studies by C.K. McDonald.

The remaining studies all related to the fate of seed once it had been set. The data on the breakdown of hard seed (Study 5) have been incorporated into the model and data on the longevity of seed banks (Study 6) will be added to existing information to enable better prediction of these attributes in relation to climate and grazing pressure.

Three studies suggest that, while it should be possible to model accurately cassia seed set and its subsequent fate in most situations, it will be difficult to do this in every specific situation. The different patterns of seed loss recorded in the 1990 and 1991 sowings (Study 6) suggest that there can be very large differences in seed loss during the winter following seed set, depending on seed quality and how wet the pasture is over the winter months when temperatures are too low for germination. Study 4 suggests that predation, probably by ants, may be a problem at some times of the year and at some sites. Furthermore, grazing pressure also affects seed set (Study 2). Predicting seed set and incorporation of seed into the seed bank is a very difficult part of modelling cassia. At present, we are unsure how much detail we need to have to model seed flow. For example, it may be that we can meet the broad objectives of our model (Jones *et al.* 1993) by using generalised relationships between seed set and soil seed reserves without going to the more detailed descriptions of seed loss. If this is so, it will mean that, in some specific site/time situations, the generalised relationships will not be appropriate.

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References

ANON (1993) Beef production from cassia/buffel grass pastures in subtropical Queensland. *Final Report, Project CSNAP P.11, Meat Research Corporation of Australia*.

ARGEL, P.J. and HUMPHREYS, L.R. (1983) Environmental effects on seed development and hardseededness in *Stylosanthes hamata* cv. Verano II. Moisture stress and illuminance. *Australian Journal of Agricultural Research*, **34**, 271–277.

ASHTON, D.H. (1979) Seed harvesting by ants in forests of *Eucalyptus regnans* F. Muell. in central Victoria. *Australian Journal of Ecology*, **4**, 265–278.

CLEMENTS, R.J., JONES, R.M., VALDES, L.R. and BUNCH, G.A. (1996) Selection of *Chamaecrista rotundifolia* by cattle. *Tropical Grasslands*, **30**, 389–394.

FLEMING, B.A. (1995) *The effect of the drying front on the survival and root expansion of germinating legume pasture seedlings*. M.Sc. Thesis. University of Queensland, Brisbane.

JONES, R.M. (1981) Studies on the population dynamics of Siratro: the fate of Siratro seed following oversowing into sub-tropical pastures. *Tropical Grasslands*, **15**, 95–101.

JONES, R.M. and BUNCH, G.A. (1988a) The effect of stocking rate on the population dynamics of Siratro in Siratro (*Macroptilium atropurpureum*)-Setaria (*Setaria sphacelata*) pastures in south-east Queensland. II Seed set, soil seed reserves, seedling recruitment and seedling survival. *Australian Journal of Agricultural Research*, **39**, 221–234.

JONES, R.M. and BUNCH, G.A. (1988b) A guide to sampling and measuring the seed content of pasture soils and animal faeces. *Technical Memorandum No. 59, Division of Tropical Crops and Pastures, CSIRO, Australia*.

JONES, R.M., CLEMENTS, R.J., BUNCH, G.A. and MCDONALD, C.K. (1990) Persistence and productivity of legume based pastures at Narayen. *Biennial Research Report 1988–90, Division of Tropical Crops and Pastures, CSIRO, Australia*. pp. 114–115.

JONES, R.M., MCDONALD, C.K. and BUNCH, G.A. (1993) Persistence of roundleaf cassia in grazed pastures — a conceptual model. *Proceedings of the XVII International Grassland Congress, Rockhampton, 1993*. III, 1902–1903.

JONES, R.M. and BUNCH, A. (1995) Yield and population dynamics of *Chamaecrista rotundifolia* cv. Wynn in coastal south-eastern Queensland as affected by stocking rate and rainfall. *Tropical Grasslands*, **29**, 65–73.

MICHALK, D. and HUANG ZHI-KAI (1994) Grassland improvement in subtropical Guandong Province, China. *Tropical Grasslands*, **28**, 129–138.

MOTT, J.J. and MCKEON, G.M. (1977) A note on the selection of seed types by harvester ants in northern Australia. *Australian Journal of Ecology*, **2**, 231–235.

MOTT, J.J., MCKEON, G.M., GARDENER, C.J. and MANNETJE, L.'t (1981) Geographic variation in the reduction of hard seed content of *Stylosanthes* seeds in the tropics and subtropics of northern Australia. *Australian Journal of Agricultural Research*, **32**, 861–869.

NORTHCOTE, K.H. (1977) *Factual Key for the Recognition of Australian Soils*. (Rellim: Adelaide).

PARTRIDGE, I.J. and WRIGHT, J.W. (1992) The value of roundleafed cassia (*Cassia rotundifolia* cv. Wynn) in a native pasture grazed with steers in south-east Queensland. *Tropical Grasslands*, **26**, 263–269.

PETERS, M., TARAWALI, S. and ALKAMPER, J. (1994) Evaluation of tropical pasture legumes for fodder banks in subhumid Nigeria. 1. Accessions of *Centrosema brasilianum, C. pascuorum, Chamaecrista rotundifolia* and *Stylosanthes hamata. Tropical Grasslands*, **28**, 65–73.

QUINLIVAN, B.J. (1971) Seed coat impermeability in legumes. *Journal of the Australian Institute of Agricultural Science*, **37**, 283–295.

STRICKLAND, R.W., GREENFIELD, R.G., WILSON, G.P.M. and HARVEY, G.L. (1985) Morphological and agronomic attributes of *Cassia rotundifolia* Pers., *C. pilosa* L., and *C. trichopoda* Benth., potential forage legumes for northern Australia. *Australian Journal of Experimental Agriculture and Animal Husbandry*, **25**, 100–108.

TAYLOR, G.B. (1972) Time distribution of seedling emergence from single seed crops of several annual pasture legumes. *Australian Journal of Experimental Agriculture and Animal Husbandry*, **12**, 628–633.

TAYLOR, G.B., ROSSITER, R.C. and PALMER, M.J. (1984) Long term patterns of seed softening and seedling emergence from single seed crops of subterranean clover. *Australian Journal of Experimental Agriculture and Animal Husbandry*, **24**, 200–212.

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