

ECOLOGY OF *CALOSTEMMA* AND *CRINUM* (AMARYLLIDACEAE) IN THE RIVER MURRAY AREA, SOUTH-EASTERN AUSTRALIA

TRACY CLARK & R. F. PARSONS

Botany Department, La Trobe University, Bundoora, Victoria 3083

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Calostemma luteum, *C. purpureum* and *Crinum flaccidum* are the only native plant species in Victoria possessing true bulbs. Their distribution at their southern limit on and near the River Murray floodplain is described. Distribution of *Calostemma* flower colour forms may be related to water dispersal of seed by various rivers entering the Murray. Whilst some stands found follow elevation contours and may be related to seed dispersal by past very high floods, others are well upslope from the present floodplain.

All three taxa produce large, buoyant, non-dormant, water-rich seeds less than six weeks after flowering. *Calostemma* seeds had more complete germination than *Crinum* at 15°/10°C but not at 25°/15°C in keeping with *Calostemma*'s more temperate range. Watered two-month-old seedlings of both genera produced small bulbs and roots, whilst unwatered ones produced large bulbs but no roots. In dry storage, all seeds had germinated by two months. At 23 months, all *Calostemma* seedlings were dead but half the *Crinum* seedlings were still alive in keeping with their larger seed size. The burial of the shoot apex by the positively geotropic cotyledon may be an adaptation to protect it from drought.

Young *Crinum* seedlings remained alive and floating after two months in both fresh and seawater; *Calostemma* seedlings remained alive in fresh water but were usually killed by seawater. Mature *Crinum* bulbs contained a number of live, unemerged inflorescences at all sampling dates while in *Calostemma* none were found between March and September, suggesting that flowers are initiated no more than once per year. The flowering time for both *Crinum* and *Calostemma* was summer-autumn following rain; rains after March produced leaf emergence but no flower emergence. In *Crinum*, even showers as light as 6 mm may produce some flowering; in *Calostemma* 15 mm produced flowering while 9 mm did not.

Both genera show low leaf palatability to grazing mammals, but predation on seeds by emus and bulbs by pigs has been reported.

WHILE most of Australia's ten native species of Amaryllidaceae occur in well-watered tropical to subtropical areas (Hewson 1987; Telford 1987), *Calostemma luteum*, *C. purpureum* and *Crinum flaccidum* (Figs 1 and 2) extend into arid and semi-arid parts of inland Australia, reaching as far south as the River Murray area around latitude 34°S. These, and two species of *Haemodorum*, are the only native plant species in temperate south-eastern Australia possessing true bulbs. All three have large flowers, those of *C. flaccidum* being the largest of any native Victorian species (Willis 1970).

This paper introduces the biology of *Calostemma luteum*, *C. purpureum* and *Crinum flaccidum* at their temperate, southern limit on the River Murray floodplain in Victoria and South Australia. The main aims were to investigate germination and seedling behaviour and the way that growth, flowering and fruiting are related to temperature and rainfall in naturally-occurring populations. As the conservation status of *Calostemma purpureum* and *Crinum flaccidum* is rare and vulnerable Victoria-wide respectively (Gullan, Cheal & Walsh

1990), we hope this paper will provide data useful for their management.

Species nomenclature follows Ross (1993) and Telford (1987).

DISTRIBUTION AND HABITAT

Crinum flaccidum occurs in all mainland states and reaches as far north as the Kimberley and inland from Townsville (Pate & Dixon 1982; Hewson 1987). North of the Murray River, *Calostemma* extends through New South Wales but only as far north as Rockhampton in Queensland (Telford 1987). Whilst *Calostemma* and *Crinum flaccidum* occupy river floodplains, swamps and other seasonally flooded sites (Pate & Dixon 1982; Telford 1987), *C. flaccidum* also occurs 'in the hills near Port Augusta' (Hannibal 1966) and *Calostemma* 'on sandstone hills and rocky rises' (Cunningham et al. 1981), indicating a capacity for non-flooded sites as well. Both genera can be found on soils ranging from deep sands (this study) to grey cracking clays (Moore 1984). They can be found



Fig. 1. Distribution maps for (A) *Crinum flaccidum*, (B) *Calostemma luteum* and (C) *C. purpureum*, from Hewson (1987), Pate and Dixon (1982) and Telford (1987). Commonwealth of Australia copyright reproduced by permission.

where flooding is short-lived, but not where water lies for long periods.

Crinum flaccidum may occur where mean annual rainfall is below 150 mm, such as in the Simpson Desert (Purdie 1984) and along the banks of the Clayton River north of Marree (Lothian 1957). In such areas, it is strictly confined to sites that receive supplementary moisture from runoff (F. J. Badman and P. K. Latz, personal communication). Less is known of *Calostemma* where it occurs in dry areas such as the Lake Eyre basin (Telford 1987).

The southernmost, temperate limit of *Crinum flaccidum* in Australia, the mouth of the Murray River at 35°30'S (Hewson 1987) is strikingly similar to the northernmost 'Crinum Line', for *C. asiaticum* in Japan at 35°21'N (Koshimizu 1938) which coincides approximately with an annual mean temperature of 15°C and an annual mean minimum of -3.5°C (Koshimizu 1938). The corresponding Australian values (Victor Harbor data) are 16°C and 12°C.



Fig. 2. *Crinum flaccidum* plant about 400 mm high, margin of Lake Wallawalla, 1977.

In Victoria, *Calostemma* and *Crinum* are confined to the western part of the River Murray floodplain. The eastern limit of *Calostemma* is just downstream of the junction of the Murrumbidgee River with the Murray (Willis 1970, J. N. Macfarlane personal communication) (Fig. 3). By contrast, *Crinum* begins its range further west, just downstream of the junction of the River Darling with the Murray (Fig. 3). This may be related to *C. flaccidum* seed dispersal into the Murray by the waters of the Darling River (Zimmer 1946). The same may be true of *C. purpureum* and the Murrumbidgee.

In Victoria, *Calostemma* and *Crinum* occur on superficial sand ridges on the Murray floodplain except for a *Crinum* stand on clay at Lock 9 on the Murray River (Ashwell 1987). *Calostemma* and *Crinum* usually occur in treeless openings or woodlands of *Eucalyptus camaldulensis* and *E. largiflorens* (Ashwell 1987, Victoria: Department of Conservation and Natural Resources unpublished, this study, Table 1).

In *Calostemma*, we treated plants with large, wholly bright yellow flowers as *C. luteum* and all other flower colour forms as *C. purpureum* (see Telford 1987). These two taxa can occur in pure or mixed stands; they may be colour variants of a single species (Telford 1987). The abrupt change of colour forms downstream of the Murray-Darling junction (Fig. 3) could mean that the yellow plus purple and purple forms were dispersed to the Murray via the Murrumbidgee, whilst the pink and yellow forms (i.e. *C. luteum*) were dispersed to the Murray via the Darling. Dispersal only by water can mean that populations on separate river systems can become genetically isolated (Renner 1992).

At Wood's Lagoon, occasional *Calostemma* plants with white flowers can be found, whilst 8.2 km ESE of Ned's Corner Homestead at least six different *Calostemma* colour forms occur, including cream and white with pink stripes (F. E. Curtis, personal communication).

Sites for detailed study of the three species (Fig. 3, Table 1) were chosen to cover two flower colour forms of *Calostemma purpureum* and an attempt was made to include sites of differing recent rainfall history. When the work started, only a single stand of *C. luteum* (site 4) was known close enough to Melbourne for us to sample (Table 1). The Victorian stands (Fig. 3) were reported to us in May 1993 (F. E. Curtis, personal communication). The field work period was largely January to September 1992.

All sites chosen were on the Murray floodplain and all three taxa have dispersal units which can

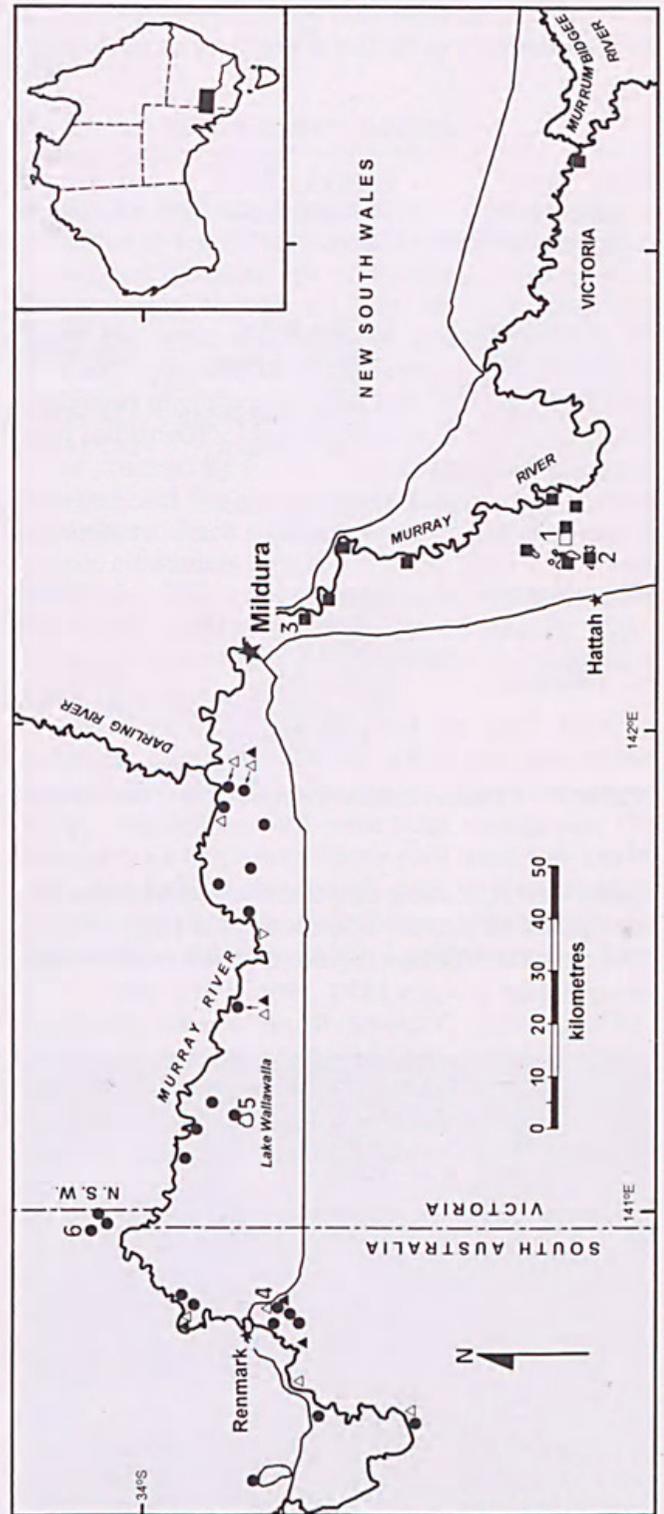


Fig. 3. Distribution of *Crinum flaccidum* (closed circles), *Calostemma luteum* (open triangles) and *C. purpureum* on part of the River Murray floodplain. For *C. purpureum*, open squares show stands with purple flowers and closed squares show stands with yellow flowers with purple markings; closed triangles show pink flowers. The open inverted triangle shows a *Calostemma* stand of unknown flower colour. The numbers show sites studied in detail.

Species	Site	Latitude, longitude	Surface soil texture	Habitat	Name of and distance to, nearest rainfall station
<i>Calostemma purpureum</i> (purple perianth)	1. Chalka Creek, Hattah Lakes area	34°43'17"S, 142°24'07"E	Loamy sand	Treeless opening just upslope from <i>Eucalyptus camaldulensis</i> woodland	Hattah-Kulkyne National Park Ranger's House, 7 km
<i>C. purpureum</i> (yellow and purple perianth)	2. Lake Bulla, Hattah Lakes area	34°45'30"S, 142°15'24"E	Loamy sand	<i>E. largiflorens</i> woodland	As above, 1.5 km
<i>C. purpureum</i> (yellow and purple perianth)	3. King's Billabong near Mildura	34°16'44"S, 142°14'34"E	Loamy sand	<i>E. largiflorens</i> woodland	Red Cliffs, 6 km
<i>C. luteum</i> (wholly bright yellow)	4. Paringa near Renmark	34°13'30"S, 140°48'32"E	Loamy sand	<i>E. largiflorens</i> woodland	Wonuarra Park homestead, 0.6 km
<i>C. flaccidum</i>	5. Lake Wallawalla, far NW Victoria	34°09'37"S, 141°11'30"E	Sand	Treeless sand ridge upslope from <i>E. largiflorens</i>	Ned's Corner homestead, 12 km
<i>C. flaccidum</i>	6. Gum Flat, Chowilla Station, E of Renmark	33°55'10"S, 140°57'19"E	Sand	Treeless sand ridge upslope from <i>E. largiflorens</i>	Chowilla homestead, 14 km

Table 1. General characteristics of the *Calostemma* and *Crinum* sites studied in detail.

float, so it is possible that distribution patterns may be related to floods. The six largest River Murray floods in the Mildura region (in order of decreasing magnitude) were in 1870, 1956, 1917, 1931, 1975, 1974 and 1981 (Victoria: Rural Water Commission 1986a). During the highest water levels since 1981 on 25–27 November 1992, none of the Victoria *Crinum* and *Calostemma* stands known to us was flooded. The floodwaters did not come close to any of the study sites (Table 1) except for site 5, where they were 10 m away in early December 1992.

Around Mildura and the Hattah Lakes, the *Calostemma* stands are elongate ones just above the 40 m contour, thus resembling a strandline. All were likely to be flooded for several months in 1956 (Victoria: Rural Water Commission 1986b), which would probably kill any submerged *Calostemma* plants. Major floods like those of 1956 and 1975 could deposit strandlines of *Calostemma* seeds, so producing linear stands along the flood margin which could subsequently colonize up- and downslope. Of course many present stands are likely to have resulted from the complex interaction of a number of such colonizing events. Concentration of water-dispersed seeds at the land-water interface is well-known in other work (Schneider & Sharitz 1988).

Downstream of the Darling River junction, *Crinum flaccidum* can be found up to 12 km from

the River Murray itself (e.g. at Boy Creek) Some, but not all, of the *C. flaccidum* sites flooded in 1956 (Victoria: Rural Water Commission 1986b, F. E. Curtis, personal communication). By contrast, in this section, *Calostemma* stands are not found more than 4 km from the river itself and most or all of them flooded in 1956 (F. E. Curtis, personal communication).

It seems certain that some *Crinum* and *Calostemma* sites in South Australia near Renmark have not been flooded since 1870 or even earlier. Some stands, quite separate from the main ones at low altitudes, occur well upslope and seem certain to be above the level of even the largest flood imaginable, suggesting a seed dispersal agent other than water is operating. Seeds being carried and dropped by ravens or other birds is one possibility (D. Frahn personal, communication). In contrast, plants of the water-dispersed Central American *Crinum erubescens* only occur in strongly linear stands right at the land-water interface (Manasse 1990).

METHODS

Morphology and development of the dispersal units

Presence and maturity of dispersal units were

recorded approximately every six weeks from 4 March 1992 to 7 September 1992 (hereafter called the sampling dates).

Morphology and development of bulbs and scapes

On the sampling dates, two to three bulbs were dug up at each site. Each was sectioned transversely one third of the way up the bulb from the base and the following recorded: depth of bulb (from soil surface to base of bulb), maximum bulb diameter, maximum leaf width, number of old scapes within bulb (present as dried remains), number of unemerged inflorescences within bulb and number of leaf bases found radially between each inflorescence.

Phenology

On the sampling dates, 50 marked plants at each site were scored for stage of flowering/fruitlet, number of inflorescences, emerged leaf number and maximum leaf length. Using the methods of Orshan (1989) for any given date, the predominant phenomorphological state is presented; in practice, this meant that if less than 20% of plants exhibited a state, this was not recorded in the diagrams. Reproductive plants were scored as 'senescent' if the scape was still alive but all seeds had been dispersed or the scape had fallen.

Climate was monitored by rain gauges and maximum–minimum thermometers at the sites for the main study period from 4 March to 7 September 1992. Before and after this, values from the nearest meteorological stations had to be used (Table 1). Only the latter data are presented; the six-weekly rain gauge values were used as a check on their applicability. The seasonal temperature pattern was very similar right across the study area.

At site 4, an area 7 m × 5 m was hand-watered with 2250 L, 2250 L and 1000 L of water on 11, 18 and 26 February respectively.

Germination and emergence

Trials were conducted on the effects of temperature on germination and seedling development. All seeds were collected in March 1992. The temperature trial used seeds from sites 2 and 6 in the following regimes; (a) 25°C day/15°C night, (b) 15°C day/10°C night and (c) 2°C in constant dark. The photoperiod in (a) and (b) was 14 h. All seeds were placed on damp, sterile sand in covered transparent dishes replicated five times, 20 seeds per replicate for *Calostemma*, 12 for *Crinum*. The 2°C treatment

was chosen to see if the taxa behaved like tropical taxa with recalcitrant seeds at low temperatures.

Responses of seeds and seedlings to burial and watering

This trial used seeds from sites 1, 2 and 6. It was designed to see if burial or watering has important effects on germination or seedling development, the watering because all taxa can germinate and grow for some time without added water.

There were two watering regimes (watered regularly and unwatered) × two burial regimes (buried and unburied) × four replicates. The buried seeds were covered by 0.5 to 1 times the seed diameter of sand and the watered treatments used drained containers. Each replicate consisted of 20 seeds in plastic containers 20 × 26 × 8.5 cm filled with sterile river sand. The trial ran in an unheated glasshouse for three months starting on 13 March 1992. Presence and length of cotyledon, leaf and root were recorded every 14 days.

The term germination will be used here to mean the emergence of the radicle and part of the cotyledon from the seed (Fig. 4). Two subsequent events studied as well were root emergence, the emergence of an adventitious root from the cotyledon just behind the radicle and leaf emergence, the emergence of the first foliage leaf through the side of the cotyledon slightly further back (see Rees

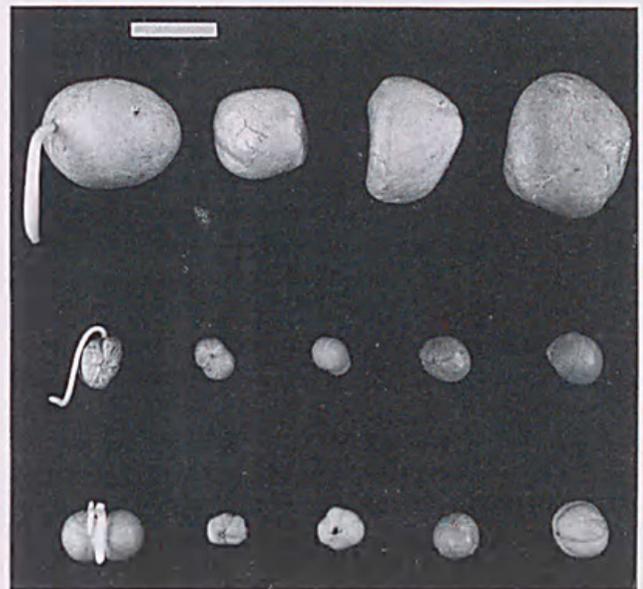


Fig. 4. Dispersal units of *Crinum flaccidum* (top row), *Calostemma purpureum* (middle row) and *C. luteum* (bottom row). The left hand units have already germinated without an external water supply. All units from site 4. Scale bar = 20 mm.

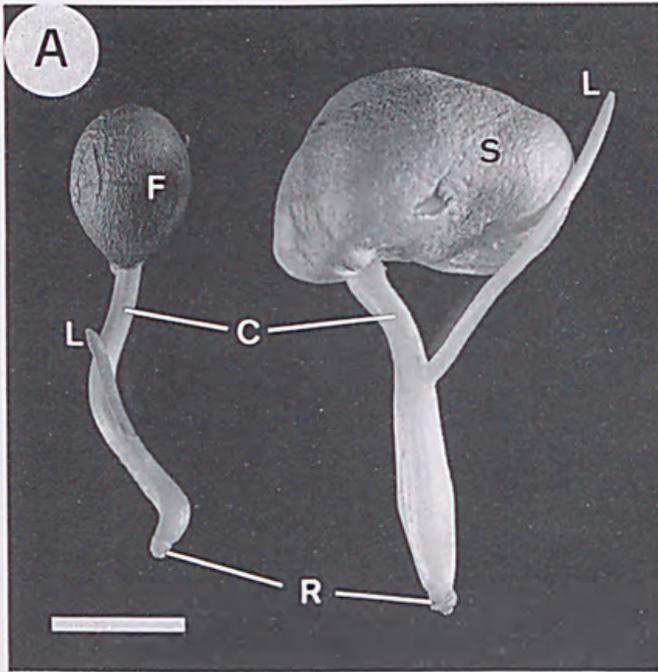
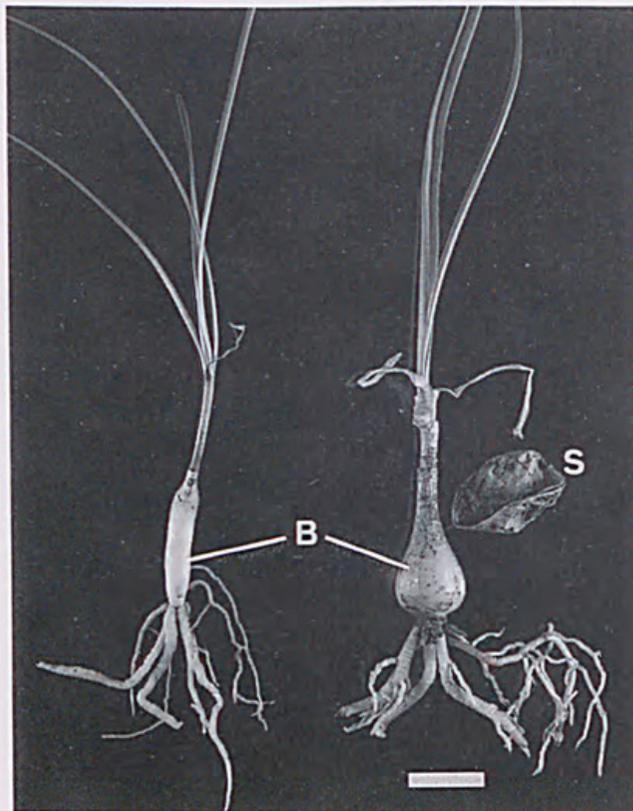
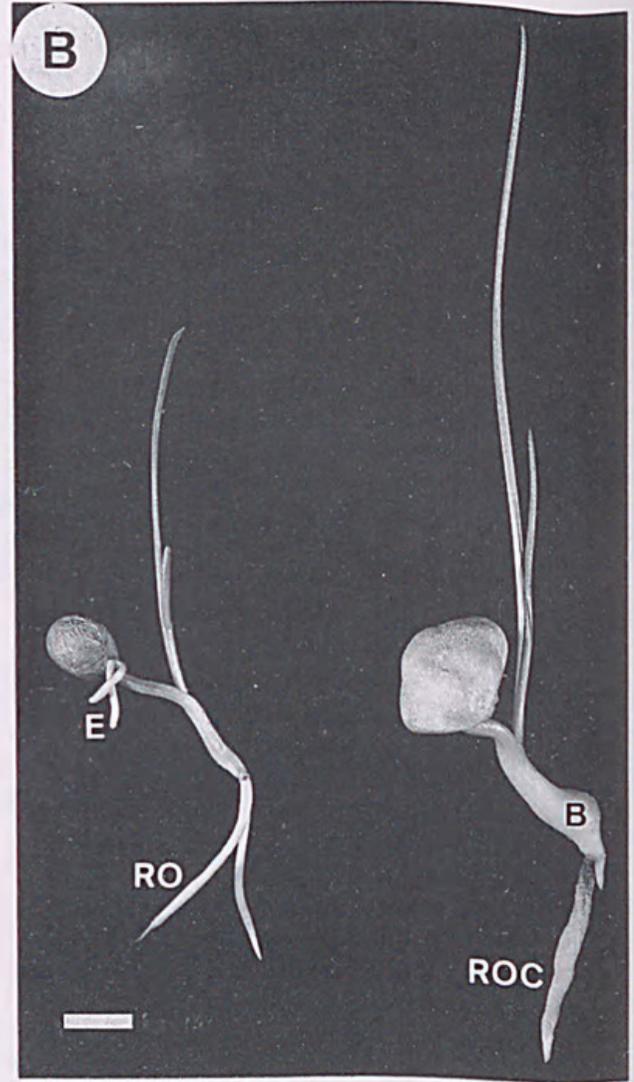


Fig. 5. A, B, seedlings of *Calostemma purpureum* (left) from Lambert Island and *Crinum flaccidum* (right) from Paringa showing bulb (B), cotyledon (C), young embryos (E), fruit (F), first leaf (L), radicle (R), root (RO), contractile root (ROC) and seed (S). A, seedlings four weeks old. B, same seedlings seven weeks old. Scale bar = 10 mm.



1972; Pate & Dixon 1982; Figs 5 and 6). These two events are seemingly independent—they do not occur in a fixed order.

Effects of seed storage

Four seeds of *Crinum* (site 5) and 11 seeds of *Calostemma* (site 3) were stored dry at 4°C for 2 months (by which time they had germinated). They were then stored dry for a further 21 months in the dark at room temperature and examined for viability.

Fig. 6. Plants of *Calostemma purpureum* (left) from site 2 seed source and *Crinum flaccidum* (right) from site 5 seed source. Plants were grown from seed in pots for 13 months. Showing bulbs (B) and remains of seed, now detached (S). Scale bar = 20 mm.

Buoyancy of the dispersal units

Ungerminated seeds of *Calostemma* (sites 1 and 2) and newly-germinated seedlings of *Crinum* (site 6) were available. These were added to containers (20 cm × 26 cm × 8.5 cm) containing either tap-water or seawater. The sea water treatment was included because many species of *Crinum* are coastal and thought to be dispersed by ocean currents (Koshimizu 1930; Hannibal 1966) and because Hannibal (1966) suggests that *C. flaccidum* may have arisen as a coastal species in the Gulf of Carpentaria. There were four replicates, with 20 (*Crinum*) or 25 (*Calostemma*) seeds per replicate. Every two weeks, the water was changed and sunken or rotted seeds or seedlings recorded. The rotted ones were removed. The trial ran in an unheated glasshouse for two months (mid-March to mid-May).

RESULTS AND DISCUSSION

Morphology and development of the dispersal units

At site 4, *Calostemma luteum* and *C. purpureum* plants in full flower on 12 April 1993 had mature seeds as few as three weeks later; for *Crinum* there the corresponding figure was 5.5 weeks (D. Frahn, personal communication). For the South African *Crinum bulbispermum*, seeds can mature two to three weeks from flowering (Oliver 1990) and for *C. erubescens* the figure is 45 days (Manasse 1990).

Crinum flaccidum produces large seeds up to 25 mm in diameter, weighing up to 11 g (mean weight 5 g) and with a high water content of 89% (Fig. 4; Howell 1984; Howell & Prakash 1990). Seeds up to 66 g in weight are known in *C. erubescens* (Manasse 1990). Vivipary—germination while the seed is still attached to the parent plant—is rare; normally it occurs 2–4 weeks from seed shed. No external water supply is required for this (Howell & Prakash 1990).

Less is known of *Calostemma*. The organ that is shed from the parent plant is a capsule. This is normally one-seeded. However, it is likely that the 'seeds' are, strictly speaking, bulbils (Telford 1987). For brevity, the dispersal units of both *Crinum* and *Calostemma* will often be referred to below as seeds.

Calostemma germination normally occurs within a few weeks after seed shed as one to three embryos extrude through the fruit wall. Again no external water supply is required. No dispersal unit differences were noted between the two species of *Calostemma*, with diameters of 5 to 12 mm, mean weights of 0.6 g and high water contents.

A group of genera in the Amaryllidaceae has large, soft dispersal units of high water content (60–90%) which lack dormancy and are often viviparous. It includes *Amaryllis*, *Brunsvigia*, *Crinum*, *Haemanthus*, and some other South African genera (Isaac & McGillivray 1965; le Maitre & Midgley 1992). Clearly, *Calostemma* should be added to this group. Such dispersal units, called 'water-rich seeds' by Dahlgren, Clifford & Yeo (1985), are similar to many recalcitrant seeds in their large size, high water content and lack of dormancy. Presumably, like non-dormant recalcitrant seeds, they are imbibed when shed and so germinate then or soon after, as is the case for *Avicennia marina* (Verbenaceae) and *Sechium edule* (Cucurbitaceae). In these cases the young seedling can then survive for months prior to either establishment or receipt of external water supplies (Chin 1988; Newstrom 1989).

Morphology and development of bulbs and scapes

Crinum. The largest bulb seen was 146 mm across and contained the remains of 8 old scapes, 7 un-emerged inflorescences and about 60 leaf bases in keeping with a genus noted for its enormous bulbs (Hitchmough 1989). Bulbs smaller than 45 mm across had never flowered and did not contain unemerged inflorescences. The latter were present in bulbs larger than 45 mm at all sample dates.

The *Crinum flaccidum* bulb appears to be made up entirely of leaf bases; nothing was recognizable as scales, so that the bulb is the *Hippeastrum* type (Rees 1972). In *C. flaccidum*, the usual number of leaf bases between inflorescences is five, with a range from three to seven.

Inflorescences are initiated in the centre of the bulb and move outwards as newer leaf and floral buds are formed (Fig. 7). At flowering, there are generally three unemerged inflorescences within the bulb, with the oldest inflorescence, furthest from the centre, being the emergent one. Thus the bulb has a sympodial branching system like *Hippeastrum* (Rees 1972) rather than the monopodial system suggested for *C. flaccidum* by Howell & Prakash (1990).

The fact that unemerged inflorescences at all stages of development separated by about five leaf bases were found at all sampling dates indicates that bulb growth and inflorescence initiation are more-or-less continuous processes, at least while emerged leaves are present. In the absence of seasonal trends, the bulb data from different sampling dates were pooled (Table 2).

Regarding the depth to which the bulbs are buried, Pate and Dixon (1982) recorded 500 mm for *Crinum asiaticum* and regarded it as 'a remarkably great depth for a bulbous species'. However, for *C. flaccidum*, we recorded 600 mm, while 900 mm (Lothian 1969) and even 1200 mm (D. Frahn, personal communication) have also been recorded.

Calostemma. No important differences were found between populations (Table 2). The largest

bulb was 56 mm across. The two smallest bulbs, 15 mm across, had never flowered but the two next-smallest ones, 18 mm across, had flowered as had nearly all the others.

By the first sampling date, the 1992 inflorescences had already emerged. In all flowering bulbs seen, three inflorescences had been initiated in the months prior to the most recent flowering, all between the same two leaf bases and at slightly different ages (Fig. 8). In the bulb sections, the remains of old scapes could again be seen. Remains

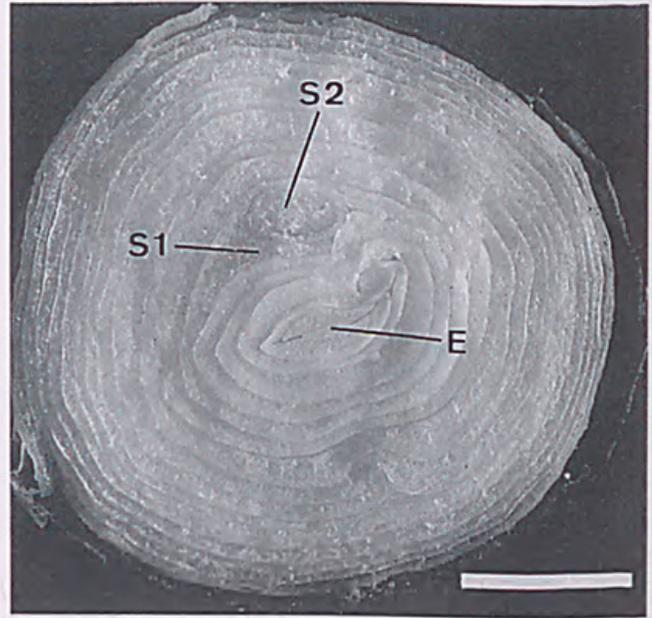
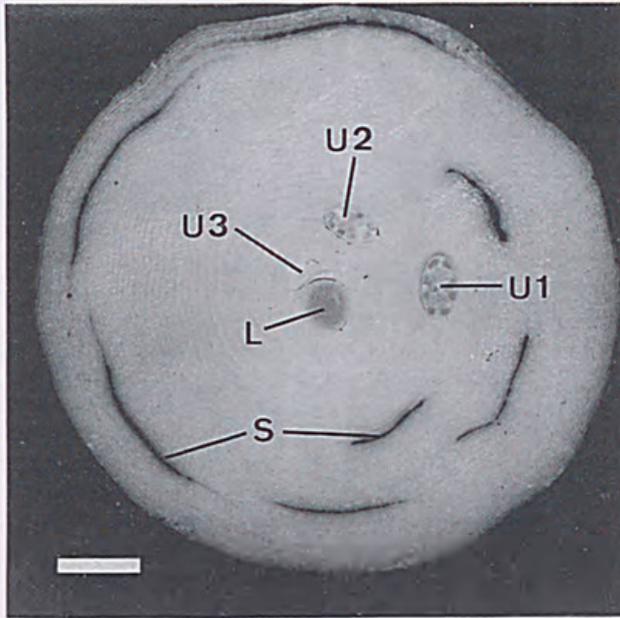


Fig. 7. Transverse section of *Crinum flaccidum* bulb collected at site 6 in June 1992 showing young unemerged leaves (L), remains of old scapes (S) and first, second and third unemerged inflorescences (U1, U2, U3). Scale bar = 20 mm.

Fig. 8. Transverse section of *Calostemma purpureum* bulb collected at site 3 on 17 May 1993 showing bases of emergent leaves (E) and two of the three scapes from the current season's flowering (S1 and S2). Scale bar = 10 mm.

Species	Site	Depth of bulb (mm)		Bulb diameter (mm)		Number of old scapes in bulb ¹		Number of unemerged inflorescences in bulb		Mean number of leaf bases between inflorescences ³	
		Mean	Range	Mean	Range	Mean ²	Range ²	Mean ²	Range	Mean	Range
<i>Crinum flaccidum</i>	5	246	150-358	68	18-116	4	1-7	4	1-6	5	3-7
<i>C. flaccidum</i>	6	303	195-600	85	47-146	4	1-8	4	1-7	5	4-7
<i>Calostemma luteum</i>	4	115	75-190	38	21-51	3	2-5	—	—	6	5-7
<i>C. purpureum</i>	1	129	85-195	36	18-47	2	1-4	—	—	7	5-9
<i>C. purpureum</i>	2	233	95-320	43	15-56	3	1-5	—	—	7	5-12
<i>C. purpureum</i>	3	139	85-205	34	15-50	3	2-4	—	—	7	5-9

Table 2. Bulb characteristics for *Crinum flaccidum*, *Calostemma luteum* and *C. purpureum*, combined over six sampling dates from March until September 1992. ¹For *Calostemma*, these numbers are the groups of three inflorescences formed each flowering season. ²These values do not include bulbs which have never initiated inflorescences. ³These are population means obtained by averaging bulb means. For *Calostemma*, they are the numbers of bases between groups of inflorescences from a single flowering season.

of groups of three inflorescences from up to five past flowering seasons were found.

At all sites in April–June, some bulbs contained the dead, dried remains of unemerged inflorescences; these are described here as being aborted (see phenology section). If less than three inflorescences emerge in a season, the remainder abort. Such abortion was never seen in *Crinum flaccidum*.

Unlike *Crinum*, no live unemerged inflorescences were found at any time from March to September, suggesting flower initiation no more than once a year rather than the more continuous *Crinum flaccidum* pattern. In the bulbs sampled on 7 September 1992, there was no sign of flower bud initiation in advance of the next summer's flowering; this presumably must occur some time in the September–January period given the normal flowering time. If flower bud initiation was not until summer, this could explain why spring to early summer rains do not produce flowering, whereas late summer rains do (see later). In *Calostemma*, leaf growth occurs between flowering periods, typically producing six to seven leaves. Unlike *C. flaccidum*, *Calostemma* inflorescences emerge from amongst the leaf rosette.

In *Crinum*, it takes from four to five years from germination to flowering (Hitchmough 1989), whilst for *Calostemma* it takes about three years (J. Belling, personal communication).

Maximum bulb depth recorded in *Calostemma* was 320 mm (Table 2).

Crinum flaccidum and *Calostemma* are often found in groups, clumps or colonies. In other bulbous geophytes, such behaviour has been related variously to bulb division and to restricted seed dispersal (see e.g. Nault & Gagnon 1993). These factors are considered here in turn.

Production of daughter bulbs by bulb division was found rarely (1 out of 41 bulbs for *Crinum*, 7 out of 72 for *Calostemma*). The daughter bulbs arise from lateral buds between the leaf bases. They are also produced occasionally by *Crinum asiaticum* (Pate & Dixon 1982) and prolifically by some African *Crinums* (Verdoorn 1973).

During fruit development of *Crinum flaccidum* and *Calostemma* the scape lengthens and bends under the weight of the fruit so that the attached fruits eventually come to lie on the soil surface. Groups of the large, heavy seeds can be found germinating exactly where they were deposited by the bent-over scapes. Given the rarity of bulb division, such restricted seed dispersal may be the main cause of clumping. Especially in *C. flaccidum*, two clumps can often be found approximately the same distance apart as the mature scape length, possibly representing offspring clumps. Similar behaviour

has been suggested in the amaryllid *Haemanthus* (Snijman 1984) and other monocot geophytes (Bierzychudek 1982) as well as in *Plantago lanceolata* and some other dicots (Gilbert 1989). Clumping can also be caused by bulb division (see e.g. Barkham 1992; Nault & Gagnon 1993) and mass germination from mice seed caches (Nault & Gagnon 1993).

In *Haemanthus*, with similar large, soft seeds to *Crinum* and *Calostemma*, there is little evidence that animals eat or disperse the seeds; these are probably too soft to survive passage through animal digestive tracts (Snijman 1984). The only animals recorded eating *Crinum flaccidum* or *Calostemma* seeds are emus, seen eating large quantities of *Calostemma* seeds at Hattah Lakes on a number of occasions (J. H. Browne, personal communication). Their faeces did not contain any intact *Calostemma* seeds, making dispersal by emus seem unlikely.

Phenology

The main aim of the account below is to examine the extent to which rainfall and temperature influence leaf and flower emergence.

Crinum. At site 5 on 4 March 1992, only 10% of plants had any live, emergent leaves and only 8% of plants were reproductive (mostly in fruit). This followed a very dry summer, with only four light showers; 0.6 mm in December, 3 mm in January and 3 mm on both 4 and 5 February. After 27 mm of rain in late March–April, 69% of plants had emergent leaves on 5 May and this reached a maximum of 90% by 16 June after further rain. However no further plants flowered additional to those which were reproductive on 4 March (Fig. 9).

The nearest rainfall station to site 6, 14 km away (Table 1), had similar rainfalls to site 5, with none in December–January and only 5 mm in February, on the 6th. We presume that site 6 itself received more rain than this because by 4 March, 75% of plants had emergent leaves and 42% were reproductive (nearly all in fruit). With no further rain, these active plants had died back by 28 March. As at site 5, April rains then produced widespread leaf emergence but no further flowering (Fig. 9).

The whole area received very high rainfall from September through to January 1993. Near Renmark, some flowers had appeared by mid-December 1992, with peak flowering in about mid-February 1993. Occasional flowers of *Crinum* can be found on a variety of dates, e.g. June and September 1992 (D. Frahn, personal communication).

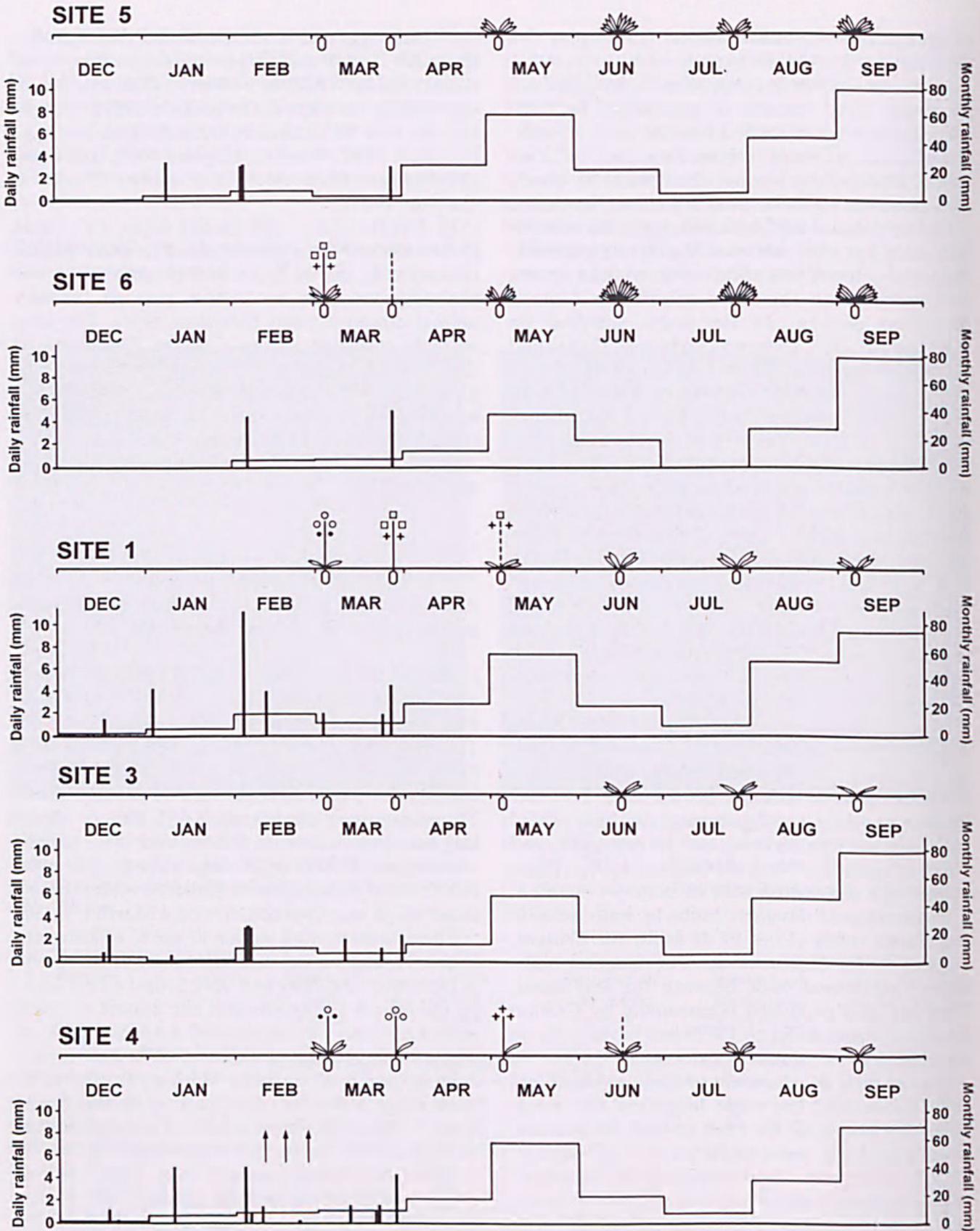


Fig. 9. Rainfall and phenology of *Crinum flaccidum* (sites 5 and 6), *Calostemma luteum* (site 4) and *Calostemma purpureum* (sites 1 and 3). Closed circles = buds, open circles = flowers, squares = fruits, crosses = seed dispersal, dashed lines = dead or senescent scapes. In the rosettes, mean leaf number is shown. Narrow, filled bars are daily rainfall (December 1991 to March 1992 only); wide, unshaded bars are monthly rainfall. For site 4, the arrows are the three irrigation events and the data shown are from the irrigated plot.

Leaf number per plant was highly variable, with up to 36 being recorded.

Our findings agree with earlier work that *C. flaccidum* generally has a summer–autumn flowering time in southern Australia (see Cunningham et al. 1981), with no flowers being found after May (see Howell 1984). In our sites, rains after March produced leaf emergence but no flower emergence.

In January–February–March, even light showers like 6 mm as at site 5 can produce some flowering (8% of plants; not shown in Fig. 9). As a result, the species flowers virtually every year in our study area (D. Frahn, personal communication). In the drier climate of Central Australia, flowers are usually seen only every two to three years (P. K. Latz, personal communication). The flowering response is very rapid. For example, 30 mm of rain on 28 February 1987 at Paringa was followed by a mass flowering event two weeks later (D. Frahn, personal communication). North of our area, earlier flowering can occur, e.g. November at Kinchega (T. Auld, personal communication) and June–July near Marree in northern South Australia (Lothian 1957).

Despite the view that *C. flaccidum* leaves die back in winter (Howell 1984), we found maximum leaf length then (see Cunningham et al. 1981) and dying back of leaves seemed more related to declining soil water supply. In *C. flaccidum*, only very young leaves showed intact leaf tips; the rest have lost their tips in such a way that they seem to have been cut off along a line straight across the leaf blade. In South African *Crinum*s, this is due to the leaves dying back to the base in winter and growing out again later (Verdoorn 1973). For *C. flaccidum*, low soil water supply seems the most likely cause. After good rains, *C. flaccidum* leaves over 1 m in length are common, up to 1.5 m (D. Frahn, personal communication).

The genus *Crinum* is regarded as basically tropical and sub-tropical, generally showing summer growth in summer rainfall climates (Hitchmough 1989). *C. flaccidum* has been treated as an exception to this, and regarded as a 'winter rainfall species' (Hitchmough 1989). However, in northern Australia *C. flaccidum* is dormant during winter, which is the dry season (Pate & Dixon 1982), so it may be more accurate to regard *C. flaccidum* as an adaptable species which grows whenever water is available.

Calostemma. Sites 1 and 2 results were similar so only the site 1 data are given. At site 1, there was only 1 mm of rain in December and 4 mm in January. However, following 11 mm on 4–5 February and 4 mm on the 12th, by 4 March

78% of plants had small emerged leaves and 74% were reproductive. After a dry March, most leaves died. Leaves, but not flowers re-appeared after April rains (Fig. 9). All plants remained in leaf but without flowers throughout winter.

Site 3 also had a very dry December–January, but only 9 mm of rain in February, spread over the 4th, 5th and 6th. On 4 March no plants were reproductive or had emerged live leaves; plants could only be found with difficulty. They remained like this through a March–April dry period and finally produced leaves after rains in May (Fig. 9). None became reproductive in 1992.

At site 4, February was even drier than site 3, with a total of only 7 mm from showers of 5, 1 and 1 mm on the 4th, 6th and 10th. As at site 3, no non-irrigated plants flowered in 1992. The irrigated plants all produced leaves by 4 March, and nearly all had flower buds or flowers. As at site 1, many leaves died back in the March dry period. Further leaves appeared after rains in May, but no further flowers (Fig. 9).

At sites 3 and 4 but not at sites 1 and 2, the unemerged inflorescences had aborted by 5 May, correlated with drier March–April conditions at the former two sites. Such abortion was not seen at sites 1 and 2 until 16 June, following good rains in May–June. It is likely that water deficit caused abortion at sites 3 and 4, but this is most unlikely at sites 1 and 2 where the cause may be related to frosts, low temperature or some other factor.

Despite the high rainfalls no flowers were seen at any *Calostemma* site from September to December 1992. In our area, flowers can be found in January but not in December. This also applies to *Crinum flaccidum* (our observations; F. E. Curtis, personal communication). Peak flowering occurred in early February 1993 both at site 3 and site 4 (J. H. Browne & D. Frahn, personal communication).

Our data agree with earlier suggestions of a summer–autumn (Cunningham et al. 1981) or January–April (Elliot & Jones 1982) flowering time for both species. As for *Crinum*, rains after March produced leaf emergence but no flower emergence.

In our study, a fall of rain of 15 mm in summer was enough to produce flowering, while 4 mm (site 4) and 9 mm (site 3) were not. Accordingly, *Calostemma* flowers much less frequently than *Crinum*; for example, at Kinchega National Park, with a mean annual rainfall of 236 mm, *Calostemma* has not been seen flowering since March 1987, while *Crinum flaccidum* has flowered several times at least (T. D. Auld, personal communication, 1992).

The most important trigger for growth in herbaceous perennials in the Mojave Desert is a fall

of rain of 25 mm or more in autumn and called by Beatley (1974) the critical rainfall event. For growth of herbaceous monocots in Perth, Western Australia, the critical rainfall event is greater than 17 mm in autumn (Bell & Stephens 1984). This is similar to the value for *Calostemma* shown here, whereas for large-bulbed species like *Crinum flaccidum* we believe that the value is significantly less.

Calostemma leaf growth continued throughout winter, confirming earlier views that *Calostemma* species show predominantly cool-season leaf growth (Cunningham et al. 1981; Hitchmough 1989). The leaves then decline in late spring (Hitchmough 1989). It is not known to what extent this is simply a reflection of declining soil moisture supply.

In our area, *Calostemma* plants are normally dormant in early summer until both leaves and scapes start growing after rain. In plants which are going to flower, the leaves usually produce 20 mm or so of green tissue and then stop, at the stage where they are either slightly emergent or not quite emergent. Leaf growth then resumes later once fruiting is over. This behaviour is probably why *Calostemma* is said to have 'leaves developing mainly after flowering' while *Crinum flaccidum* is said to have 'leaves well-developed during flowering' (Jessop 1981).

General discussion. Regarding geophyte life cycle types, the Amaryllidaceae is one of the main families in which many species in South Africa and the Mediterranean show hysteranthous behaviour (Dafni, Shmida & Avishai 1981), namely the flowers and leaves appear at separate times of the year, the flowers in early autumn before rain has fallen to break the summer drought, and the leaves a month or so later with the first rains (Dafni, Cohen & Noy-Meir 1981). In Israel, all autumn-flowering geophytes are hysteranthous (Dafni, Shmida & Avishai 1981). Although *Calostemma* (and *Crinum*) can flower in autumn (and summer), they show some leaf growth at flowering and do not flower in the absence of rain, so are not hysteranthous in the sense of Dafni, Cohen & Noy-Meir (1981). Hysteranthous is seen as an adaptation to declining rainfalls (le Maitre & Midgley 1992).

The flowering behaviour of *Crinum flaccidum* and *Calostemma* contrasts strongly with the predominantly spring flowering of the geophytes introduced to southern Australia from Europe and South Africa (see e.g. Parsons & Cuthbertson 1992). While the geophytes of southern Africa mostly flower in spring (Pierce & Cowling 1984), those in the Amaryllidaceae mostly flower in

autumn, presumably because the lack of seed dormancy in those with fleshy seeds restricts flowering and seed dispersal to the period shortly before the winter rains (Johnson 1993). The present data accord with this in general, although the flowering times are somewhat earlier than typical for taxa with fleshy seeds. Similarly, the bulbous Amaryllidaceae of the Sonoran Desert only produce leaves and flowers following summer rains, while some bulbous Liliaceae there are only active after winter rains (Shreve & Wiggins 1964). For *Crinum* and *Calostemma* in our area, at least some summer rain seems to be important for flowering to occur. It is not known if there are temperate areas where lack of such rainfall excludes them.

For the species studied here, growing in highly variable rainfall and flood regimes, relatively wet conditions allow both vegetative and reproductive development to occur, as at sites 1, 2 and 6, whilst drier conditions allow only vegetative development (e.g. sites 3 and 4). Given the extension of all three species into far drier areas than the study area, we assume that in drought conditions the bulbs can remain totally dormant for at least a year and probably for much longer (see also Evenari, Shanani & Tadmor 1971; Boeken & Gutterman 1989).

Germination and emergence

In the temperature trial, germination and leaf and root emergence were reduced at 2°C. Final percentages for all three processes were higher for *Calostemma* than *Crinum* at 15°C, while the reverse was true at 25°C (Table 3). This is consistent with the fact that *Calostemma* has a more temperate range, being restricted to areas south of the Tropic of Capricorn whilst *Crinum flaccidum* extends up to 18°S (Hewson 1987; Telford 1987). Germination

Temperature	2°C	15°C	25°C
Germination (%)			
<i>Crinum</i>	58	75	83
<i>Calostemma</i>	37	100	75
Leaf emergence (%)			
<i>Crinum</i>	10	45	70
<i>Calostemma</i>	0	77	53
Root emergence (%)			
<i>Crinum</i>	0	67	77
<i>Calostemma</i>	0	77	53

Table 3. Germination, leaf emergence and root emergence for *Calostemma* (site 2) and *Crinum* (site 6) after 68 days at three temperature regimes.

and seedling survival were surprisingly high at 2°C. In this, the populations behaved similarly to temperate taxa with recalcitrant seeds like some *Quercus* sp. rather than to most tropical taxa with recalcitrant seeds (Chin 1988).

Responses of seeds and seedlings to burial and watering

No effects of watering or burial on germination were found, but in the watered, buried treatment 24% of *Crinum* and 6% of *Calostemma* seedlings were killed by rotting of the cotyledon and seed as occurs in *Crinum erubescens* (Manasse 1990). In all treatments, every seed which germinated subsequently produced a foliage leaf. However rate of leaf growth and final leaf length was small in the unwatered treatments, bigger in the unburied watered treatment and bigger still in the buried watered one (Fig. 10). Root emergence occurred in all the watered seeds but not the unwatered ones; seed burial did not have significant effects on this. All three taxa showed similar treatment response (Fig. 10).

At the end of the trial, all taxa had produced more swelling in the area where the bulb forms in unwatered than watered treatments, suggesting that growth is somehow flexibly partitioned between either bulbs or roots depending on water regime. Maximum bulb size was 2.5 cm in diameter (in *Crinum*). Final leaf number was two to three. For *Crinum*, final root number was two, of which the oldest had a transversely enfolded surface and so was probably contractile.

Effects of seed storage

In the long-term dry seed storage trial, all seeds had germinated by 2 months. At 23 months, all *Calostemma* seedlings were desiccated, shrunken and dead. Most had produced the first, and some the second, leaf before dying. Some swelling in the bulb region occurred. However, half the *Crinum* seedlings were still alive, having produced two to three leaves of which the most recent on each plant was still alive. Bulbs were up to 15 mm diameter and still contained moist, white tissue, although they had begun to shrink. The seeds were totally desiccated and shrunken as before. In both taxa, roots had not developed beyond a tiny protrusion. However, the surviving *Crinum* seedlings, when planted in moist soil, rapidly produced healthy, normal roots. The longer survival time of *Crinum* than *Calostemma* seedlings is probably related to the much larger seed size of the former. For *Crinum asiaticum* seeds after two years in a desiccator, 62%

were still alive (made up of 28% seedlings and 34% ungerminated seeds) (Koshimizu 1930).

The positive geotropism of the elongating cotyledon means that the shoot apex can become buried, so that cryptocotyledon germination can occur as described for other Amaryllidaceae. This is thought to be an adaptation which protects shoot apices from drought or fire (Fahn & Cutler 1992). Whilst this can occur in *Calostemma* and *Crinum* without an external supply of water, our results suggest that further shoot burial due to root contraction cannot, as root growth was negligible in dry soil. The maximum extent to which the cotyledon can elongate is about 70 mm in *Crinum* and 50 mm in *Calostemma*. A preliminary trial placing seeds on dry coarse sand showed that in some cases the cotyledon elongates without burying the shoot apex while in others the shoot apex can be buried to maximum depths of 18 mm (*Crinum*) or 17 mm (*Calostemma purpureum*) after 2.5 months.

Buoyancy of the dispersal units

All *Calostemma* seeds germinated during the trial, so that, for all populations, treatment effects were on seedlings.

Nearly all *Crinum* seedlings remained alive throughout the trial (Table 4). Those in seawater showed little new growth. In fresh water, growth was faster, with all developing roots and leaves. Buoyancy remained high and after 62 days ranged from 86% in fresh water to 92% in seawater.

In *Calostemma*, in strong contrast to *Crinum*, most seedlings were killed by seawater and rotted, with final viable seedling percentages of 14 and 1 for the two populations (Table 4). None of these viable seedlings was still floating. All seedlings in fresh water remained viable, with buoyancies at 62 days of 56% (site 1) and 83% (site 2).

The data from fresh water strongly suggest that both *Crinum* and *Calostemma* are capable of water-borne dispersal in rivers and streams. In *Crinum flaccidum* and other *Crinums*, seed buoyancy is thought to be related to corky layers in the endosperm (Howell & Prakash 1990). For those Amaryllidaceae with large, soft, fleshy seeds, seed buoyancy may be a common corollary of their seed morphology. For example, water-borne seed dispersal has been suggested for most species of *Haemanthus* (Snijman 1984). In *Crinum erubescens*, seeds only sink if they are inviable (Manasse 1990).

While the salt water treatment did not adequately simulate wave action, ocean temperatures or risk of damage by marine organisms, the present buoyancy and viability data certainly make dis-

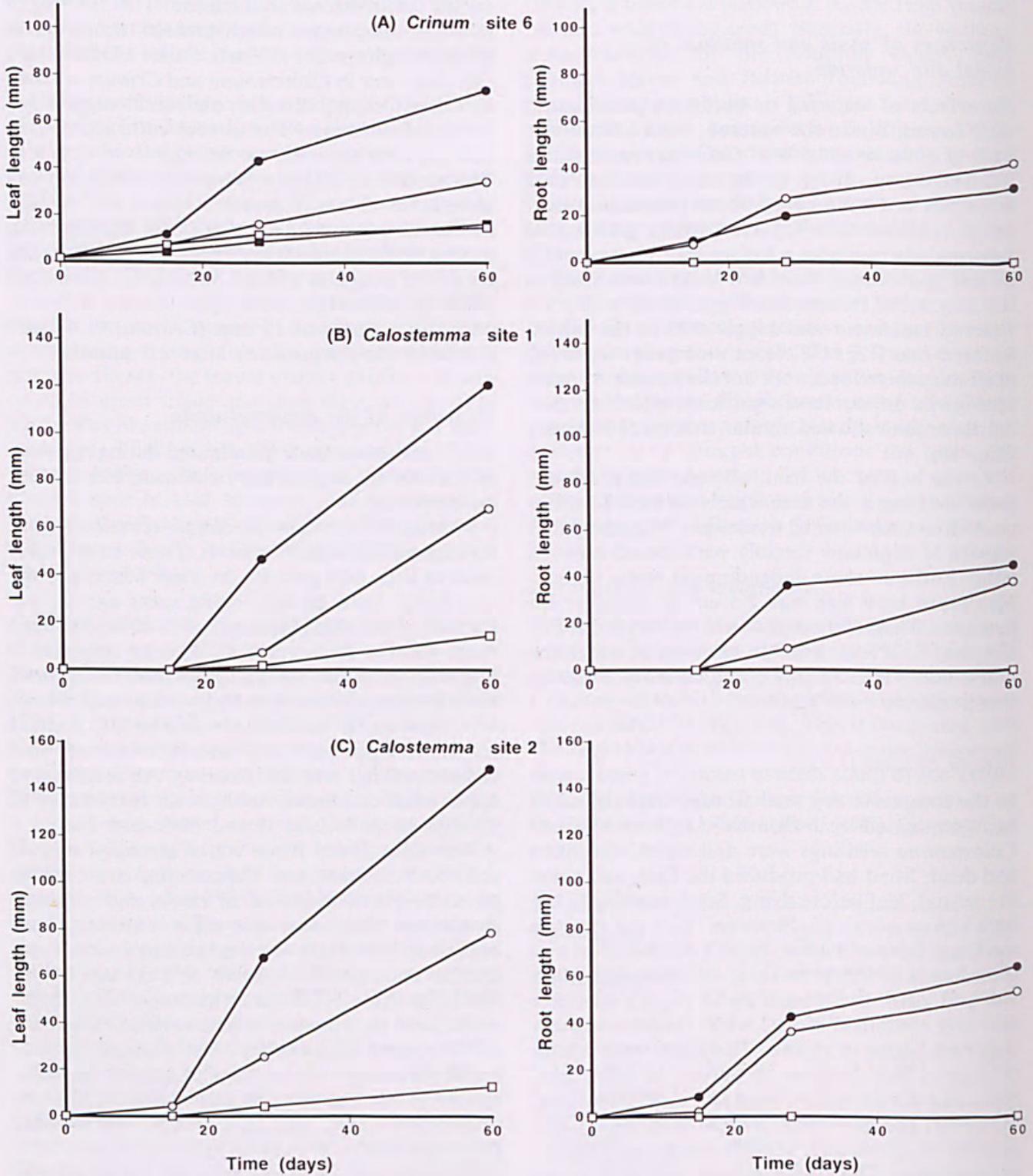


Fig. 10. Leaf and root growth for seedlings of *Crinum flaccidum* and two populations of *Calostemma purpureum* in four treatments; watered, buried (closed circles); watered, unburied (open circles); unwatered, buried (closed squares); unwatered, unburied (open squares). Closed squares not shown when coincident with open squares.

Species		Time (days)			
		22	35	49	62
<i>Crinum flaccidum</i>	Seawater	100	100	100	95
	Fresh water	100	100	100	100
<i>Calostemma purpureum</i>	Site 1	Seawater	100	1	1
		Fresh water	100	100	100
	Site 2	Seawater	100	26	14
		Fresh water	100	100	100

Table 4. Viability (%) of dispersal units of *Calostemma purpureum* and *Crinum flaccidum* in seawater and fresh water. N=80 for *Crinum* and 100 for *Calostemma*.

persal via ocean currents a possibility for *Crinum flaccidum*. Similar trials show that seedlings of the coastal *C. asiaticum* can float and remain viable for more than two years (Koshimizu 1930) and seeds and seedlings of both it and *C. americanum* are said to float in seawater for at least a month and to be washed up live on beaches (Gunn & Dennis 1976). Thus the behaviour of *C. flaccidum* in seawater echoes that of other members of the genus, even though its present distribution is explicable without invoking dispersal by ocean currents. The majority of plant dispersal units are thought not to float in either fresh water or seawater (Gunn & Dennis 1976).

Calostemma purpureum dispersal units are clearly much less able both to float and to remain viable in seawater than those of *Crinum flaccidum*, not surprisingly in a genus with no known coastal connections.

CONSERVATION

It is hard to assess the conservation status of these taxa. In Victoria, the Mallee Survey of 1985–86 sampled five stands of *Calostemma* and seven of *Crinum* on public land (Cheal & Parkes 1989 and personal communication). There are other public land stands as well and probably at least half the public land stands are in biological reserves. Low palatability to grazing mammals is also in favour of these taxa (Cunningham et al. 1981). Sheep and/or rabbit grazing damage has been seen on *Calostemma* leaves at times but not on those of *Crinum* (F. E. Curtis, personal communication). It has been reported to us that wild pigs dig up and eat *Crinum flaccidum* bulbs over big areas on Lindsay Island (J. Hart, personal communication). Work is needed on this, on the extent of seed

predation by emus (as seen at Hattah–Kulkyne National Park) and on whether there is an effect of changing flood regimes on the ecology of these taxa before we understand whether there are significant threats to them. Our sites would not have been flooded since 1981 and probably earlier. From the wide range of plant sizes present (including bulb diameters), we assume that flooding is not necessary for recruitment.

The low palatability of *Crinum* and *Calostemma* is not surprising given the widespread development of poisonous alkaloids in geophytes including those in the Amaryllidaceae (Tomlinson 1980; Dahlgren et al. 1985).

After a paddock containing *Crinum flaccidum* was ploughed in the Paringa area, the adult *C. flaccidum* plants survived by resprouting from the bulbs (D. Frahn, personal communication).

CONCLUDING DISCUSSION

When the main seasonal stress is drought, the stored water and carbohydrate found as part of the bulbous habit allow the plant to survive prolonged drought and then to sprout as soon as rain falls in *Calostemma* and *Crinum flaccidum*. Flowering can occur as little as two days after heavy rain in *Habranthus* (Solbrig & Simpson 1977). Possession of a bulb both gives the plant temporary independence from an external water supply and allows preformation of flower buds within the protection of a storage organ (Burt 1970). Such preformation (found in both *Calostemma* and *Crinum*), in turn allows plants to respond immediately to favourable growing conditions and to complete their life cycles quickly (Caldwell 1969), the rain merely serving as a trigger for final development of the inflorescence (Danin 1983). The bulb also facilitates partial or complete uncoupling of the leafing and flowering phenophases (Johnson 1993).

Apart from behaviour related to their bulbs, *Calostemma* and *Crinum flaccidum* also share with many other Amaryllidaceae the possession of large, buoyant, non-dormant, water-rich seeds. These characteristics have important implications for seed dispersal (see above). The effects of non-dormancy of seeds on seedling establishment are not well-understood. It has been suggested that seed non-dormancy is a strategy allowing seedlings of *Crinum flaccidum* to become established either before winter frosts (Howell 1984) or at a time when other species are competitively disadvantaged (Howell & Prakash 1990). Further work is needed before this issue will be understood.

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