

The 'inch flora': some observations on the morphology and seed biology of annual plant species common in semi-arid woodlands of western Victoria

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Abstract

Annual plants are an under-studied component of the Victorian flora. We describe the morphology and seed biology of ten species common to semi-arid woodlands in far western Victoria: *Actinobole uliginosum*, *Blennospora drummondii*, *Calandrinia granulifera*, *Centrolepis strigosa*, *Millotia tenuifolia*, *Podotheca angustifolia*, *Pogonolepis muelleriana*, *Quinetia urvillei*, *Rhodanthe pygmaea*, *Triptilodiscus pygmaeus*. Two forms of growth morphology were observed—'erect' and 'branched'. Three species were found to have myxospermous seeds. Here, the seed coat contains a mass of dry mucilage which hydrates and swells rapidly on contact with water. Eight species appear to have dormant seed at the time of dispersal, presumably a strategy to avoid germination in summer. This dormancy was overcome when seed was heated to 35°C for 4 weeks. Our preliminary studies confirm that annuals are a fascinating group of plants which warrant much better ecological understanding. Further quantitative investigation of the seed biology (particularly the extent and role of myxospermy), seed germination requirements (including dormancy-breaking mechanisms) and developmental anatomy are clearly necessary. (*The Victorian Naturalist* 129 (1) 2012, 4-9).

Keywords: germination, growth form, myxospermy, seed dormancy, annual flora

Introduction

Annual plants of the world's arid ecosystems can be divided into those that flower and seed in the summer and those that carry out those activities in winter-spring. Annual species from low rainfall zones in western Victoria fit comfortably into the winter-spring active group, using the winter-dominant rainfall that occurs in this region. While annuals are a common component of semi-arid woodlands and mallee shrublands in southern Australia (e.g. Rice and Westoby 1983; van der Moezel and Bell 1989; Morgan *et al.* 2011), few species have received detailed ecological study. Indeed, of the species we studied, only the seed dormancy and germination of *Actinobole uliginosum* has been previously reported (Hoyle *et al.* 2008). Hence, in this contribution, we introduce aspects of the morphology and seed biology of a suite of annual species common to semi-arid eucalypt woodlands in Victoria based on our observations of these much-overlooked plants.

Morphology and seed biology

We studied 10 species typically found in the 'inch flora' of semi-arid woodlands in western and north-western Victoria (Table 1). One spe-

cies (*Quinetia urvillei*) is classified as rare in Victoria. The maximum height of all species is <100 mm, with several species strictly <30 mm tall at maturity. All species we have observed demonstrate one of two characteristic growth morphologies (Table 1). Species either develop (i) a single shoot which bears just one terminal inflorescence ('erect' habit; Fig. 1), or (ii) one or more additional shoots are produced from lateral buds on the primary axis ('branched' habit; Fig. 2). These lateral shoots appear to grow diageotropically and then curve upwards, bearing either inflorescences or further shoots that, in turn, bear inflorescences in a more or less erect position. Six species have 'branched' habit but there is much variation. *Blennosperma drummondii*, for instance, omits the development of the lateral shoot stage and has either just one single shoot with a terminal inflorescence, or two or more laterals that grow at an angle that is steeply inclined to the vertical, each terminated by a single smaller inflorescence. In *Pogonolepis muelleriana*, it is very clear that when additional branches arise from the diageotropic laterals, the size of the inflorescences produced are smaller than those produced terminally by

Table 1. Height, growth form morphology and evidence of myxospermy for ten annual plant species common to semi-arid woodlands in western Victoria. * Height <30 mm; ** Comprising a single shoot which may bear just one terminal inflorescence (erect), or one or more additional shoots are produced from lateral buds on the primary axis (branched); *** Seeds rich in mucilage which hydrates rapidly on wetting; **** Seeds surrounded by hairs that turn mucilaginous on wetting.

Species	Family	Inch Plant*	Morphology**	Myxospermous***
<i>Actinobole uliginosum</i>	Asteraceae	Strict	Branched	Yes
<i>Blennospora drummondii</i>	Asteraceae	Strict	Branched	Yes
<i>Calandrinia granulifera</i>	Portulacaceae	Strict	Branched	No
<i>Centrolepis strigosa</i>	Centrolepidaceae	Strict	Branched	No
<i>Millotia tenuifolia</i>	Asteraceae	No	Erect	No
<i>Podotheca angustifolia</i>	Asteraceae	Variable	Branched	No
<i>Pogonolepis muelleriana</i>	Asteraceae	Strict	Branched	Yes
<i>Quinetia urvillei</i>	Asteraceae	No	Erect	No
<i>Rhodanthe pygmaea</i>	Asteraceae	Variable	Erect	No****
<i>Triptilodiscus pygmaeus</i>	Asteraceae	Variable	Erect	No

the original diageotropic shoot. This is equally true with *Blennospora drummondii*.

Three species (*Actinobole uliginosum*, *Blennospora drummondii*, *Pogonolepis muelleriana*) have myxospermous seeds. Here, the seed coat contains a mass of dry mucilage when the seeds are shed. The mucilage hydrates and swells rapidly on contact with water, in some cases in as

little as a few minutes (Fig. 3). In *Rhodanthe pygmaea*, seeds are surrounded by hairs that turn mucilaginous on wetting. Myxospermy

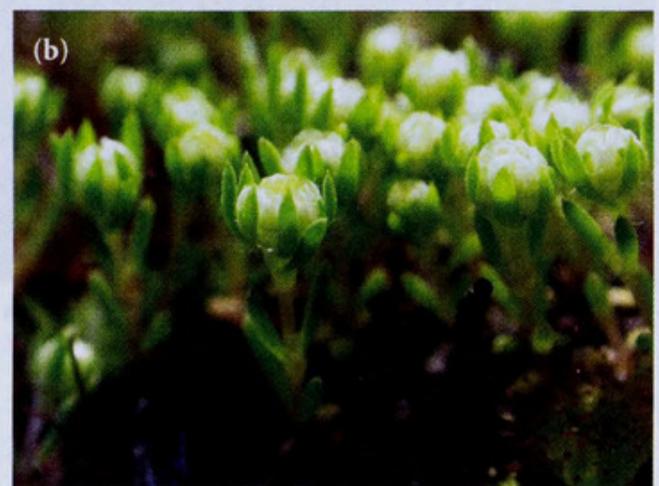


Fig. 1. Examples of annual plants with 'erect' growth morphology where a single shoot bears a terminal inflorescence. (a) *Millotia tenuifolia*, (b) *Siloxerus multiflorus* and (c) *Gnephosis drummondii*. Photos by Pete Green.



Fig. 2. *Actinobole uliginosum* is an example of a species with 'branched' growth morphology where one or more shoots are produced from lateral buds on the primary axis. Photo by Pete Green.

has been studied in many species of desert plants (reviewed by Fahn and Cutler 1992), and been found to be common in plant families such as Plantaginaceae and Asteraceae. Interestingly, myxospermy is common in winter annuals of Israel and South Africa (van Rheede van Oudtshoorn and van Rooyen 1998); however, it does not appear to have been investigated much in Australian annual species. A number of theories have been suggested about its significance and myxospermy might be important when seeds are both wet and dry. We are inclined to the idea that it assists the seed to attach to the soil, giving the radicle something to push against as it starts to elongate, minimising the risk of pushing the root hair zone away from the soil surface. This might be particularly important where the substrate is covered by a biological soil crust as is common in semi-arid areas. Clearly this is an area in need of much greater study.

Observations on developmental anatomy

A feature of annual plants is their ability to grow rapidly after germination, establish one or more shoots that bear inflorescences, and then to flower and produce seed rapidly. One can speculate that achieving this end has sparked the creation of the 'branched' morphology we observed. First, photosynthetic tissue needs to be close to the sites at which photosynthates are consumed, because it is almost an axiom of phloem function that the shorter the distance between source and sink, the more rapidly photosynthetic products are moved to their destination. In plants with this 'branched' morphology, such morphology guarantees that the sinks and the source of photosynthates are never more than a few centimetres apart.

The water and mineral nutrition for these axes will be drawn from soil and the root systems, and some water will no doubt be taken up



Fig. 3. Evidence of myxospermy in *Blennosperma drummondii* (foreground) compared to a species which is not myxospermous (*Podotrocha angustifolia*, background). In this example, the mucilage had hydrated and swelled rapidly on contact with water applied 15 minutes previously. Photo by John Morgan.

by absorption through growing leaf surfaces, in some cases as dew; however, there are no studies on the developmental anatomy and histology of any of these species with these issues in mind. The uptake of water, photosynthates and minerals into the developing flower heads and seeds of these species, with the urgency created by the relatively short growing season, and its timing with respect to vascular development, will likely be of considerable interest to ecophysiologicalists.

Our preliminary observations suggest that the root system engages in a similar pattern of development to that of the shoots. A primary radicle emerges rapidly from below the hypocotyl which may or may not have a corona of hypocotyl hairs. During this stage, many seedlings have their cotyledons still encased in a seed coat and, in the case of myxospermous species, the seed coats are firmly stuck to the substrate. This radicle grows vertically and rapidly, reaching a depth of 70 mm when the coty-

ledons have barely finished unfolding. In soil, this primary root develops lateral branches at regular intervals (5–10 mm), laterals which are also strongly diageotropic from the moment they emerge from the stele of the parent root. These laterals then produce vertical roots with numerous root hairs which can adhere strongly to sand grains in the soil. A detailed analysis of the root morphology, including development of the mycorrhizas known to be a feature of plants growing in these habitats (Warcup and McGee 1983), and of the soil sheaths identified by McCully (1987), which have been shown to permit non-rhizobial N_2 fixation, await detailed study.

Preliminary studies of germination

We collected ripe seeds from all species in October–November 2009 from a number of state forests between Horsham, Dimboola and Goroke in western Victoria to examine the cues for germination in annuals. In particular, we were interested in the temperatures that promote germination and the environmental cues

Table 2. Summary of the germination response of ten annual plant species to move-along (MA1-3) treatments on fresh seed. A fourth germination treatment on fresh seed was preceded by heating seeds at 35°C for four weeks prior to sowing.

Species	Experimental Treatment			
	MA1: 30°C (12 hrs light/dark)	MA2: 20°C (12 hrs light/dark)	MA3: GA ₃ @ 20°C (12 hrs light/dark)	Seed heating @ 35°C then 20°C (12 hrs light/dark)
<i>Actinobole uliginosum</i>	No	No	No	Yes
<i>Blennospora drummondii</i>	Yes - substantial	Not tested	Not tested	Yes
<i>Calandrinia granulifera</i>	No	Yes - substantial	Not tested	Yes
<i>Centrolepis strigosa</i>	No	No	Yes - minimal	No
<i>Millotia tenuifolia</i>	No	No	No	Yes
<i>Podotheca angustifolia</i>	No	No	No	Yes
<i>Pogonolepis muelleriana</i>	No	No	Yes	Yes
<i>Quinetia urvillei</i>	No	No	No	Yes
<i>Rhodanthe pygmaea</i>	No	No	No	Yes
<i>Triptilodiscus pygmaeus</i>	No	No	Yes	Yes

that might be necessary to overcome dormancy. We do not report germination experiments *per se*; rather, we make observations of likely germination strategies in these species as a precursor to more formal study.

Within two months of seed collection, we started Germination Trial 1. We placed 70-100 filled seeds of each species on Whatman No. 1 filter paper in individual 90 mm Petri dishes and placed them at 30°C constant temperature in a Thermoline growth cabinet (12 hrs light/12 hrs dark). We were interested in whether fresh seed would resist germination upon wetting at high temperature. Within one week, *Blennosperma drummondii* had produced a few germinants; all other species showed no signs of activity. After 3 weeks, *Blennosperma* had achieved a germination of approximately 70%, but no other species germinated at this temperature. At this time, we moved all Petri dishes to 20°C constant temperature (12 hrs light/12 hrs dark) (Germination Trial 2) in a 'move-along' experiment (i.e. seed exposed to one treatment that does not induce germination are moved to a second treatment in an attempt to do so).

Calandrinia granulifera germinated rapidly when seeds were moved to 20°C; >80% germination was observed within three days of starting this trial. No germination, however, was recorded for any other species at this temperature suggesting that seeds have a physiological dormancy upon being shed.

After another 3 weeks, we started Germination Trial 3 in an attempt to overcome dormancy of seeds. Gibberellic acid (GA₃), known from the literature to be capable of breaking dormancy in some desert annuals (Plummer and Bell 1995), was added to all Petri dishes where no germination had previously been recorded (i.e. 8 of the 10 species). We treated each Petri dish with 7.5 ml of GA₃ (at 200 mg/l), and then returned dishes to the growth cabinet at 20 °C (12 hrs light/12 hrs dark). This experiment released the dormancy of some species including *Centrolepis strigosa*, *Pogonolepis muelleriana* and *Triptilodiscus pygmaeus*; however, for *Actinobole uliginosum*, *Millotia tenuifolia*, *Podotheca angustifolia*, *Quinetia urvillei* and *Rhodanthe pygmaea*, no germination was observed.

Finally, in Germination Trial 4, we exposed filled seed of all species to 28 days of heating at 35 °C. This is considered a form of dry after-ripening. Heating was achieved by placing seeds in paper bags inside a thermostatically controlled oven. After heating, 70-100 seeds of each species were placed on Whatman No. 1 filter paper in 90 mm Petri dishes, as before, and placed at 20 °C constant temperature, with 12 hrs light / 12 hrs dark. All species, except *Centrolepis strigosa*, germinated in the 3 weeks after we started this trial. Germination was high; 60-80% germination was observed in all species. We summarise these outcomes in Table 2.

We conclude from these observations that the common seasonal pattern of high summer temperatures and a variable period of low rainfall combine to render the seed of many annual species initially dormant upon dispersal. *Blennospora drummondii* and *Calandrinia granulifera* would appear to be exceptions; they await the arrival of appropriate temperatures and moisture to germinate. As the summer progresses, the high temperatures that seeds experience at (or near) the soil surface appear likely to slowly reduce the dormancy of the embryo, which eventually responds to the combination of cooler conditions and moisture by rapidly germinating. *Actinobole uliginosum*, *Millotia tenuifolia*, *Podotheca angustifolia*, *Quinetia urvillei* and *Rhodanthe pygmaea* all appear to respond in this manner.

Conclusions

The ecology of annual plants has largely been overlooked in southern Australia, despite the important contribution they make to diversity in semi-arid woodlands and mallee shrublands. Hence, our observations were undertaken in the almost complete absence of published literature. By describing the variation that exists in morphology and seed biology of this group, we have demonstrated that annual plant species exhibit a fascinating array of strategies to cope with their environment. We hope that this stimulates further quantitative study of the 'inch flora'.

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One hundred and twenty-eight years ago

MALLEE HENS AND THEIR EGG MOUNDS

BY A.J. CAMPBELL

(Read before the Field Naturalists' Club of Victoria, Dec. 8, 1884)

...When anything is mentioned about the Mallee country, there is instantly conveyed to the mind of many people a vivid picture of desert land, the abode only of wild dogs and latterly of rabbits. Never was there a greater error. It is predicted that in the near future the Mallee country will be among the most fruitful and productive parts of the Colony of Victoria. The Mallee scrub is a species of dwarf gum-tree or Eucalyptus, and 10 to 12 small trees spring from the one root. The foliage spreads over-head 10 to 20 feet above the ground. The wood is hard and durable, the bark as a rule smooth and thin.

This scrub generally grows in a loose yellowish sandy soil, and in long belts varying from half a mile to miles in breadth. Between the belts there are corresponding good tracts of country more openly timbered with bull-oak, and still more thickly in parts where they are interspersed with one or more varieties of gum trees, Murray pine, &c.

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