Chapter 2

GERMINATION IN TWO AUSTRALIAN SPECIES OF *FRANKENIA* L., *F. SERPYLLIFOLIA* LINDL. AND *F. FOLIOSA* J.M.BLACK (FRANKENIACEAE) – EFFECTS OF SEED MASS, SEED AGE, LIGHT, AND TEMPERATURE.

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ABSTRACT

Easton, L.C. & Kleindorfer, S. (2008) Germination in two Australian species of *Frankenia* L., *F. serpyllifolia* Lindl. and *F. foliosa* J.M.Black (Frankeniaceae) – effects of seed mass, seed age, light, and temperature. *Transactions of the Royal Society of South Australia* 132(1): 29-40.

We test the effects of seed mass, temperature (16°C, 24°C, 30°C), and seed age (1 year, 7 years, 20 years) on the germination rates of two arid zone plant species that differ in seed mass, but occur within the same genus (*Frankenia*) to determine if these factors, or a combination of these factors, influence germination rates. *Frankenia serpyllifolia sens. lat.* produces one or two larger seeds per fruit whereas *F. foliosa* produces up to 27 smaller seeds per fruit. Both of these species co-occur geographically in northern South Australia and experience similar abiotic conditions (unpredictable rainfall, extremes in temperature, poor soil conditions). The results showed that germination success by Day 21 was similar between the species, whereas we found significant differences in germination rates during the first week of germination. *Frankenia serpyllifolia sens. lat.* seeds germinated rapidly and were less temperature dependant for germination success. *Frankenia foliosa* seeds were relatively slower to germinate and germination rates were higher at lower temperatures. Differences in germination rates were demonstrated to result from an interaction between seed mass/seed age (η_p^2 = 0.30), and an interaction between seed age/temperature (η_p^2 = 0.19), but only minimally from an interaction between seed mass/seed age/temperature (η_p^2 = 0.08).

Key words: *Frankenia*, Australian arid zone plants, germination rates, seed mass, halophytes

INTRODUCTION

This paper reports on germination in two of the 46 endemic Australian species of *Frankenia* L., *F. serpyllifolia* Lindl. *sens. lat.,* and *F. foliosa* J.M.Black, that both occur in the arid 'Far North' of South Australia, southern Northern Territory, far western New South Wales, and north-western Victoria (Barnsley 1982). Data on life history strategies in *Frankenia* are limited. In particular, published data on *Frankenia* germination strategies are sparse. One notable exception is Brightmore's (1979) studies on *F. laevis* L. in Britain.

Knowledge of the germination of seeds of arid zone plants, and halophytes in particular, is limited (Ungar 1978). In Australia seed germination and its relationship to various environmental factors is still poorly understood for many arid zone endemic plants (Groves *et al*. 1982). The most widely studied flora in Australia are taxa from temperate or tropical zones (reviewed in Bell 1999). The relatively fewer published studies examining arid zone species generally focus on annual or ephemeral species, notably species with agricultural importance, significance to mine-site rehabilitation, or seed dormancy breaking by fire (e.g. Mott 1974; Tothill 1977; Bell & Bellairs 1992; Roche *et al.* 1997; but see Jurado & Westoby 1992; Bell *et al*. 1993; Leishman & Westoby 1994).

Arid zone and halophytic plants are subjected to unpredictable abiotic conditions including long periods of water stress, extremes in temperature, high levels of sodicity, poor nutrient availability, sporadic and inconsistent rain, and poor soil texture. Arid zone and halophytic plants have therefore developed germination, seedling establishment, and reproduction strategies that allow for perpetuation of the species in these conditions (Orozco-Almanza *et al*. 2003).

Frankenia is interesting in that some species have fruits with low ovule numbers and consequently few larger seeds, while other species have fruits with numerous ovules and many smaller seeds. While this is not unusual within taxa, these two strategies are usually associated with differing specific environmental conditions. For example, in some closely related Proteaceae species, larger-seeded species occur in colluvial sands that are low in nutrients and soil-water, and smaller-seeded species occur in the more nutrient rich, higher water-holding capacity limestone (Mustart & Cowling 1992). In *Frankenia*, species representing these two strategies often occur together (Easton personal observation).

A cornerstone of life history theory addresses an individual's decision to invest all available, albeit limited, resources for reproduction into many small or a few large offspring. This differential reproductive allocation often represents a trade-off in the quantity versus quality of offspring (Smith & Fretwell 1974), and in plants, this is reflected in the size of seeds versus the number of seeds per fruit. Experimentally, large seeds have been shown to have an advantage over small seeds by having greater nutrient reserves for the young seedlings to enable them to grow larger and to tap resources earlier (e.g., water, sunlight, mineral nutrients). Thus, seedlings from large-seeded species could establish under a range of environmental conditions that could not be tolerated by seedlings from small-seeded species, notably competition for resources, and the capricious drought prone environments (Salisbury 1942, 1974; Wulff 1986; Geritz *et al*. 1999; Susko & Lovett Doust 2000; Leishman *et al*. 2000; Westoby *et al*. 2002; Moles & Westoby 2004).

Further to this, *Frankenia* may have potential in revegetation, mine-site rehabilitation, or salinity remediation projects. The revegetation potential of *Frankenia* has largely been overlooked, as little is known of its ecology (Semple & Waterhouse 1994). Advantages in utilizing species of *Frankenia* for revegetation projects are recognized by their vast biogeographical range which includes many inhospitable regions. *Frankenia* is an halophytic genus, and some species (e.g. *F. foliosa*) can tolerate highly saline areas such as the margins of salt lakes and salt pans (Whalen 1986). Their unpalatability, even to endemic fauna, promotes species of *Frankenia* as valuable taxa in revegetation programs (Semple & Waterhouse 1994).

Here we test the effects of seed mass, temperature, and seed age on the germination of *F. serpyllifolia sens. lat.* and *F. foliosa* to determine if these factors, or a combination of these factors, influence germination. Germination of seeds to temperature is important as it determines the time of year (season) for successful seedling establishment (Mott 1974; Bell *et al*. 1993). Optimal temperature range for successful germination has been demonstrated to be related to seed mass (Bell *et al*. 1995). Seed age has been demonstrated to be related to seed mass in that smaller seeds can remain viable (in seed banks) over longer periods than larger seeds (Leishman *et al*. 2000). We also test for the requirement of light for seed germination.

We test seed from *F. serpyllifolia sens. lat.* and *F. foliosa* under a standardized set of treatment conditions to compare interspecific variation in germination. We predict: (1) higher germination success and faster germination rates in *F. serpyllifolia sens. lat.,* the larger-seeded species, at each temperature, (2) a narrower optimal temperature range for germination success in *F. foliosa*, the smaller-seeded species, and (3) higher germination success for the older seed age categories in *F. foliosa,* the smaller-seeded species.

MATERIAL AND METHODS

Test species

The focal *Frankenia* species in this study were *F. serpyllifolia sens. lat.* and *F. foliosa*, two species commonly occurring in the arid 'Far North' of South Australia. This study follows the taxonomic relationships described by Whalen (1986) whereby species closely related to *F. serpyllifolia*, including *F. planifolia* Sprague & Summerh. and *F. connata* Sprague, are considered con-specific with *F. serpyllifolia.* In this study, *F. planifolia*, *F. connata,* and *F. serpyllifolia* populations comprise the group '*F. serpyllifolia sens. lat.*' and are subsequently referred to as *F. serpyllifolia*. Seeds from populations with voucher registrations prefix 'LE' were collected by one of the authors (L. Easton). The remaining seeds were obtained from collections in the School of Biological Sciences, Flinders University[1].

Frankenia serpyllifolia is a small shrub that grows to 20 cm in height, has one or two large seeds per fruit (mean seed mass 0.55 mg ± 0.005 se), and is often associated with, but not restricted to, red, clayey sands and clay-pans. *Frankenia foliosa* is a compact dwarf shrub that grows to 10 cm in height, has up to 27 seeds per fruit (mean seed mass 0.072 mg ± 0.001 se), and is often associated with, but not restricted to, saline, gypseous salt-pans and salt lakes. Seeds were collected from naturally occurring populations in early autumn in 1985, 1997, and 2001, and stored in their respective fruit at room temperature in paper bags at optimal storage conditions (i.e. <21°C, <30% humidity, away from sunlight – see Wrigley & Fagg 2003). Seeds from all species were periodically germinated over time to check for loss of viability. No degradation in seed germinability, or indication of seed dormancy was found during this time period. *Frankenia* seeds have been demonstrated to retain *ex situ* viability for at least seven years (but see Chapter 8). Seed age at the time of experimentation was 1, 7, or 20 years. Preliminary studies demonstrated that *F. serpyllifolia* and *F. foliosa* seeds germinate without a period of after-ripening and do not require any pre-treatment (Easton unpublished data). This

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* Herbarium voucher specimens, collection details including year of seed collection, and number of plants sampled per population are available at Flinders University, School of Biological Sciences.[1]

supports observations of *F. laevis* from Europe (Brightmore 1979), and *F. ericifolia* Chr. Sm. ex DC from the Cape Verde Islands (Brochman *et al*. 1995).

Light requirements for germination

In order to establish our germination experimentation protocol, it was first necessary to determine the light requirement of *Frankenia* species for germination. Four replicates of 15 seeds were sown on Whatman Number 1 filter paper in 500 ml plastic containers. The filter papers were placed on round perforated PVC disks supported by 10 mm legs, thus suspending the filter paper and seeds over a 100 ml reservoir of distilled water (adapted from Zubrinich 1990). The filter paper and the seeds were in constant contact with water. Containers were sealed to prevent evaporation. One treatment (dark) was covered with aluminium foil, and therefore kept in total darkness, while the other treatment (light) was subjected to a 14 hour day and 10 hour night regime with Silvanian Gro-lights (25 µmol $m^{-2}s^{-1}$, 400 – 700 nm). Containers were placed into a 24°C controlled temperature room for 21 days. On Day 21, the aluminium foil was removed from the replicates of the 'dark' treatment, and germination rates of 'light' and 'dark' treatments were scored. Seeds were considered germinated with the emergence of the radicle. Containers from the 'dark' treatment were left uncovered for an additional 7 days to test for further germination. Ungerminated seeds were dissected (cut test) to establish their possible viability (see Verger *et al*. 2003).

The light requirement for germination was calculated using the Relative Light Germination (RLG) index (Milberg *et al*. 2000);

$$\mathbf{RLG = Gd/(Gd + Gl)}$$

where **Gd** is the number of seeds that germinated when not subjected to light, and **Gl** is the number of seeds that germinated when subjected to periods of light. RLG indices represent a range of values from 0 (light essential for germination) to 1 (no light required for germination). Chi-squared analyses calculated differences in germination success between the two species.

Effects of seed mass, seed age, and ambient temperature

Table 1 lists the locations of populations from which seeds of *F. foliosa* and *F. serpyllifolia* were collected for this study. Experimental design followed a completely randomized block design, whereby the following arrangement of effects were tested; population/species effect (three populations per species with four replicates per population), species effect (categorically 'larger seed' and 'smaller seed'), seed age effect (1 year, 7 years, 20 years), and ambient temperature effect (16°C, 24°C, 30°C). This experimental design produced a total of 216 units (containers).

Containers were placed in constant temperature rooms and illuminated on a 14-hour day and 10-hour night regime with Silvanian Gro-lights (25 µmol $m^{-2}s^{-1}$, 400 – 700 nm). Seeds were checked every second day, at which time, germinated seeds were removed. Seeds were considered germinated with the emergence of the radicle. The experiment was terminated after 21 days, and ungerminated seeds were dissected (i.e. cut test) to establish their viability (see Verger *et al*. 2003).

Statistical analyses

Statistical analyses were calculated using SPSS Version 10 (SPSS Inc. 2002). To satisfy requirements of normality for statistical analyses, data were arc-sine transformed. Germination rate was calculated using a modified Timson Index of germination velocity;

$$\textbf{Germination rate} = \Sigma \mathbf{G}/\boldsymbol{t},$$

where **G** is the percentage of seed that germinated at 2-day intervals, and ***t*** is the total number of days of the germination period (Khan & Ungar 1984). The greater the value of the Timson index, the more rapid is the germination rate. The maximum value for germination rate at Day 8 was 12.50, and the maximum value at Day 21 was 4.76. A Repeated Measures ANOVA investigated differences in germination rates between the two species at 2-day intervals. Repeated Measures ANOVA manages the non-independence of sampling the same populations over time (Dytham 2003). Partial Eta Squares (η_p^2), a measure of effect size, quantified the degree of association or correlation between the effects (seed size/seed age/temperature) and germination rate (SPSS Inc. 2002). Thus η_p^2 is the proportion of variance in germination rates that are attributed to each effect (SPSS Inc. 2002).

Germination success was calculated as the percentage of seeds per treatment factor that had germinated by Day 21. A Single Factor ANOVA examined differences in germination success at Day 21.

RESULTS

Light requirements for germination

Table 2 lists germination success for *F. serpyllifolia* (larger-seeded) and *F. foliosa* (smaller-seeded) in total darkness (no light requirement) and in the day/night regime (light requirement) after 21 days. Germination success was higher in total darkness for *F. serpyllifolia* (RLG = 0.31) than *F. foliosa* (RLG = 0.03) (χ^2 = 22.28, P<0.001). *Frankenia foliosa* had a high percentage of further germination when seeds previously in total darkness were exposed to light (from 3% to 57%).

Effect of seed mass, seed age, and temperature

Table 3 lists the germination rates of *F. foliosa* and *F. serpyllifolia*, calculated by a modified Timson Index, at Day 8 and at Day 21. Germination rates for both species were highest during the first eight days. For both species 1-year old seed in an ambient temperature of 16°C germinated fastest. Germination was faster at 24°C for *F. foliosa* than *F. serpyllifolia* 1- and 7-year seed. No 20-year old *F. foliosa* germinated, but there was nominal, albeit slow, germination for *F. serpyllifolia* in this age category. Figure 1 compares the percentage of seeds that germinated per species at each 2-day interval over the first 14 days at 16°C, 24°C, and 30°C. Figure 2 compares the percentage of 1-year old and 7-year old seeds that germinated per species at each 2-day interval over the first 14 days. A Repeated Measures ANOVA examined differences in germination rates at Day 2, Day 4, Day 6, and Day 8 (all N = 60 per species per treatment). The results showed a significant difference in germination rates on Day 2, where a higher percentage of the *F. serpyllifolia* compared with *F. foliosa* germinated (F = -3.08, P<0.01), but by Day 4 the pattern was reversed, with higher rates in *F. foliosa* (F = 4.89, P<0.001). There was no significant difference in germination rates across seed size at Day 6 or Day 8 (F = 0.13, P = 0.8; F = -0.91, P = 0.3 respectively).

Table 4 lists the results of a Single Factor ANOVA examining differences in germination success between *F. serpyllifolia* and *F. foliosa* after 21 days. Partial Eta Squares, (η_p^2) quantified the degree of association between the 'effect' categories. All combinations of factor levels (seed mass/seed age; seed mass/temperature; temperature/seed age; seed mass/seed age/temperature) were significantly different. However the η_p^2 indices showed that germination success was only minimally correlated to the combined interactive effect of seed mass/seed age/temperature (η_p^2 = 0.08), indicating that something other than the combined interactive effect of all three factors were causing the differences (e.g. the effect of population differences). This is also evident in the combined interactive effect of seed mass/temperature ($\eta_p^2 = 0.05$). However an interaction of seed mass/seed age, and of temperature/seed age were significant predictors of germination success ($\eta_p^2 = 0.30$; $\eta_p^2 = 0.19$ respectively). Figure 3 compares differences in germination success (calculated as the percentage of seeds that had germinated by Day 21), between *F. serpyllifolia* and *F. foliosa* for seed (age categories 1, 7, 20 years). Figure 4 compares differences in germination success between *F. serpyllifolia* and *F. foliosa* at ambient temperatures of 16°C, 24°C, and 30°C. There was higher germination success in *F. foliosa* at 24°C, with approximately equal germination success for 1-year old seeds and 7-year old seeds. Germination success in *F. serpyllifolia* was highest at 16°C, but with significantly higher success for 1-year old seed than 7-year old seed. Germination success for *F. serpyllifolia* decreased with increasing temperatures, albeit gradually.

DISCUSSION

Light requirements for germination

Our results suggest that a light requirement for germination is more important for *F. foliosa* (the smaller-seeded species) than for *F. serpyllifolia* (the larger-seeded species). Seeds that experience limited germination when subjected to continual darkness may be demonstrating a response to burial (Wood 1937; Facelli & Ladd 1996). Small seedlings covered by soil are often unable to emerge from the soil (Baskin & Baskin 1998).

Effects of seed mass/seed age/temperature on germination

This study showed that germination success by Day 21, was not significantly different between *F. serpyllifolia* and *F. foliosa.* There was, however, a significant difference between species (and by association, seed mass) and germination rates during the first eight days. On Day 2, *F. serpyllifolia,* the larger-seeded species, had greater germination rates than did *F. foliosa,* the smaller-seeded species, at age category 1-year, and at all ambient temperatures. The difference in germination rates at the higher temperatures was almost three-fold higher in *F. serpyllifolia*. At Day 4, *F. foliosa* had greater germination rates for all age categories and at all ambient temperatures. Germination rates in 1- and 7-year old *F. foliosa* seeds were similar to each other, especially at the lower temperatures.

Our results provide evidence that germination rates in relation to seed mass and under similar conditions, runs a different course, with faster germination in the young, larger-seeded *F. serpyllifolia,* and somewhat slower germination in all seeds of the smaller-seeded *F. foliosa,* regardless of age category. In the oldest seeds (age category 20-years), only the larger-seeded *F. serpyllifolia* exhibited any germination by Day 21.

Both species had high germination rates, but at different temperatures. *Frankenia serpyllifolia* had high germination rates at all temperatures, however *F. foliosa* had highest germination rates at 24°C. It is possible that each species has experienced a different selection regime that allows it to cope in areas with unpredictable rainfall. In Australia, *Frankenia* generally occur in areas that experience winter rainfall during the cooler months. High germination rates have been demonstrated to be correlated with temperatures that corresponded to the usual rainfall season (Bell *et al*. 1993). Thus temperatures associated with winter months should be correlated to the highest germination rates in *Frankenia*. Daily mean temperatures for July in the region of the distribution of these two species are around 16°C (e.g. Leigh Creek 16°C (1982–2007) – Australian Bureau of Meteorology, 2007). At 16°C there were high germination rates for both species. However *F. foliosa* had highest germination rates at 24°C. This temperature is more typical of early spring temperatures in the region (e.g. Leigh Creek 23°C (1982–2007) – Australian Bureau of Meteorology 2007) and may relate to the season for favourable seedling establishment.

Australia is divided into two distinct rainfall zones, with northern Australia experiencing the heaviest rainfall during February from monsoonal troughs from the north, and southern Australia experiencing the heaviest rainfall in July from southerly Antarctic depressions (Wood 1937; Specht 1972). The area of distribution for *F. serpyllifolia* and *F. foliosa* lies at the intersection of these two rainfall zones. While the mean annual rainfall in this area is about 100 mm, this rainfall may occur in a single downpour, or may be scattered over a number of small showers (Wood 1937; Specht 1972). It can occur in the hot or the cool season. Also droughts are frequent and periods of two years in which less than 25 mm of rainfall occurs are common (Wood 1937).

Frankenia serpyllifolia, with additional resources within their seeds for successful seedling establishment, and with high germination rates at 16°C, 24°C, and some germination at 30°C, may be adapted to germinate after any rainfall event, including scattered small showers, providing the seed is relative young. The 1-year old larger-seeded *F. serpyllifolia* was less affected by temperature than the 1-year old smaller-seeded *F. foliosa*, but the germination rates in *F. serpyllifolia* decreased with seed age at all temperatures. This suggests that *F. serpyllifolia* germination, especially in young seeds, is stimulated by any rainfall event regardless of temperature, thus behaving like an opportunistic ephemeral.

Frankenia foliosa seeds may be adapted to preferentially germinate after rainfall at cooler temperatures. There is reduced evaporation during the cooler winter temperatures, thus moisture remains in the soil longer (Philippi 1993). This is advantageous if seedling growth and establishment is retarded by less nutrient reserves within the seed. One year old and 7-year old *F. foliosa* seeds had equal germination rates but these rates decreased with increasing temperatures. Equally high germination in 7-year old seed as in 1-year old seed may indicate that the appropriate temperatures for high germination success (and subsequent seedling establishment) for *F. foliosa* may occur less frequently. It appears that the ability to time emergence is more important in the smaller-seeded *F. foliosa* than the larger-seeded *F. serpyllifolia* with large nutrient reserves for rapid root growth.

The results of our study are comparable to those of Jurado and Westoby (1992), who reported high germination rates in central Australian arid zone plant species. Their study demonstrated that germination of 105 large- and small-seeded species (*Frankenia* was not included) was greatest over the first 10 days and 90% of the species had commenced germinating within three days. This time period would correspond to the germination response of a single large rainfall event and would match an environment with uncommonly, albeit short-lived, wet soil (Jurado & Westoby 1992). *Frankenia* also responded quickly to the availability of water with 84% of the total germination occurring by Day 8, although *F. serpyllifolia* had higher germination rates pre Day 3 than *F. foliosa*. Variations between seed mass have been predicted to be of the greatest significance to initial seedling establishment in arid zones (Susko & Lovett Doust 2000).

This is one of only a few studies on arid zone plants that have compared germination rates across seed mass within a genus. Studies have generally investigated seed mass variation within an individual plant (e.g. Wulff 1986; Van Noordwijk & De Jong 1986), within a plant species (e.g. Harper *et al.* 1970; Werner & Platt 1976; Leishman & Westoby 1994), or within a plant community (e.g. Werner & Platt 1976; Shipley & Dion 1992; Greene & Johnson 1994; Jakobsson & Eriksson 2000; Henery & Westoby 2001; Leishman 2001). Knowledge of what controls timing of seed germination will assist with the development protocols for revegetation and conservation. Information on seed germination is also important for propagation of potentially economically important plant species. Only a few *Frankenia* species are currently cultivated (Elliot & Jones 1989) despite being salt and drought tolerant. Further studies are underway to examine germination across Australian *Frankenia* species, and the effects of larger-seededness and smaller-seededness.

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Species	Voucher ID	Seed age	Population location
Frankenia serpyllifolia	MAW707	20 yrs	4.8 km north of Marree, Oodnadatta Track
	MAW812	20 yrs	Birdsville Track
	MAW918	20 yrs	Near Marree, Oodnadatta Track
	'Site 15'	7 yrs	69km west of Oodnadatta, Oodnadatta Track
	'Site 16'	7 yrs	Near Oodnadatta
	'Site 18'	7 yrs	Strzelecki Track
	LE02008a	1 yr	10 km from Alandale H/S, Oodnadatta Track [S27°40'38" E135°32'36"]
	LE01002	1 yr	Borefield Track, Roxby Downs [S30°03'28" E135°32'36"]
	LE02003	1 yr	3 km north of Kalamanna H/S, Birdsville Track [S27°57'30" E138°39'36"]
Frankenia foliosa	MAW701	20 yrs	Near Marree, Oodnadatta Track
	MAW702	20 yrs	Near Marree, Oodnadatta Track
	MAW703	20 yrs	Near Marree, Oodnadatta Track
	'Site 5'	7 yrs	26.4 km northwest of Marree, Oodnadatta Track
	'Site 6'	7 yrs	60.2 km northwest of Marree, Oodnadatta Track
	'Site 12'	7 yrs	7.9 km northwest of Marree, Oodnadatta Track
	LE01004	1 yr	Finnis Springs, Oodnadatta Track [S29°30'05" E137 24'29"]
	LE02006	1 yr	Blanche Cup mound springs, Oodnadatta Track [S29°27'17" E136°51'25"]
	LE01005	1 yr	West of Marree, Oodnadatta Track

Table 1. Locations (with GPS co-ordinates where available), seed age, and voucher ID for populations of *Frankenia* included in this study. Seeds with herbarium vouchers with prefix 'LE' were collected by the authors. All other seeds were obtained from collections in the School of Biological Sciences, Flinders University. 'H/S' indicates 'homestead'.

	F. serpyllifolia	***F. foliosa***
% germinated in day/night	83	89
% germinated in darkness	38	3
Post-exposure to light	25	54

Table 2. Percentage seeds that germinated over 21 days (germination success) in total darkness, and in day/night regime. **"Post-exposure to light"** indicates the percentage of seeds that did not germinate in darkness, but did germinate after exposure to light. For each treatment N=180. Seeds are pooled in equal numbers from 3 populations of *Frankenia serpyllifolia* (LE01002, LE02003, LE02005) and *Frankenia foliosa* (LE01004, LE01005, LE02006).

Frankenia serpyllifolia			***Frankenia foliosa***		
Age/temperature (°C)	**T_8**	**T_{21}**	**Age/temperature (°C)**	**T_8**	**T_{21}**
1/16°	12.22	4.74	**1/16°**	12.08	4.68
2/16°	7.50	3.15	**2/16°**	10.97	4.34
3/16°	0.21	0.21	**3/16°**	0.00	0.00
1/24°	8.96	4.26	**1/24°**	9.93	3.94
2/24°	4.93	2.30	**2/24°**	10.56	4.15
3/24°	0.28	0.19	**3/24°**	0.00	0.00
1/30°	7.15	3.12	**1/30°**	4.38	2.46
2/30°	4.72	2.01	**2/30°**	8.13	3.54
3/30°	0.28	0.11	**3/30°**	0.00	0.00

Table 3. Germination rates (calculated as Timson Indices) for *F. serpyllifolia* (larger-seeded species) and for *F. foliosa* (smaller-seeded species) on Day 8 and Day 21, per age categories 1 (1-year old seed), 2 (7-year old seed), and 3 (20-year old seed), per temperature (16°, 24°C, and 30°C). Higher Timson indices equate to faster germination rates. Maximum value for T_8 is 12.50. Maximum value for T_{21} is 4.76.

	df	F	Significance	η_p^2
Seed mass/temperature	2	4.93	P<0.01	0.05
Seed mass/seed age	2	43.03	P<0.001	0.30
Temperature/seed age	4	11.32	P<0.001	0.19
Seed mass/temperature/seed age	4	4.09	P<0.01	0.08

Table 4. Results of a Repeated Measures ANOVA examining differences in germination success between *F. serpyllifolia* (larger-seeded species) and *F. foliosa* (smaller-seeded species) after 21 days. The fixed factors were seed mass (small, large), temperature (16°C, 24°C, 30°C), and seed age (1-, 7-, 20-years). Partial Eta Squares, (η_p^2) quantify the degree of association between categories.

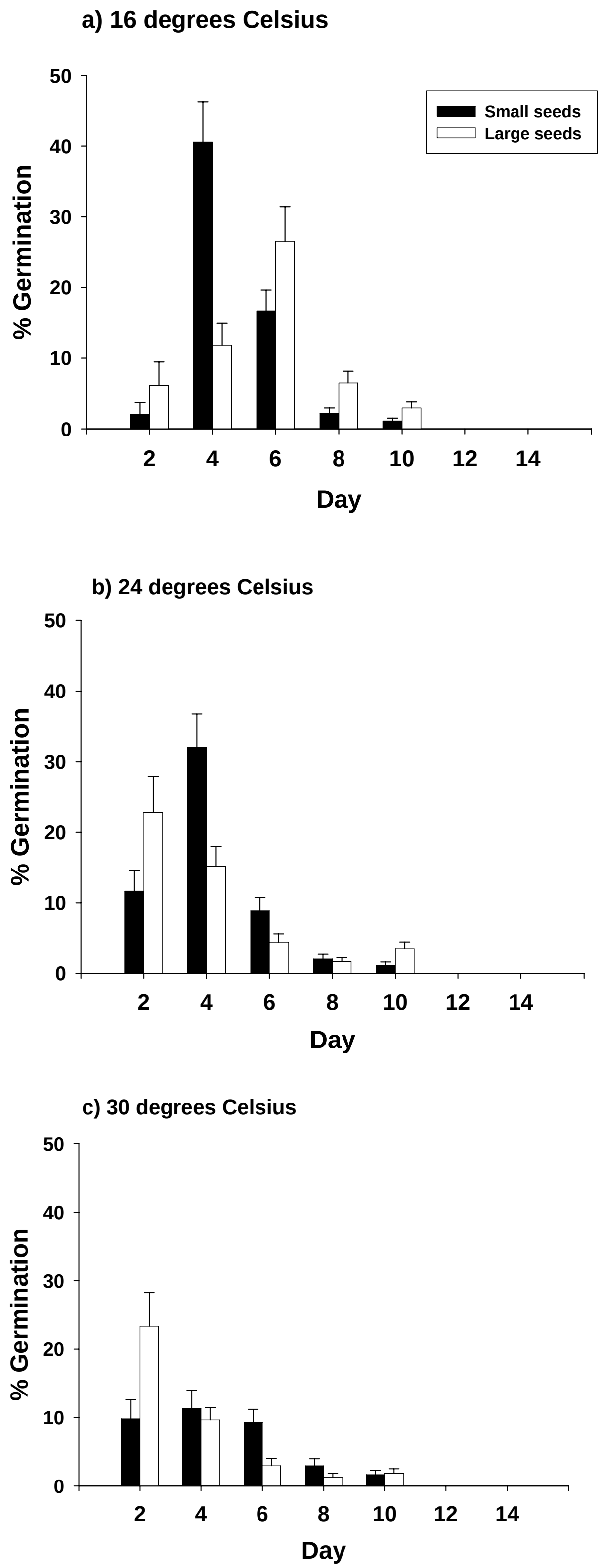

Fig 1. Total germination rates for 20-, 7-, and 1-year old seeds of *F. serpyllifolia* (larger-seeded species) and *F. foliosa* (smaller-seeded species) for temperatures 16°C, 24°C, and 30°C during the first 14 days.

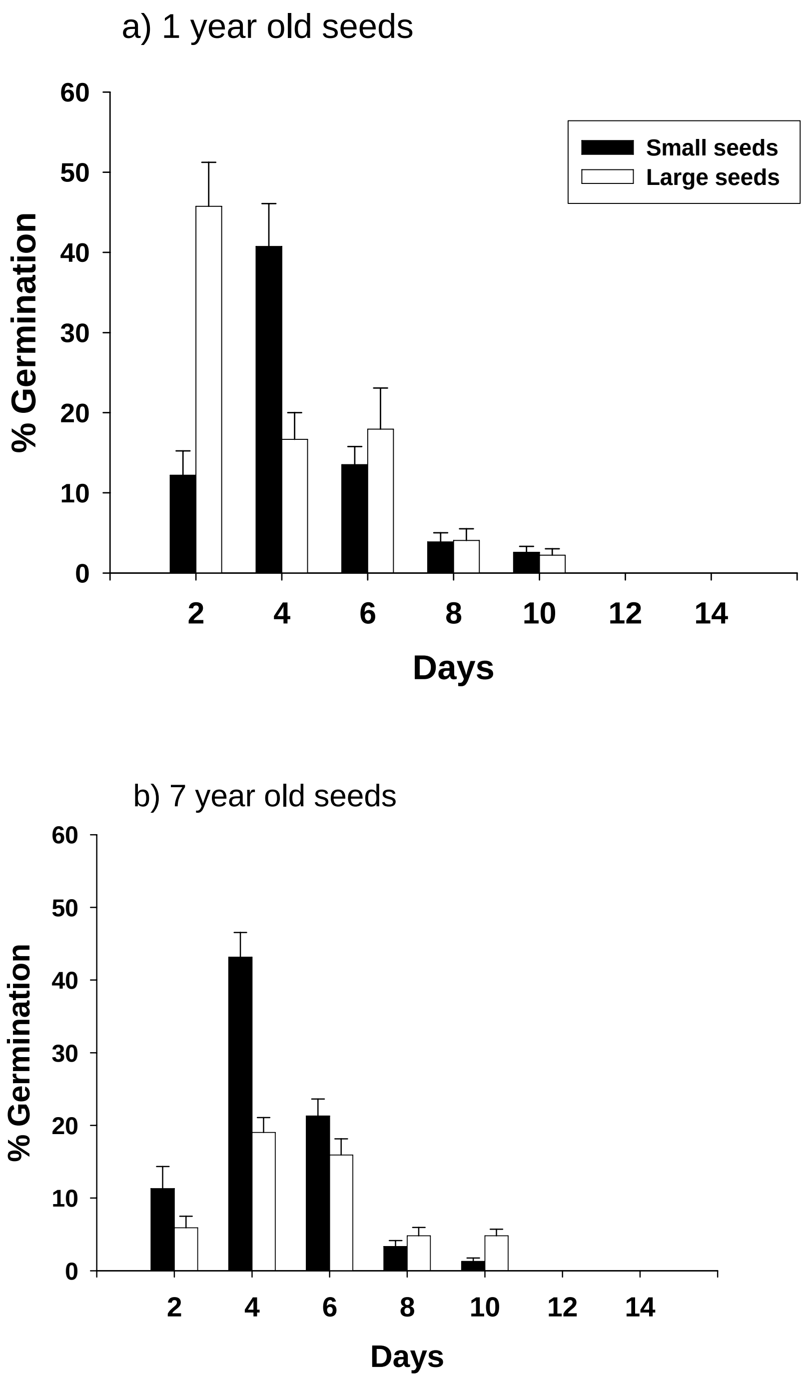

Fig. 2. Total germination rates at 16°C, 24°C and 30°C for *F. serpyllifolia* (larger-seeded species) and *F. foliosa* (smaller-seeded species) for seed age categories 1- and 7-years during the first 14 days.

Fig. 3. Total germination success at 16°C, 24°C, and 30°C for *F. serpyllifolia* (larger-seeded species) and *F. foliosa* (smaller-seeded species) after 21 days for seed age categories 1-, 7-, and 20-years.

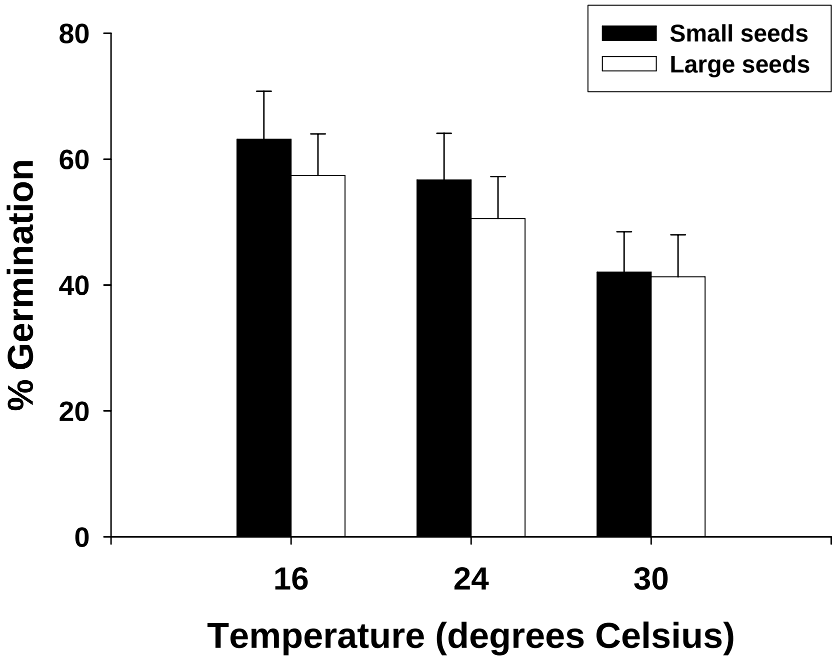

Fig. 4. Total germination success for 20-, 7-, and 1-year old seeds of *F. serpyllifolia* (larger-seeded species) and *F. foliosa* (smaller-seeded species) after 21 days at temperatures 16°C, 24°C, and 30°C.