

## Chapter 8

### DISCUSSION

The aim of this thesis was to investigate basic germination requirements for Australian species of *Frankenia* in relation to seed age, light requirements, temperature preferences, salinity tolerance, and soil properties. Germination strategies play a major role in the persistence of all plant taxa, particularly in arid zone halophyte species. The evolution of germination strategies is a consequence of plant taxa responses to environmental cues. Arid zone halophytes have evolved germination strategies under selective pressures – notably in relation to seed age, light requirements, temperature preferences, salinity tolerance, and soil properties – whereby they respond to a sequence of environmental cues that indicate periods of relatively high probability of subsequent seedling survival. Elucidating these strategies is of fundamental importance to the understanding of halophyte life histories. *Frankenia* in particular has several rare and little known species, and the vulnerability of these species cannot be assessed without basic life history data. This data is also a prerequisite for the consideration of *Frankenia* in salinity remediation, mine-site remediation, and coastal revegetation projects. (A summary of the findings per species in this thesis is given in **APPENDIX A**).

The underpinning aim of this study was to investigate reproductive strategies, and in particular the large-seeded versus small-seeded strategies in relation to environmental variables that are commonly experienced by arid zone halophyte plant taxa. Previous research has shown that larger-seededness arose several times in Australian *Frankenia* as a result of evolution towards fewer ovule numbers per fruit, although both the larger- and smaller-seeded species still co-occur in biogeographical proximity. By restricting the analysis of seed packaging strategy variations to similar habitats and within a genus, it was possible to uncover ecological correlates that would otherwise have been masked by the strong effects of habitat differences and phylogenetic constraints on seed mass. I could thus test the hypothesis that large-seededness is favoured over small-seededness in drought and/or saline stressed environments.

In **Chapter 2** I found differing germination patterns between a larger-seeded species (*F. serpyllifolia* has 1–2 seeds per fruit), and a smaller-seeded species (*F. foliosa* has up to 27 seeds per fruit) despite occurring in close geographical proximity. The seeds of the larger-seeded species required less specific abiotic conditions for germination success than the

smaller-seeded species. Overall, the smaller-seeded species had lower germination rates, did not germinate without exposure to light, and were more temperature specific (a cooler temperature preference) for germination success. However, while seeds of up to 7-years in age were highly viable in both seed mass categories, 7-year old seeds of the smaller-seeded species germinated as successfully as 1-year old seeds, providing the temperature was 24°C or less. The 7-year old seeds of the larger-seeded species were slightly less viable than the 1-year old seeds. After 21-days, germination success was not significantly different between the two seed mass categories. It appeared that large-seededness was only favoured during the first few days after rainfall. This suggested that the larger-seeded species could take advantage of any rainfall (albeit capricious) for germination, whereas the smaller-seeded species delayed germination pending favourable conditions for seedling establishment. As seed viability was high for 7-year old seeds, smaller-seeded species could delay germination over many years if favourable conditions were irregular. Note that cooler temperatures are associated with the rainy season (thus higher soil-water availability) in regions of *Frankenia* distribution in Australia.

**Chapter 3** further investigated the temperature/seed mass interaction effect on germination in 12 *Frankenia* species, (six larger-seeded species and six smaller-seeded species). The larger-seeded species had faster germination rates than smaller-seeded species at temperatures from 17°C to 29°C. Germination success by Day 28 was not significantly different between seed mass categories at 17°C. As temperature increased, germination success in both seed mass categories decreased, but the rate of decrease was higher in smaller-seeded species. This suggested that the temperature/seed mass interaction effect was more important in smaller-seeded species than larger-seeded species, as both germination rates and germination success were delayed at higher temperatures in the smaller-seeded species. This supports the hypothesis that smaller-seeded species are more reliant on specific abiotic conditions (specifically cooler weather and, by inference, the rainy season) for successful germination and consequent seedling establishment.

However, within the seed mass categories there were differences in germination rates and germination success between species. **Chapter 4** investigated germination in 17 *Frankenia* species in relation to light requirements for germination, and temperature preferences (equated as time to  $T_{50}$ ), and examined seedling emergence success from soil. This information is pivotal when considering species suitability for inclusion in rehabilitation, remediation and revegetation projects. Light did not inhibit germination in any species; moreover it appeared necessary for promoting germination in many species. Consequently

seeds covered or buried by soil would be less likely to germinate. Germination decreased with temperature in all but three species (two larger-seeded species and one smaller-seeded species), which had higher germination at 23°C than 17°C. The *F. pauciflora* complex, especially the WA varieties and including *F. confusa*, had low germination even at 17°C, suggesting that a more specific temperature cue was necessary for germination success. Seedling emergence from soil was very low for all species. While seeds from most *Frankenia* species are highly viable, the conditions for successful seedling emergence appeared far less certain. Furthermore, seedling survival to six months was variable between species, and poor overall. Significantly, species with a higher percentage of seedling survival were species with slower initial germination rates.

In central and southern Australia, *Frankenia* distribution is disjunct, and species rarely co-occur within a single community. **Chapter 5** investigated whether specific soil properties influenced species or seed mass category distribution. For soil elements, there were significant differences in the proportions of calcium, aluminium, potassium, magnesium and sulfur in the crustal and sub-crustal layers between species and between seed mass categories. For soil properties, the inter-relationship of available soil-water, exchangeable cation ratios, and incidence of calcium compounds (limestone, gypsum) were significant in assigning species and seed mass category distribution. Overall, soils associated with smaller-seeded species were more highly saline and sodic, and had a higher pH, carbonate (CO<sub>3</sub>) content, and K<sup>+</sup>:Na<sup>+</sup> ratio. However, populations of most species were distributed over saline, non-saline, sodic and non-sodic soils, suggesting that while *Frankenia* is salt-tolerant, the genus is not an obligate halophyte. *Frankenia foliosa* was the only species that appeared to be a gypsophile; however, populations of this species occurred over a wide range of soil types. *Frankenia foliosa*, *F. sessilis*, and the SA varieties of *F. pauciflora* were proposed to be suitable species for inclusion in salinity remediation programs due to their natural occurrence in highly saline soils, although these species did take slightly longer to establish.

Because *Frankenia* occurs on saline and non-saline soils, **Chapter 6** investigated the salinity level/seed mass interaction effects on germination. Overall, germination decreased as salinity levels (as indicated by EC) increased from 0.4 dS/m to 38.87 dS/m. In Chapter 5, it was revealed that the smaller-seeded species appeared to tolerate more highly saline soils than the larger-seeded species. However, Chapter 6 demonstrated that the larger-seeded species had higher germination rates and germination success at higher salinities. These results were influenced by the extremely poor germination of WA *F. pauciflora* seeds. This species germinated poorly in all experiments suggesting that the requirements for high germination

success in WA *F. pauciflora* were not uncovered in this thesis. Decreased germination at high salinity levels in the smaller-seeded species, despite their natural distribution in highly saline soils, infers that they have mechanisms to delay germination under highly saline conditions. Salt stress is not conducive to successful seedling establishment. Prolonged rainfall would decrease salinity levels by diluting the saline soil-water. Prolonged rainfall would also extend soil-water availability for the relatively more slowly growing seedlings from the smaller-seeded species.

Finally, **Chapter 7** investigated seed mineral nutrient content to disclose any differences between species and/or seed mass categories. In general, the proportions of elements per 0.4 grams of seeds were consistent between species. Thus, seedlings of larger-seeded species would have more of the proscribed (and possibly phylogenetically constrained) proportion of resources for establishment, and by inference, tolerate more stressful environments by being less reliant on it for successful establishment. However, proportions of three elements were significantly different between seed mass categories: (1) boron (which is instrumental in root elongation), and (2) sodium (which is instrumental in the  $K^+Na^+$  salt-exclusion pump) were in higher proportions in larger-seeded species, while (3) copper (which is instrumental in redox reactions) was higher in smaller-seeded species.

### ***Conclusion***

Overall, larger-seedness is advantageous for rapid germination after transitory water availability, and for providing resources to seedlings if resources become limiting before their successful establishment. Smaller-seeded species delay germination until both soil-water availability and cooler temperatures persist over a long time period, improving the chances of successful establishment for the more slowly growing seedlings that are reliant on their surroundings for resources.

### ***Limitations of the thesis and further work***

This research is the first comprehensive study on *Frankenia* ecology. The original research proposal for this study was heavily based on seedling survival in relation to water stress and salt tolerance. The proposal argued that larger seeds produce larger seedlings, and that larger seedlings are better able to establish and survive under harsh conditions. The proposal also included investigations into pollination strategies (i.e. selfing versus out-crossing). However, it rapidly became clear that the lack of knowledge on basic *Frankenia* germination was impeding experimental protocols.

A change in supervision, resulting from a prolonged medical intermission during my research, resulted in a narrower and more focused research aim. The revised research program mainly addressed germination in an evolutionary and ecological framework to address the relevance of differing reproductive packages (i.e. seed size and number) found in geographically co-occurring species. The outcomes of this research have raised new questions that need to be considered when expanding on future research directions. Most pointedly is the need to do seed physiological testing. Due to time restraints, no histology, and most importantly, no investigation into embryo types (see Martin 1946; Baskin & Baskin 2007)<sup>1</sup> were conducted during this study. The E:S ratios (embryo length:seed length) of the various species were not determined. The results of these tests, along with microscope derived images of the various seed types, would have been useful to confirm comments/statements made throughout the thesis on the absence of dormancy, which in this thesis is alluded to by germination results alone. The addition of imbibition curves, along with the E:S ratios, would also significantly add to research on differences in germination rates between smaller-seeded species and larger-seeded species of *Frankenia*. Finally, the lower temperature limits for successful germination, especially in the Western Australian *F. pauciflora* group, could be extended in future studies.

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<sup>1</sup> Baskin, C.C. & Baskin, J.M (2007) A revision of Martin's seed classification system, with particular reference to his dwarf-seed type. *Seed Science Research* **17**: 11-20.  
Martin, A.C. (1946) The comparative internal morphology of seeds. *The American Midland Naturalist* **36**: 513-660.