Chapter 5

SOIL PROPERTIES ASSOCIATED WITH THE HABITATS OF CENTRAL AND SOUTHERN AUSTRALIAN SPECIES OF *FRANKENIA* L. (FRANKENIACEAE).

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ABSTRACT

Easton, L.C. & Kleindorfer, S. (In review) Soil properties associated with the habitats of central and southern Australian species of *Frankenia* L. (Frankeniaceae). *Plant and Soil.*

We examine the soil properties (soil texture, soil elements, pH, EC, exchangeable cations, water content at field capacity, gypsum content, carbonate content) from sites where populations of *Frankenia* species naturally occur in central and southern Australia. We test whether any suites of soil properties are correlated to species distribution. We also test whether any suites of soil properties are associated with seed packaging strategies (categorically larger-seeded species, smaller-seeded species). Discriminant Function Analyses revealed that populations clustered into species groups and into seed packaging categories based on soil properties. The inter-relationships of water content at field capacity, proportions of exchangeable cations, and gypsum and/or carbonate content provided the maximum discrimination to identify species clusters. The additional inter-relationship between pH and the K^+:Na^+ ratio further clustered populations into seed packaging categories. We demonstrate that the evolution of seed packaging strategies may have been directed by soil properties. We discuss this information in the context of considering the inclusion of *Frankenia* in salinity remediation, mine-site rehabilitation, or coastal revegetation projects.

Key words arid zone plants, halophytes, salinity remediation, seed mass/seed number, soil preferences

INTRODUCTION

Australia has the largest area of saline soils of any continent (Peverill *et al.* 1999). More than one third of the country is affected by primary or secondary salinity. Saline soils generally occur in the arid, semi-arid, and Mediterranean climates where rainfall is highly variable in timing, duration, and intensity. Available water for plants in these areas is unpredictable and unreliable. Consequently, Australia has a high number of endemic plant species adapted to cope with varying degrees of salinity and drought.

Soil characteristics are important in the study of plant ecology as they affect the likelihood of survival at all life history stages (Meyer 1986). The distribution and abundance of plant species is governed by their germination requirements, and by a seedling's ability to survive to reproductive age. The principal factors affecting these life history stages – especially in arid regions – are soil-nutrient and soil-water availability (Rivas-Arancibia *et al.* 2006). Soil-nutrient availability is highly variable even within populations. Moreover, species vary in their ability to utilize available soil-nutrients and soil-water, and this in turn is influenced by temperature, season, dormancy mechanisms, and soil properties. Consequently, there is often substantial inter-communal diversity in plant species that make up the arid and semi-arid floral communities. As there is little difference in rainfall and temperature between proximal communities at a given time, it is suggested that differences in soil properties play an important role in explaining the differences in inter-communal plant diversity (Rivas-Arancibia *et al.* 2006).

This paper investigates soil properties from sites where populations of the halophyte plant genus *Frankenia* L. occur in central and southern Australia. Data on the ecology of *Frankenia* taxa are sparse. Detailed data on soil properties of *Frankenia* habitats in particular are limited to Brightmore's (1979) study on *F. laevis* L., a European species, and Whalen's (1987) monograph of American *Frankenia*. Soil properties associated with the naturally occurring Australian *Frankenia* species have been referred to in only a small number of vegetation surveys (e.g. Murray 1931; Jessup 1951; Symon 1963; Boyland 1970; Badman 1999).

Although *Frankenia* species only occur in arid, semi-arid, and Mediterranean climates, there are differences between species in their reproductive strategies – notably in ovule number per flower and seed mass. Easton and Kleindorfer (2008a) categorized *Frankenia* species – based on seed packaging strategies – into 'larger-seeded species' (3–6 ovules per flower; mean seed

mass 400 µg ±12 s.e.), and 'smaller-seeded species' (up to 45 ovules per flower; mean seed mass 90 µg ±2 s.e.). The consequences of seed packaging strategies on germination and seedling establishment in relation to temperature, salinity levels, seed age, and light requirements are discussed in Chapters 2, 4, and 6. Furthermore, *Frankenia* species appear to be site specific. Rarely do they occur in a single community and when they do occur in a single community, the species are segregated (Easton & Kleindorfer 2008a, 2008b). This segregation may be influenced by differences in soil properties. Whalen (1987) noted a correlation between *Frankenia* species in America and the electrical conductivity (EC), pH, sodicity (ESP), and gypsum content of soils. Semple and Waterhouse (1994) also noted site specificity for several Australian arid zone species, including three species of *Frankenia*, and suggested that it was caused by the different soluble salt concentrations between the sites.

Secondary salinity is a major problem in Australia with 30% of agricultural land affected by salinity. One method to ameliorate salinity affected areas is through phytoremediation (Boyko 1966). Salt-tolerant shrubs can lower soil salinity levels by extracting salts from the soil, while providing groundcover to reduce soil erosion. However, efforts to utilize species in artificial revegetation have met with mixed success due in part to a lack of knowledge about the specific germination requirements for the species (Mikhiel *et al.* 1992). However, knowing the environmental preferences and limitations of plant species, including soil associations, is vital when restoring degraded areas (Northcote & Skene 1972).

Although previously not included in reclamation and remediation projects primarily due to the lack of knowledge on its ecology, *Frankenia* has the potential to be included in reclamation and revegetation projects. We examine soil properties, specifically soil texture (particle size), pH, EC, cation exchange capacity (CEC), exchangeable cation ratios, water content at field capacity, and the presence of gypsum ($CaSO_4.2H_2O$) and carbonate (notably $CaCO_3$), from population sites of 12 *Frankenia* species that occur in central and southern Australian. The aim of this study was to test whether specific suites of soil properties were associated with individual *Frankenia* species, and/or with seed packaging strategies. We test the hypothesis (based on overall *Frankenia* distribution) that there are differences in soil properties between species. We predict that (1) smaller-seeded species with high ovule numbers per fruit occur in gypseous soils with a high sand content and a high EC (highly saline), and (2) that larger-seeded species with low

numbers of ovules per fruit occur in non-gypseous soils with a higher clay content and a lower EC.

MATERIALS AND METHODS

Test species

Frankenia are cosmopolitan salt-tolerant shrubs, sub-shrubs, or cushion bushes. Currently, 47 Australian species are recognized and only one, *F. pulverulenta* L., is not endemic (Barnsley 1982; Whalen 1986; but see Craigie 2007). In Australia, *Frankenia* are found south of the latitude 17°S in Mediterranean, arid, and semi-arid climates (Summerhayes 1930). Populations often occur in isolated, disjunct pockets and generally cover only several square metres.

Soil analyses

To examine the soil properties associated with *Frankenia* habitats, soil to a depth of 15cm was sampled from five sites per population (see Table 1) in close proximity to *Frankenia* plants, following the protocol of Whalen (1987). In general, soil associated with *Frankenia* had a negligible A horizon and a deep B horizon with limited stratigraphy. Soil profiles for species of Australian *Frankenia* distribution, based on McKenzie *et al.* (2004) and in accordance with the Australian Soil Classification (Isbell 1996), were designated Hypercalcic Calcisol, Endosalic Calcisol, Calcic Solonchak, Vertic Solonchak, Endopetric Plinthosol, or Alcalic Solonetz.

In the laboratory, the five soil samples from each population were mixed to create a single homogenous representative sample per population. Soils were air dried and then sieved through a 2mm sieve to remove extraneous materials.

Soil elements

Preliminary investigations tested homogeneity in the soil elements from population sites of eight species occurring in South Australia. Samples from 21 population sites (see Table 1) representing a cross section of the South Australian distribution of this genus were analysed by Inductively Coupled Plasma Atomic Emission Spectrometry (ICPAES) after digestion with

nitric/perchloric acid, at Waite Analytical Services, Urrbrae, South Australia. Note that the resultant potassium values were indicative only because nitric/perchloric acid digestion has the potential to decrease the fraction of this element due to the precipitation of potassium perchlorate.

Soil properties

Exchangeable cations, pH, and EC were analysed by CSBP, Bibra Lake, Western Australia. Exchangeable cations were extracted using 1M NH_4Cl buffered at pH 8.5 (Rayment & Higginson 1992). This extraction method was chosen due to the suspected CO_3 and gypsum content in the soil samples. Electrical conductivity (EC) and pH were analysed by 1:5 soil/water extract (Rayment & Higginson 1992). Cation exchange capacity was calculated as the sum of all cations. Exchangeable sodium percentage was calculated as the percentage of Na^+ in the CEC.

Soil texture, water retention at field capacity, and the presence of gypsum and/or carbonate for 41 population sites (see Table 1) were analysed at CSIRO Land and Water, Urrbrae, South Australia. Gypsum content (%) was determined first using the EC conversion method following the protocol of Burt (2004). The presence of gypsum in soil samples causes flocculation, thus rendering many soil analyses fallacious. Soil samples identified as containing gypsum therefore required intensive pretreatment before some analyses could be undertaken (see below). Each soil sample was partially dispersed by an ultrasonic probe for 15 minutes. Next, CO_3 content was estimated using the 'fizz test'. Hydrochloric acid was added to dry soil and the strength of the chemical reaction was recorded categorically as 'no reaction', 'slight reaction', 'moderate reaction', or 'strong reaction' (Bowman & Hutka 2002). Soils were then pre-treated to remove organic matter (by hydrogen peroxide) and CO_3 (by acetic acid). This modified method uses acetic acid rather than hydrochloric acid to remove CO_3 because acetic acid has less effect on sensitive clay materials. Soluble salts (including gypsum) were removed by washing and the samples dispersed by shaking with sodium hexametaphosphate and sodium carbonate (Method Code 517.13). This procedure was repeated until the EC of the soil:water sample was <0.4 dS/m. Soil texture (particle size) analyses were undertaken by dispersion, wet sieving, and pipette sub-sampling following the protocol of Bowman and Hutka (2002). The sample was wet sieved through 63µm fine mesh. Pipette sub-samples from the <63µm sample were taken at specified times and depths relevant to the partition of silt from clay. The >63µm sample was not further separated and recorded as homogenous sand.

Soil-water retention for determining moisture content was measured by the volumetric water retention percentage (θ_v) at field capacity (henceforth noted as 'θ_vFC'). This depicts the plant-available water (Janik *et al.* 2007). For the initial 23 population sites, θ_vFC was measured by pressure plate extractors for a matrix suction of 10 kPa (ψm = -10 kPa) following the protocol of McKenzie *et al*. (2002). For the subsequent 18 sites (see Table 1), θ_vFC was predicted using an estimate of soil density analysed by Mid Infrared (MIR) spectroscopy. Mid Infrared spectroscopy is sensitive to soil composition. Volumetric soil retention can be derived via Mid Infrared Partial Least Squares models from the MIR spectra of soils and from reference data. These are used to predict the water retention of unknown samples (Janik *et al.* 2007). Soils for MIR analyses were prepared and analysed following the protocol of Janik *et al.* (2007).

Statistical analyses

All analyses were calculated using SPSS Version 15. Means and standard errors of all soil properties were calculated for each species and for each seed packaging category. Results of the analyses were subjected to Discriminant Function Analysis (DFA) to examine possible causal relationships between soil properties and *Frankenia* species distribution, or seed packaging strategies (see Meyer *et al.* 1992). Cadmium was included in the original ICPAES analyses; however, the amount present in all population samples was less than the limit of detection for ICPAES, and they were therefore excluded from further analyses.

Discriminant Function Analysis (multivariate ANOVA) was used to provide weightings for the combination of all soil variables to provide a maximum discrimination between populations (Dytham 2003). This analysis showed whether any inter-relationships of soil properties (henceforth called the SPIR effect) identified clusters of species groups, or seed packaging categories. We also tested whether individual populations would be assigned to the correct species groups or seed packaging categories if the population was excluded and then reassigned based on the Discriminant Function scores. This approach gave an overall efficiency score for the discrimination of groups based in the SPIR effect (Dytham 2003). Wilks lambda – the proportion of the total variance in the Discriminant Function scores not explained by the differences among groups – tested the equality of group means between species and between seed packaging categories. Single factor ANOVA tested for significant differences per individual soil property, between species and/or seed packaging strategies.

RESULTS

Soil elements

Table 2 lists the mean percentages (±s.e.) of soil elements per species and per seed packaging category for 21 populations of *Frankenia* included in this part of the study. Figure 1 is the scatterplot generated for the soil elements based on DFA results. The Ca component accounted for the largest absolute correlation and explained 91.1% of the variation between populations (i.e. the SPIR effect).

There was observable (and statistically significant) clustering of populations into species based on the SPIR effect (Wilks Lambda: $\chi^2 = 144.04$, df = 84, $P<0.001$). Individually, there were also significant differences between species clusters for Ca content, as expected due to its significance in the SPIR effect ($F = 32.75$, $df_{(7,14)}$ $P<0.001$), and also K content ($F = 3.69$, $df_{(7,14)}$ $P<0.05$), Fe content ($F = 436$, $df_{(7,14)}$ $P<0.01$), and Al content ($F = 7.42$, $df_{(7,14)}$ $P<0.01$).

Furthermore, there was observable (and statistically significant) clustering of populations into seed packaging categories based on the SPIR effect (Wilks Lambda: $\chi^2 = 27.14$, df = 14, $P<0.05$). The SPIR effect of the S, Al, Mg, and K contents accounted for the largest absolute correlation. Individually, there was a significant difference between seed packaging categories for S content ($F = 4.70$, $df_{(1,20)}$ $P<0.05$) and Al content ($F = 4.39$, $df_{(1,20)}$ $P<0.05$).

Relationships between species and soil properties

Table 3 summarizes the overall means (±s.e.) and range of soil properties for the 41 *Frankenia* populations included in this part of the study. Table 4 lists the means (±s.e.) for soil properties per species. Discriminant Function Analyses were calculated to identify which soil properties would maximize the differences between the 41 populations, and to investigate whether populations would cluster into species groups and/or seed packaging category based on soil properties (see Figure 2).

There was an observable (and statistically significant) clustering of populations into species groups (Wilks Lambda: $\chi^2 = 3.15.57$, df = 192, $P<0.001$). The SPIR effect of the CO_3 content, θ_vFC, and K^+:Na^+ accounted for the largest absolute correlation and explained 58.3% of the variation between populations. Individually, there were significant differences between species clusters in percentage sand content ($F = 3.11$, $df_{(12,28)}$ $P<0.01$), percentage clay content (F

= 3.69, $df_{(12,28)}$ P<0.01), CO_3 content (F = 9.56, $df_{(12,28)}$ P<0.001), and θ_vFC (F = 6.46, $df_{(12,28)}$ P<0.001).

Relationship between seed packaging categories and soil properties

Table 3 also lists the means (±s.e.) of soil properties for *Frankenia* population sites when divided into seed packaging categories. The SPIR effect of CO_3 content, Mg content, CEC and pH accounted for the largest absolute correlation. There was observable (and statistically significant) clustering of larger-seeded species and of smaller-seeded species (Wilks lambda: χ^2 = 46.14, df = 16, P<0.001). Independently, there were significant differences between the seed packaging categories for CO_3 content (F = 35.4, $df_{(1,39)}$ P<0.001), CEC (F = 5.95, $df_{(1,39)}$ P<0.05), θ_vFC (F = 4.69, $df_{(1,39)}$ P<0.05), pH (F = 5.55, $df_{(1,39)}$ P<0.05), Mg content (F = 5.52, $df_{(1,39)}$ P<0.05), and K^+:Na^+ (F = 4.89, $df_{(1,39)}$ P<0.05).

Notable imprecision in the clustering included (1) *F. sessilis*, a coastal larger-seeded species, clustering closely to *F. foliosa*, an inland smaller-seeded species, and (2) *F. eremophila*, also a coastal larger-seeded species, clustering within the *F. pauciflora* varieties, which are coastal smaller-seeded species.

DISCUSSION

Given the increasing incidence of secondary salinity in Australia, the underpinning aim of this study was to identify the soil properties of *Frankenia* species from primary salinity habitats to ascertain their potential for salinity remediation, mine-site rehabilitation, and/or coastal revegetation. While the soil properties *per se* were comparable between *Frankenia* species, there was evidence that individual species were affiliated with specific combinations of these soil properties. Furthermore, there was evidence that seed packaging strategies were also affiliated with specific combinations of soil properties

Soil elements

Soil element content generated clustering of species and seed packaging categories in the DFA. Specifically, Ca content was the key predictor for the clustering of species groups, while

the SPIR effect of S content, Mg content, and K content was the key predictor for the clustering of seed packaging categories. The biological relevance of variation in the soil elements is unclear because at any instance, only 1% of the total nutrient content of soil is available to plants (McKenzie *et al.* 2004). However, *Frankenia* species have differing requirements for peak germination and seedling establishment (see Chapter 4). The effect of soil elements (notably Ca and S) on soil pH, EC, or morphology may impact on seed germination and seedling establishment. The presence of S in conjunction with high Ca content generally indicates a gypseous soil. (Note also that low K content is also characteristic of gypseous soils – see Meyer *et al.* 1992.) The presence of gypsum in soils at some *Frankenia* sites was confirmed by its confounding affects on several of the tests performed in this study – notably the flocculation in the soil texture analyses.

Gypsophily in arid zone plant species is well documented (e.g. Parsons 1976; Escudero *et al.* 2000; Palacio *et al.* 2007). *Frankenia* have been associated with gypseous soils in North and South America. In particular, *F. jamesii* Torrey ex A. Gray is considered an indicator for the presence of gypsum (Parsons 1976; Brightmore 1979; Whalen 1987). Gypseous soils have a relatively high hydraulic conductivity. Thus, soil-water is drawn to the soil surface in response a gradient created by soil surface evaporation and drying (Meyer *et al.* 1992; Escudero *et al.* 2000). This creates a near surface water regime suitably for shallow rooted and slow establishing species such as small-seeded *Frankenia*. Gypsum is also effective at reducing exchangeable unfavourable Na^+ (Peverill *et al.* 1999). Gypsum exposures are widespread in central and southern Australia (Bonython & King 1956). Despite this, of all the central and southern Australian *Frankenia* species, only *F. foliosa* (and possibly *F. eremophila*) showed a bias for gypseous soils. All populations of *F. foliosa* occurred in soils that contained substantial gypsum.

Species delineation - θ_vFC, K^+:Na^+, and Ca compounds

The SPIR effect of θ_vFC, K^+:Na^+ and the Ca compounds (calcium carbonate and gypsum) were significant predictors for delineating species clusters in the DFA. Water retention at field capacity is related to soil texture. Soil texture affects the water potential – i.e. how tightly water is held by the soil. While the effect of 'soil texture' *per se* was not included as a discriminating factor in the SPIR effect, the independent effects of 'percentage clay content' and 'percentage sand content' were significantly different between species clusters. Overall, clay content ranged

from 29% to 52%, and sand content ranged from 25% to 96%. In general, the larger-seeded species occurred in soils with a higher clay content and lower sand content than smaller-seeded species. Soils with higher clay content can retain higher θ_vFC (McKenzie *et al.* 2004).

However, few *Frankenia* population sites had a mean θ_vFC greater than 30%. For this reason, θ_vFC related to *Frankenia*, based on McKenzie *et al.* (2004), was rated as 'very poor'. The few populations that recorded θ_vFC of greater than 30% – notably the two *F. pauciflora* varieties – also had a high CO_3 content. The θ_vFC was estimated by MIR's for all of the *F. pauciflora* populations. Bertrand *et al.* (2002) demonstrated that the presence of $CaCO_3$ can cause MIR spectra to become atypical of the remaining calibration set, thereby leading to difficulties in predictors. Thus, the MIR θ_vFC values for *F. pauciflora* in this study may have been over-estimated.

The θ_vFC and the way it is utilized by plants influences species distribution, particularly in arid, semi-arid, and Mediterranean climates. For *Frankenia*, it appears that the larger-seeded species have adapted to soils that retain higher θ_vFC through higher clay content, whereas smaller-seeded species have adapted to soils that retain higher θ_vFC through higher proportions of carbonate compounds (gypsum, calcium carbonate).

The third soil property in the SPIR delineator for species groups was the K^+:Na^+ ratios. Many authors have emphasized the importance of CEC and the ratios of these cations – including K^+:Na^+ – on vegetation patterns (e.g. Cantero *et al.* 1998; Rogel *et al.* 2000), and on germination and radicle survival (Tobe *et al.* 2002). Pertinent to the K^+:Na^+ ratio, Na^+ can be toxic to plants: however, high levels of K^+ in the soil depresses Na^+ (Ungar 1991; Tobe *et al.* 2002). The proportion of K^+ was lower for smaller-seeded species than larger-seeded species. The significance of this finding is discussed below.

Seed packaging strategies delineation – CO_3, CEC, and pH

Seed packaging category clusters were delineated in DFA by the SPIR effect of CO_3 content, CEC, Mg content, and pH. The CO_3 content was five-fold higher for the smaller-seeded species than larger-seeded species. The CEC was generally two-fold higher for sites with the smaller-seeded species. The exception was K^+, which was lower for smaller-seeded species than larger-seeded species. Magnesium cations, as with Na^+, can be toxic to plants. High levels of Ca^{2+} or K^+ in the soil can also depress Mg^{2+} uptake (Ungar 1991; Tobe *et al.* 2002). High Mg^{2+}

levels may be tolerated by *Frankenia* species (especially the smaller-seeded species) due to the reduced uptake of these cations by the high levels of Ca^{2+}. Higher levels of Ca^{2+} may be necessary in soils of the smaller-seeded species due to the lower levels of K^{+} in these soils than in soils of the larger-seeded species.

The presence of soluble salts – notably CO_3 – raises pH. The pH is instrumental in regulating chemical and biological reactions, including nutrient extraction and absorption. It appears that smaller-seeded species can tolerate higher pH levels for these reactions.

Role of* Frankenia *in salinity remediation

In this study, soil salinity levels were analysed in three ways – by EC, by Na^{+} content, and by ESP. The EC for *Frankenia* sites ranged from 0.04 dS/m to 11.4 dS/m. An EC >4 dS/m indicates saline soil. Furthermore, soil with an EC >8 dS/m can only support salt-tolerant plants. More populations of the smaller-seeded *Frankenia* species occurred in saline soils than larger-seeded species (21% *cf.* 14%). At EC's >8 dS/m, this became even more apparent (16% *cf.* 4.5%). Thus, while *Frankenia* are salt-tolerant, they are not necessarily obligate halophytes. Indications are that smaller-seeded species are more salt-tolerant and thus more suitable for salinity remediation projects.

In contrast to saline regions on other continents, Australian saline soils are NaCl rich (DeDekker 1983). Consequential problematic 'sodic' soils are characterized by poor water infiltration and poor aeration (which also creates water-logging after rains). This reduces plant-available water and inhibits seedling emergence and root development. Sodic soils are indicated as having a Na^{+} content exceeding 20 cmol(+)/kg (Peverill *et al.* 1999), or an ESP of >6% (McKenzie *et al.* 2004). Soil associated with *Frankenia* populations had Na^{+} concentrations ranging from 0.32 to 49 cmol(+)/kg. The smaller-seeded species generally occurred in sites with a higher Na^{+} content than larger-seeded species. The mean ESP per species ranged from 10% (*F. connata*) to 56% (*F. sessilis*). According to the criteria for sodicity as measured by ESP, all *Frankenia* populations occurred in sodic soils.

Conclusion

Efforts directed towards artificial revegetation have met with mixed success due in part to a lack of knowledge about specific germination requirements and soil preferences for the species

included in revegetation projects (Mikhiel *et al.* 1992). Our results suggest that *Frankenia* should be included in salinity remediation, mine-site rehabilitation, and coastal revegetation projects. In particular, *F. foliosa, F. pauciflora,* and *F. sessilis* should be included in general revegetation and rehabilitation projects (also see Semple & Waterhouse 1994; Barrett & Bennett 1995; Barrett 2006). *Frankenia foliosa* is particularly suitable due to its wide range of soil tolerances. Furthermore, its dense cushion-bush habit would make *F. foliosa* amenable for the prevention of soil erosion. Bio-geographically, *F. foliosa* commonly occur in monocultures on the margins of salt-lakes, and particularly around the mound springs of the Great Artesian Basin. The soils near mound springs are highly saline and the spring waters are high in CO_3 and sulfates (Badman 1999).

The closely related larger-seeded inland species (see Whalen 1986) appear to be adapted to a more specific combination of soil properties, which include lower salinity levels, higher clay content and negligible gypsum and/or carbonate content. One of these larger-seeded species (*F. connata*) was represented in this study by one population only; however this has shown to be noteworthy and may have implications for the ongoing phylogenetic and systematic revisions. In relation to phylogenetic and systematic revisions, *Frankenia planifolia* Sprague and Summerh. is suggested to be conspecific with *F. serpyllifolia* (Whalen 1986), although it is morphologically distinct in leaf shape and colour, degree of hirsuteness, and flower colour. The *F. planifolia* population was not clustered within the *F. serpyllifolia* populations based on SPIR effects. *Frankenia connata* Sprague is closely related to *F. latior* Sprague and Summerh., separated only by leaf shape and degree of hirsuteness on the calyx (Whalen 1986). The *F. connata* population likewise was not clustered within the *F. latior* populations based on SPIR effects.

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REFERENCES

Badman, F.J. (1999) **The Lake Eyre South study: Vegetation**. Gillingham Publishing, South Australia.

Barnsley, B. (1982) Frankeniaceae. *In:* George A.S. (ed.) **Flora of Australia Volume 8**. Australian Government Publishing, Canberra. pp 112–146.

Barrett, G. (2006) Vegetation communities on the shores of a salt lake in semi-arid Western Australia. *Journal of Arid Environments* **67**: 77–89.

Barrett, G.S. & Bennett, I. (1995) Research into revegetation of salt-affected land after mining in the goldfields of Western Australia. *In:* Khan, M.A. & Ungar, I. (eds.) **Biology of salt tolerant plants.** Book Crafters, USA.

Bertrand, I., Janik, L.K., Holloway, R.E., Armstrong, R.D. & McLaughlin, M.J. (2002) The rapid assessment of concentrations and solid phase associations of macro- and micronutrients in alkaline soils by mid-infrared diffuse reflectance spectroscopy. *Australian Journal of Soil Research* **40**: 1339–1356.

Bonython, C.W. & King, D. (1956) The occurrence of native sulphur at Lake Eyre. *Transactions of the Royal Society South Australia* **79**: 121–129.

Bowman, G.M. & Hutka, J. (2002) Particle size analysis. *In:* McKenzie, N., Coughlan, K. & Cresswell, H. (eds.) **Soil physical measurement and interpretation for land evaluation**. CSIRO Publishing, Australia.

Boyko, H. (1966) **Salinity and aridity.** D.W. Junk Publishing, The Hague.

Boyland, D.E. (1970) Ecological and floristic studies in the Simpson Desert National Park, South Western Queensland. *Proceedings of the Royal Society Queensland* **69**: 3–17.

Brightmore, D. (1979) Biological flora of the British Isles. *Frankenia laevis* L. *Journal of Ecology* **67**: 1097–1197.

Burt, R. (2004) **Soil survey laboratory methods manual – soil survey investigations report No. 42, Version 4.** Natural Resources Conservation Service. pp 273–277.

Cantero, J., Cisneros, J.M., Zobel, M. & Cantero, A. (1998) Environmental relationships of vegetation patterns in salt marshes of central Argentina. *Folia Geobotanica* **33**: 133–145.

Craigie, A.I. (2007) **Systematic studies of the Australian species of *Frankenia* L. (Frankeniaceae).** PhD thesis, Flinders University, Adelaide, Australia.

De Dekker, P. (1983) Australian salt lakes: their history, chemistry, and biota – a review. *Hydrobiologia* **105**: 231–244.

Dytham, C. (2003) **Choosing and using statistics: a biologist's guide** (2nd ed). Blackwell Publishing.

Easton, L.C. & Kleindorfer, S. (2008a) 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 South Australia* **132**: 29-40.

Easton, L.C. & Kleindorfer, S. (2008b) Interaction effects of seed mass and temperature on germination in Australian species of *Frankenia* L. (Frankeniaceae). *Folia Geobotanica* **43(4).**

Escudero, A., Iriondo, J.M., Olano, J.M., Rubio, A. & Somolinos, R.C. (2000) Factors affecting establishment of a gypsophyte; the case study of *Lepidium subulatum* (Brassicaceae). *American Journal of Botany* **87**: 861–871.

Isbell, R.F. (1996) **The Australian soil classification.** CSIRO, Melbourne.

Janik, L.J., Merry, R.H., Forrester, S.T., Lanyon, D.M. & Rawson, A. (2007) Rapid prediction of soil water retention using mid infrared spectroscopy. *Soil Science Society America Journal* **71**: 507–514.

Jessup, R.W. (1951) The soils, geology and vegetation of north-western South Australia. *Transactions of the Royal Society South Australia* **74**: 189–273.

McKenzie, N., Coughlan, K. & Cresswell, H. (2002) **Soil physical measurement and interpretation for land evaluation.** CSIRO Publishing, Australia.

McKenzie, N., Jacquier, D., Isbell, R. & Brown, K. (2004) **Australian soils and landscapes: an illustrated compendium**. CSIRO Publishing, Australia.

Meyer, S.E. (1986) The ecology of gypsophile endemism in the eastern Mojave Desert. *Ecology* **67**: 1303–1313.

Meyer, S.E., Garcia Moya, E. & Lagunes-Espinoza, L. (1992) Topographic and soil surface effects on gypsophile plant community patterns in central Mexico*. Journal of Vegetation Science* **3**: 429–438.

Mikhiel, G.S., Meyer, S. & Pendleton, R.L. (1992) Variation in germination response to temperature and salinity in shrubby *Atriplex* species. *Journal of Arid Environments* **22**: 39–49.

Murray, B.J. (1931) A study of the vegetation of the Lake Torrens plateau, South Australia. *Transactions of the Royal Society South Australia* **55**: 91–112.

Northcote, K.H. & Skene, J.K.M. (1972) **Australian soils with saline and sodic properties.** Australian Division of Soils, Soil Publication #27. CSIRO, Australia.

Palacio, S., Escudero, A., Montserrat-Martí, G., Maestro, M., Milla, R. & Albert, M. (2007) Plants living on gypsum: beyond the specialist model. *Annals of Botany* **99**: 333–343.

Parsons, R.F. (1976) Gypsophily in plants – a review. *American Midland Naturalist* **91**: 1–19.

Peverill, K.I., Sparrow, L.A. & Reuter, D.J. (1999) **Soil analysis: an interpretation manual.** CSIRO Publishing, Australia.

Rayment, G.E. & Higginson, F.R. (1992) **Australian laboratory handbook of soil and water chemical methods.** Inkata Press, Melbourne.

Rivas-Arancibia, S.P., Montaña, C., Hernández, J.X.V. & Zavala-Hurtado, J.A. (2006) Germination responses of annual plants to substrate type, rainfall, and temperature in a semi-arid inter-tropical region in Mexico. *Journal of Arid Environments* **67**: 416–427.

Rogel, J.A., Ariza, F.A. & Silla, R.O. (2000) Soil salinity and moisture gradients and plant zonation in Mediterranean salt marshes of southeast Spain. *Wetlands* **20**: 357–372.

Semple, W.S. & Waterhouse, D. (1994) Performance of halophytes from semi-arid areas on two saline seepage scalds of the Central Western slopes of NSW. *Cunninghamia* **3**: 595–608.

Summerhayes, V.S. (1930) A revision of the Australian species of *Frankenia*. *Linnean Journal of Botany* **48**: 337–387.

Symon, D.E. (1963) A checklist of flowering plants of the Simpson Desert and its immediate environs. *Transactions of the Royal Society South Australia* **93**: 17–37.

Tobe, K., Li, X. & Omasa, K. (2002) Effects of sodium, magnesium and calcium salts on seed germination and radical survival of a halophyte, *Kalidium caspicum* (Chenopodiaceae). *Australian Journal of Botany* **50**: 163–169.

Ungar, I.A. (1991) **Ecophysiology of Vascular Halophytes.** CRC Press.

Whalen, M.A. (1986) Frankeniaceae. *In:* Jessop, J. & Toelken, H.R. (eds.) **Flora of South Australia.** South Australia Government Printing Division, Adelaide. pp 873-881.

Whalen, M.A. (1987) Systematics of *Frankenia* (Frankeniaceae) in North and South America. *Systematic Botany Monographs* **17**: 1–93.

Species	Ref. No.	Location	GPS co-ordinates	Site description
Frankenia connata	LE01025	Roxby Downs, SA [a,b,c]	S30°02'55" E137°04'34'	
Frankenia cordata	LE05006	Ormiston Gorge, NT [b,c,d]	S23°40'45" E132°42'42"	Pink/orange clayey sand, scree
	LE05011	Curtin Springs, NT [b,c,d]	S25°21'01" E131°50'47"	Red sand
Frankenia eremophila	LE01006	Cactus Beach, SA [a,b,c]	S32°04'49" E132°59'31"	Sand dunes
Frankenia foliosa	LE01004	Finnis Springs, SA [a,b,c]	S29°30'05" E137°24'29"	White sand, saline, traventine
	LE01005	Oodnadatta Track, SA [a,b,c]	NR	
	LE01014	Marree, SA [a,c,d]	S29°39'34" E137°40'19"	Pink/orange clayey sand
	LE01015	Strzelecki Track, SA [a,b]	S29°33'15" E139°25'16"	
	LE01019	Strzelecki Track, SA [a,b,c]	S30°11'54" E138°38'31'	
	LE02006	Blanche Cup, SA [b,c,d]	S29°27'17" E136°51'25"	White gypseous sand, saline
Frankenia gracilis	LE01002	Roxby Downs, SA [a,b]	S30°03'28" E137°04'00"	Red clayey sand
	LE01012	Roxby Downs, SA [b]	S30°03'28" E137°04'11"	
	LE01033	Beltana, SA [a,b]	NR	Red clayey sand, ironstone
	LE01034	Parachilna, SA [a,b]	NR	
	LE02003	Birdsville Track, SA [b,c,d]	S27°57'30" E138°39'36"	Gypsum, ironstone conglomerate
	LE04003	Salisbury Lake, NSW [b,c,d]	S29°41'16" E142°38'58"	Orange clayey sand, saline
Frankenia latior	LE01003	Woomera, SA [a,b]	S31°19'48" E136°51'44"	
	LE01011	Roxby Downs, SA [a,b]	S30°17'44" E136°56'12"	Heavy clay
	LE01023	Woomera, SA [b]	S30°57'25" E136°54'22"	
	LE01029	Marree, SA [a,b]	S29°38'51" E137°38'17"	Clayey sand
	LE04004	Fords Bridge, NSW [b,c,d]	S29°42'27" E145°28'22"	Pale red/brown claypan
Frankenia pauciflora **var. *fruticulosa***	LE01010	Thevernard, SA [a,d]	S32°08'33" E133°40'35"	Low limestone cliff
	LE05024	Corney Point, SA [b,c,d]	S34°35'53" E137°00'00"	Limestone cliff
	LE05025	Pt Rickaby, SA [b,c,d]	S34°40'50" E137°29'37"	Sand dune
	LE05026	Pt Gawler, SA [b,c,d]	S34°38'35" E138°26'22"	Shelly sand over clayey sand
Frankenia pauciflora **var. *gunnii***	LE01001	Goolwa, SA [a,b]	S35°31'56" E138°49'37"	Saltmarsh
	LE03086	Kangaroo Island, SA [b,c,d]	S35°47'22" E137°45'58"	Shelly sand
	LE03087	Kangaroo Island, SA [b,c,d]	S36°03'32" E136°42'06"	
	LE04020	Coorong, SA [b,c,d]	S36°19'47" E139°45'00"	Grey boggy, clayey sand
	LE04021	Coorong, SA [b,c]	S36°03'20" E139°35'21"	Clay
	LE06001	Robe, SA [b,c,d]	S37°00'59" E139°44'32"	Sand, base of cliff
	LE06002	Beachport, SA [b,c,d]	S37°29'02" E139°59'59"	Sand
	LE06003	Kingston SE, SA [b,c,d]	S36°49'45" E139°52'13"	Sand
Frankenia planifolia	LE02011	Evelyn Downs Station, SA [b,c,d]	S28°10'12" E134°24'07"	Slope of ironstone scree
	LE03076	Alandale Station, SA [b,d]	S27°40'38" E135°32'37"	Red gibber, sandy wash-away
Frankenia plicata	LE05009	Anna Creek Station, SA [b,c,d]	S29°38'57" E135°45'19"	Gypseous dunes and scree
	LE05010	Anna Creek Station, SA [b,c,d]	S29°40'22" E135°46'07"	Gypsum, limestone, scree
Frankenia serpyllifolia	LE01018	Strzelecki Track, SA [a,b,d]	S30°02'02" E138°56'51"	Red clayey sand
	LE01022	Pimba, SA [a,b]	S31°18'56" E136°51'11"	
	LE02001	Mt Gason, SA [b]	S27°13'39" E138°45'44"	Red ironstone
	LE02013	Mt Barry Station, SA [b,c,d]	S28°12'40" E134°48'12"	Red clay, pebbles, dam run-off
	LE03077	Oodnadatta Track, SA [b]	S27°38'20" E135°29'58"	
	LE04002	Tibooburra, NSW [b,c]	S29°06'26" E131°55'48"	Gibber mesa
Frankenia sessilis	LE01007	Cactus Beach, SA [a,b]	S32°03'56" E132°59'37"	Clayey sand, gypsum, limestone
	LE01008	Fowlers Bay, SA [a,b]	NR	Brown/red silty sand, saline
Frankenia subteres	LE01017	Moolawattana Station, SA [a,b]	S29°51'01" E139°39'53"	Traventine
	LE01030	Lyndhurst, SA [a,b]	S29°12'38" E138°23'58"	White sand, saline

Table 1. Sites of soil collections with *Frankenia* species association, and a general description of the soil. **Superscript 'a'** indicates soils analysed by ICPAES, **superscript 'b'** indicates soil analysed by CSBP, **superscript 'c'** indicates soil analysed at CSIRO, and **superscript 'd'** indicates water retention at field capacity estimated by MIR analyses. 'NR' denotes that this information was not recorded.

Species	N	Calcium	Magnesium	Sodium	Potassium	Sulfur	Iron	Phosphorus	Aluminium	Manganese
Larger-seeded species	**11**	**13.6 (±5.2)**	**1.1 (±0.1)**	**0.3 (±0.1)**	**0.6 (±0.1)**	**0.5 (±0.3)**	**2.3 (±0.5)**	**0.04 (±0.00)**	**3.2 (±0.7)**	**0.030 (±0.006)**
F. eremophila	1	35.0	1.3	0.3	0.1	2.7	0.4	0.04	0.5	0.008*
F. gracilis	3	0.4 (±0.04)	0.9 (±0.1)	0.1 (±0.8)	0.9 (±0.1)	0.03 (±0.0)	3.5 (±0.3)	0.34 (±0.01)	5.0 (±0.0)	0.046 (±0.007)
F. latior	2	1.0 (±0.5)	0.9 (±0.1)	0.3 (±0.04)	0.72(±0.2)	0.2 (±0.1)	3.6 (±0.2)	0.05 (±0.01)	4.5 (±1.5)	0.038 (±0.005)
F. serpyllifolia	2	2.60(±0.0)	0.9 (±0.1)	0.2 (±0.1)	0.7 (±0.2)	0.7 (±0.6)	3.0 (±0.6)	0.03 (±0.00)	4.8 (±1.2)	0.039 (±0.014)
F. sessilis	3	35.3 (±2.4)	1.6 (±0.1)	0.6 (±0.1)	0.12(±0.02)	0.2 (±0.02)	0.3 (±0.1)	0.04 (±0.00)	0.4 (±0.1)	0.008 (±0.002)
Smaller-seeded species	**11**	**8.2 (±0.7)**	**2.1 (±0.6)**	**0.6 (±0.2)**	**0.3 (±0.1)**	**1.9 (±0.6)**	**1.5 (±0.4)**	**0.03 (±0.01)**	**1.5 (±1.1)**	**0.025 (±0.010)**
F. foliosa	7	7.6 (±1.6)	2.5 (±0.8)	0.6 (±0.4)	0.3 (±0.1)	2.6 (±0.8)	1.4 (±0.5)	0.02 (±0.01)	1.4 (±0.4)	0.024 (±0.017)
F. pauciflora	2	15.4 (±4.7)	1.0 (±0.1)	0.7 (±0.8)	0.2 (±0.04)	0.1 (±0.02)	1.1 (±0.2)	0.06 (±0.01)	1.1 (±0.0)	0.018 (±0.002)
F. subteres	2	3.0 (±2.1)	2.0 (±0.9)	0.3 (±0.1)	0.5 (±0.2)	1.3 (±1.3)	2.2 (±0.9)	0.04 (±0.01)	2.5 (±1.4)	0.034 (±0.001)
All *Frankenia* species	**22**	**10.9 (±2.8)**	**1.6 (±0.3)**	**0.5 (±0.1)**	**0.4 (±0.1)**	**1.2 (±0.4)**	**1.9 (±0.3)**		**2.4 (±0.4)**	**0.027 (±0.006)**

Table 2. Percentage (%) means (±s.e.) for soil element content (ICPAES analysis) at sites per *Frankenia* species, and per seed packaging category. 'N' indicates the number of populations sampled per species (see Table 1 for sites included in ICPAES analysis). Note that zinc, nickel, boron, cobalt and copper percentages are not included, as content of these elements were <0.00%.

	Larger-seeded species	Smaller-seeded species	All species	Range
Number of populations	22	19	41	41
% sand	65.4 (±4.6)	73.8 (±3.4)	69.3 (±3.0)	25.0 – 96.3
% clay	22.3 (±3.4)	16.3 (±2.2)	19.6 (±2.1)	29.0 – 52.5
% <20µm particles	30.6 (±4.5)	25.0 (±3.2)	28.0 (±2.8)	3.7 – 70.0
EC (dS/m)	1.62 (±0.56)	3.11 (±0.77)	2.31 (±0.47)	0.04 – 11.40
Gypsum	0.37 (±0.24)	2.09 (±1.27)	1.17 (±0.61)	0.00 – 21.80
Carbonate (^{o})	0.5 (±0.2)	2.2 (±0.2)		0 – 3
Field capacity (Vol %)	21.9 (±1.6)	27.7 (±2.2)	24.6 (±1.4)	6.2 – 40.0
pH	8.22 (±0.13)	8.63 (±0.11)	8.40 (±0.09)	6.90 – 9.80
Calcium (cmol(+)/kg)	11.41 (±1.8)	20.75 (±5.3)	15.74 (±2.7)	2.92 – 93.65
Magnesium (cmol(+)/kg)	3.03 (±0.5)	7.60 (±2.0)	5.15 (±1.0)	0.33 – 28.14
Sodium (cmol(+)/kg)	7.65 (±2.1)	14.00 (±3.4)	10.60 (±2.0)	0.32 – 48.79
Potassium (cmol(+)/kg)	0.86 (±0.1)	0.66 (±0.1)	0.77 (±0.1)	0.12 – 2.28
Ca2+ : Mg2+	5.0:1	9.2:1	6.85	
Ca2+ : Na+	3.9:1	4.7:1	4.24	
K+ : Na+	0.4:1	0.1:1	0.25	
CEC (cmol(+)/kg)	22.95 (±3.4)	43.02 (±7.9)	32.25 (±4.3)	3.82 – 134.16
ESP (%)	27.6 (±4.2)	29.0 (±4.3)	28.3 (±3.0)	2.8 – 83.5

Table 3. Means (± s.e.) for soil properties examined for Australian *Frankenia* species overall and per seed packaging strategy. Note that the smaller-seeded species includes two varieties of *F. pauciflora* (as per Craigie 2007). 'Range' indicates the minimum and maximum values recorded for all populations of *Frankenia* included in this study.

Species	N	% sand	% clay	% <20µm	Gypsum	Carbonate (°)	FC (Vol)%
F. connata	1	80.0 *	12.5 *	15 *	0.00 *	0.00 *	6.0 *
F. cordata	2	94.5 (±1.9)	3.7 (±0.8)	5.6 (±1.9)	0.00	0.00	26.0 (±10.0)
F. eremophila	1	77.7*	13.8 *	22.3 *	0.40 *	3.0*	22.0 *
F. foliosa	6	71.1 (±5.4)	13.7 (±2.9)	29.0 (±5.4)	6.6 (±3.5)	1.3 (±0.4)	18.0 (±1.5)
F. gracilis	5	62.3 (±9.1)	23.3 (±5.4)	31.9 (±7.9)	0.0	0.00	24.4 (±1.5)
F. latior	4	59.1(±10.0)	27.0 (±7.9)	35.0 (±10.5)	0.99 (±1.0)	0.3 (±0.3)	21.8 (±1.5)
F. pauciflora f	3	83.7 (±2.3)	8.7 (±0.7)	16.2 (±2.3)	0.00	3.0 (±0.0)	34.3 (±1.2)
F. pauciflora g	8	76.2 (±5.5)	17.2 (±4.5)	22.1 (±5.2)	0.00	2.6 (±0.3)	34.8 (±2.6)
F. planifolia	1	84.8 *	8.9 *	15.2 *	0.00 *	0.00 *	30.0 *
F. plicata	2	79.7 (±3.1)	12.5 (±1.2)	20.3 (±3.1)	0.00	0.00	35.0 (±3.0)
F. serpyllifolia	4	36.9 (±4.8)	45.4 (±2.9)	60.7 (±4.7)	0.97(±0.0)	0.5 (±0.5)	21.8 (±2.8)
F. sessilis	2	75.9 (±3.4)	8.7 9±0.4)	13.2 (±1.6)	0.00	2.0 (±0.0)	13.0 (±1.0)
F. subteres	2	57.5 (±12.5)	20.0 (±0.)0	37.5 (±12.5)	0.00	2.0 (±0.0)	20.5 (±4.5)

Species	EC (dS/m)	pH	Calcium cmol(+)/kg	Magnesium cmol(+)/kg	Sodium cmol(+)/kg	Potassium cmol(+)/kg
F. connata	0.12 *	8.50 *	4.8 *	0.5 *	0.7 *	0.3 *
F. cordata	0.48 (±0.15)	8.65 (±0.05)	3.7 (±0.3)	0.8 (±0.1)	2.3 (±0.6)	0.5 (±0.0)
F. eremophila	3.11 *	8.00 *	17.1 *	2.0 *	7.5 *	0.5 *
F. foliosa	3.82 (±1.40)	8.48 (±0.28)	38.2 (±14.0)	6.7 (±4.4)	17.4 (±7.2)	0.5 (±0.2)
F. gracilis	0.35 (±0.10)	8.38 (±0.34)	11.9 (±3.5)	2.4 (±0.8)	2.7 (±0.7)	0.8 (±0.2)
F. latior	0.63 (±0.40)	7.88 (±0.35)	9.4 (±3.9)	3.1 (±1.0)	4.2 (±2.4)	0.6 (±0.1)
F. pauciflora f	0.82 (±0.10)	8.80 (±0.06)	10.5 (±1.2)	2.5 (±0.7)	3.5 (±0.6)	0.3 (±0.0)
F. pauciflora g	3.72 (±1.42)	8.70 (±0.14)	11.2 (±2.2)	11.7 (±3.7)	16.9 (±5.7)	0.9 (±0.3)
F. planifolia	0.08 *	7.90 *	4.2 *	1.7 *	1.4 *	1.6 *
F. plicata	1.45 (±1.01)	7.95 (±0.35)	8.8 (±2.3)	3.1 (±0.3)	9.5 (±6.8)	0.9 (±0.1)
F. serpyllifolia	3.09 (±2.33)	8.25 (±0.47)	17.4 (±6.4)	4.5 (±2.2)	10.8 (±5.1)	1.1 (±0.2)
F. sessilis	5.88 (±1.83)	8.40 (±0.20)	16.6 (±2.8)	5.9 (±1.6)	30.8 (±5.9)	1.3 (±0.7)
F. subteres	2.03 (±1.62)	8.55 (±0.35)	21.1 (±13.5)	1.9 (±0.1)	8.0 (±5.7)	0.5 (±0.2)

Species	Ca^{2+}:Mg^{2+}	Ca^{2+}:Na^{+}	K^{+}:Na^{+}	CEC cmol(+)/kg	ESP (%)	Seed mass (µg)
F. connata	9.1:1 *	7.3:1*	0.5:1*	6.29 *	10.5 *	77 (±3)
F. cordata	5.1:1	1.8:1	0.2:1	7.27 (±0.5)	31.3 (±6.3)	35 (±0.9)
F. eremophila	8.4:1 *	2.3:1 *	0.1:1 *	27.12 *	27.7 *	45 (±0.8)
F. foliosa	20.8:1	10.4:1	0.1:1	63.08 (±19.3)	25.8 (±10.0)	9 (±0.3)
F. gracilis	5.7:1	7.3:1	0.6:1	17.92 (±4.5)	19.9 (±7.0)	75 (±2)
F. latior	4.7:1	4.1:1	0.4:1	17.32 (±6.6)	18.7 (±5.0)	36 (±1)
F. pauciflora f	4.6:1	3.0:1	0.1:1	16.78 (±2.4)	20.8 (±0.5	15 (±0.1)
F. pauciflora g	1.4:1	1.4:1	0.1:1	40.69 (±9.4)	36.0 (±6.6)	11 (±0.9)
F. planifolia	2.4:1 *	3.0:1 *	1.1:1 *	8.91 *	15.8 *	61 (±1)
F. plicata	2.8:1	1.6:1	0.2:1	22.40 (±9.2)	36.1 (±15.5)	30 (±0.7)
F. serpyllifolia	5.6:1	3.1:1	0.2:1	33.84 (±4.9)	32.8 (±17.0)	61 (±0.9)
F. sessilis	2.9:1	0.5:1	0.0:1	54.52 (±10.9)	56.6 (±0.5)	72 (±18)
F. subteres	11.9:1	2.9:1	0.1:1	31.50 (±19.3)	23.0 (±4.0)	15 (±0.6)

Table 4. Means (± s.e.) for soil properties sampled from populations included in this study. (*) denotes where only 1 population for that species was sampled. 'N' is the number of populations sampled per species. Note the two varieties of *F. pauciflora* – F. *pauciflora* var. *fruticulosa* and *F. pauciflora* var. *gunnii* – *sensu* Craigie (2007).

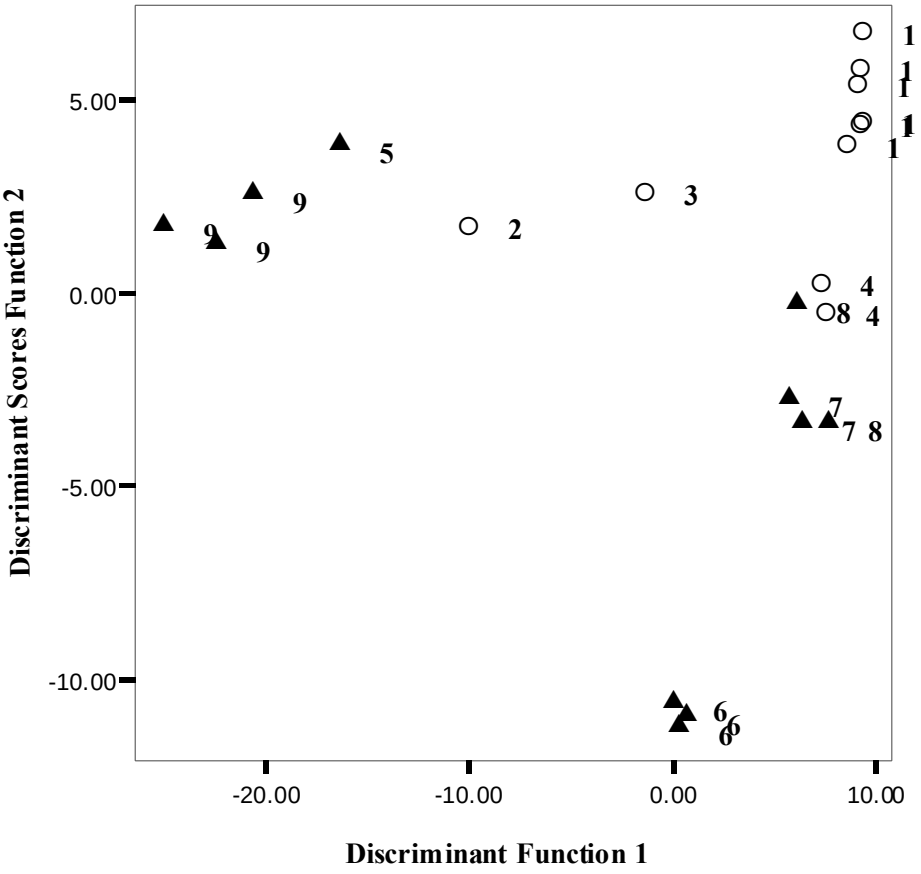

Figure 1. Scatterplot generated by the first 2 Discriminant Function scores calculated to identify element interaction effect that maximize the differences between the 20 *Frankenia* populations included in this study. Open circles represent smaller-seeded species. Closed triangles represent larger-seeded species. Label numbers represent species as follows: (1) *F. foliosa*, (2) *F. pauciflora* var. *fruticulosa*, (3) *F. pauciflora* var. *gunnii*, (4) *F. subteres*, (5) *F. eremophila*, (6) *F. gracilis*, (7) *F. latior*, (8) *F. serpyllifolia*, and (9) *F. sessilis*.

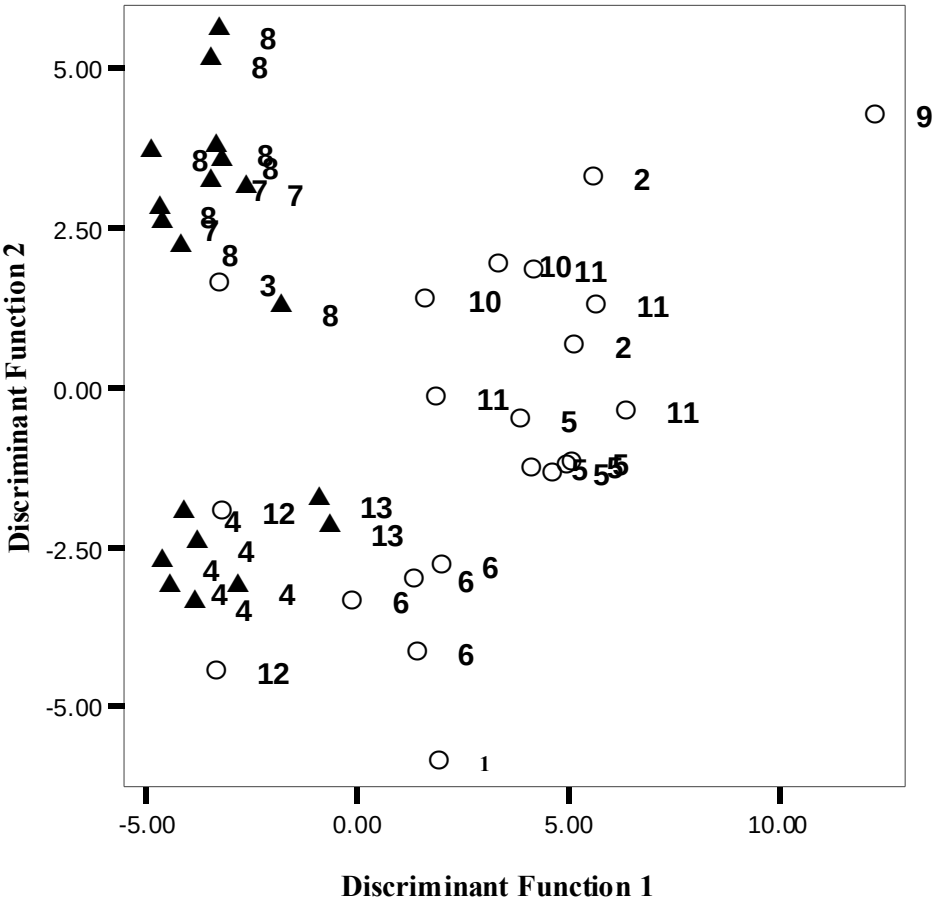

Figure 2. Scatterplot generated by the first 2 Discriminant Function scores calculated to identify soil property interaction effect that maximize the differences between the 41 *Frankenia* populations included in this study. Open circles represent larger-seeded species. Closed triangles represent smaller-seeded species. Label numbers represent species as follows: (1) *F. connata*, (2) *F. cordata*, (3) *F. eremophila*, (4) *F. foliosa*, (5) *F. gracilis*, (6) *F. latior*, (7) *F. pauciflora* var. *fruticulosa*, (8) *F. pauciflora* var. *gunnii*, (9) *F. planifolia*, (10) *F. plicata*, (11) *F. serpyllifolia*, (12) *F. sessilis*, and (13) *F. subteres*.