Chapter 7

SEED MINERAL NUTRIENT CONTENTS IN AUSTRALIAN SPECIES OF *FRANKENIA* L. (FRANKENIACEAE).

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ABSTRACT

Easton, L.C. & Kleindorfer, S. (In review). Seed mineral nutrient contents in Australian species of *Frankenia* L. (Frankeniaceae). *Folia Geobotanica.*

We examine the relationship between seed mineral nutrient contents and seed mass in Australian species of the genus *Frankenia* L. This genus includes two divergent reproductive strategies – some species have flowers with a low number of ovules and accordingly, produce fruit with a few larger seeds, while other species have flowers with numerous ovules and thus produce fruit with a large number of smaller seeds. Both strategies occur in nutrient poor soils. The proportion of mineral elements allocated to seed production was consistent between *Frankenia* species despite variations in seed packaging strategies, soil characteristics, and environmental conditions. However, the proportions in three mineral elements (sodium, boron, and copper) were significantly different between seed packaging strategies, and the proportion of one mineral element (nickel) was significantly different between species.

Key words: arid zone plants, germination strategies, halophytes, seed size and number, seed mineral nutrient content

INTRODUCTION

In the early stages of seed germination and seedling establishment, seedlings are largely reliant on the mineral nutrient reserves contained within the seed. Both the quantity of the mineral reserves and the proportions of different elements in seeds across species raise important ecological and evolutionary questions (Thompson 1993). For example, does seed nutrient content reflect mineral deficiencies in the soil? Do phylogenetic constraints on seed size (mass) influence the balance of mineral nutrient content per seed?

Soil properties are thought to be a selective factor in the evolution of seed mass, seed number, and seed nutrient content (Esler *et al.* 1989). It is proposed that large seeds are an adaptation for enhancing seedling establishment in nutrient poor soils, as the storage tissue of seeds provides the primary source of mineral nutrients to seedlings (Milberg & Lamont 1997). Hypothetically, infertile soil would be a strong selection for larger seeds with higher mineral content to ensure successful seedling establishment. In the more fertile soils, seeds could be smaller since seedlings would be less dependent on seed reserves for successful establishment (Esler *et al.* 1989). However, little information is available on the relationship between inter-species variation in seed mineral content allocation and seedling establishment success in nutrient poor soils (see Fenner 1986b; Lee & Fenner 1989; Milberg & Lamont 1997). Furthermore, available data on the allocation of mineral nutrients to the reproductive structures in the arid zones predominantly relates to annuals (Williams & Bell 1981).

This paper investigates seed mineral content in 18 Australian species of *Frankenia*. *Frankenia* is a cosmopolitan genus that occurs in Mediterranean, semi-arid, and arid regions, and frequently on saline, sodic, or gypseous soils. Pertinent to allocation of seed mineral content, the genus includes two divergent reproductive strategies. Some species have flowers with a low number of ovules and accordingly, produce only a few larger seeds per fruit, while other species have flowers with numerous ovules and fruit contain a large number of smaller seeds (Easton & Kleindorfer 2008a, 2008b). While this is not uncommon within taxa, these divergent seed packaging strategies are usually associated with distinct environmental conditions (e.g. Milberg *et al.* 1996). However, both larger- and smaller-seeded *Frankenia* species often occur in close geographical proximity. This provides a good opportunity to examine selective pressures that have shaped these geographically co-occurring reproductive strategies.

Comparisons between related species have the advantage of similar morphology and of phylogenetic history. We investigated seed mineral content in closely related species to examine variation in the allocation of mineral elements between seed packaging strategies. This provided an opportunity to examine whether mineral nutrient composition of seeds within *Frankenia* varied between seed packaging strategies, or if there was a conservative phylogenetic regulation of nutrient allocation to fruit. In previous chapters, we have uncovered differences in germination between the larger- and smaller-seeded *Frankenia* species in relation to temperature, salinity levels, light requirements, and soil properties. Here we investigate whether the differences in germination between seed packaging strategies correlate to seed nutrient concentrations.

MATERIALS AND METHODS

The species

Frankenia are salt-tolerant shrubs, sub-shrubs or cushion-bushes. Their habitat includes coastal cliffs and saltmarshes, and the margins of inland salt lakes and salt-pans. Populations often occur in isolated, disjunct pockets and generally cover only several square metres. *Frankenia* species can be categorized, based on their ovule number per flower and mean seed mass, 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. – *sensu* Easton & Kleindorfer 2008a).

Seed mineral content

Seeds were collected from naturally occurring populations in early autumn from 2001 to 2006. Seeds were removed from their fruits under a dissecting microscope and stored in vials at optimal conditions (see Wrigley & Fagg 2003). A subset of 150 seeds per population was weighed individually on Mettler Toledo MX/UMX microbalance to ascertain mean seed weight per population.

Seed mineral content per population was tested using batches of 0.4 gm of seeds per population (see Table 1). Seeds were oven-dried, and then digested with nitric acid and hydrochloric acid. Seed nutrient analysis was undertaken by Radial CIROS Inductively Coupled Plasma Atomic Emission Spectrometry (ICPAES) at the Waite Analytical Services, Urrbrae, South Australia.

Statistical analysis

Data were arc-sine transformed to satisfy the requirements of normality for percentage data (Dytham 2003). All analyses were calculated using SPSS Version 15 (SPSS Inc. 2006). Descriptive statistics, including means and standard errors, were calculated for all mineral elements per each species and per seed mass category. Discriminant Function Analysis was used to provide weightings for the combination of all mineral concentrations to provide a maximum discrimination between populations (Dytham 2003). This analysis showed whether inter-relationships of mineral concentrations identified clusters of species groups or seed mass category groups. We also tested whether individual populations would be assigned to the correct species cluster 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 (Dytham 2003). Wilks lambda – the proportion of the total variance in the discriminant scores not explained by the differences among groups – tested the equality of group means between species and between seed mass categories.

RESULTS

Results of the ICPAES analyses were subjected to Discriminant Function Analysis (DFA) to test the null hypotheses of no differences in the seed mineral contents between seed mass category and/or species. Molybdenum, cobalt, titanium, chromium, cadmium, lead and selenium were included in the ICPAES analysis; however the levels recorded (in mg/kg) were less than the limit of determination for the sample (calculated as 10x the standard deviation of the 'blank' samples) for ICPAES. Table 1 lists the means (±s.e.) of seed mineral contents per species. Table 1 also lists the number of seeds needed per population to make up the 0.4 grams needed for the ICPAES analysis, based on the mean seed weight per population. Table 2 lists the means (±s.e.) of seed mineral contents per seed mass category.

The structure matrix of the DFA for differences between seed mass categories shows that the inter-relationship between sodium, copper, and boron accounted for the largest absolute correlation. Calcium, phosphorus, zinc and manganese were least accountable for the correlation. Classification Results, predicting group membership, showed that 62.5% of the cross-validated grouped cases were correctly classified. Seed mass categories did not cluster and there were no significant differences in seed mineral nutrient content interactions between the two seed mass categories ($\chi^2 = 17.47$, df = 13, P = 0.179). The 'Test of Equality of Group

Means' (the proportion of the total variance in the discriminant scores not explained by the differences among groups) showed that individual proportions of three elements were significantly different between seed mass categories; sodium (F = 6.308, $df_{(1, 38)}$ $P<0.05$), boron (F = 5.149, $df_{(1, 38)}$ $P<0.05$), and copper (F = 6.132, $df_{(1, 38)}$ $P<0.05$).

For the larger-seed mass category, all of the variance in the discriminant scores of the interaction effects of the proportions of mineral elements between species was explained by differences between the species. However, for the smaller-seeded mass category, there was a significant difference in the proportion of nickel between species (F = 10.06, $df_{(8, 12)}$ $P<0.001$). This resulted from the high nickel content in the seeds from both of the populations of *F. magnifica*. However, the proportion of nickel was not significantly different between the other species (ANOVA: F = 0.57, df = 3, P = 0.64). We re-analysed the data, omitting nickel from the analysis as a possible confounding property. Figure 1 is the scatterplot generated by the interaction of the weighted scores for each population for the first two axes of the DFA.

DISCUSSION

This study supports the hypothesis that plant taxa allocate a set amount of resources to seed production. The proportion of mineral elements allocated to seed production was consistent between *Frankenia* species despite variations in seed packaging strategies (Chapters 2 and 3), soil properties (Chapter5), and environmental conditions (Chapters 4 and 6). Consistent allocation of resources to reproduction has been shown in other arid zone plant species. For example, Lee and Fenner (1989) found that the mineral nutrient allocation to seeds of 12 *Chionochloa* species was uniform between species despite variation in soil fertility. Fenner (1986a) described the apparent priority given to supplying a consistent nutrient allocation to seeds – possibly at the expense of the parent plant – as being comparable to that seen in human foetal nutrition.

The mineral nutrient requirements for successful seedling establishment in nutrient deficient soils are facilitated by the seed reserves. The proportion of stored nutrients may reflect the availability of nutrients in the soils to which the particular species is adapted. For Australian species of *Frankenia,* proportions of three elements (sodium, boron, and copper) were significantly different between seed mass categories. These differences in proportion of elements should reflect differences in soil characteristics. In Chapter 5, we demonstrated that there were differences in soil characteristics between seed mass categories that occur in central and southern Australia. Soil characteristics associated with habitats of Western Australian species were not covered in this thesis. However, some trends between seed mineral content and soil properties, especially between seed mass categories, are apparent.

There was a significantly higher proportion of sodium ions in the seeds of the larger-seeded species. In Chapter 5, we demonstrated that the smaller-seeded species of central and southern Australian *Frankenia* occurred in more highly saline and sodic soils than the larger-seeded species. Consequently, sodium is readily available from the surrounding soil for the smaller-seeded species and storage of sodium within the seeds is superfluous. But sodium is toxic to plants. In saline/sodic soils, the osmotic pressure across seed cell membranes causes water to move out of the seeds due to the lower solute concentration (i.e. higher water potential) in the plant cells. This can lead to seed death. In addition, sodium ions (Na^+) are preferentially absorbed over potassium ions (K^+) during osmosis, which may deprive the plant of adequate supplies of an essential nutrient that is required to activate enzymes (Raven *et al.* 1999). Specific Na^+ levels are likely to be important for efficient functioning of the K^+:Na^+ membrane pump. If Na^+ is not readily available from soil in sufficient quantities, it needs to be stored in the seeds, as in the larger-seeded species. In many halophytes, a K^+:Na^+ pump plays a major role in maintaining low Na^+ concentrations within cells while simultaneously ensuring that a sufficient supply of K^+ enters the plant (Raven *et al.* 1999). Higher internal solute concentrations also result in water imbibing into the seeds rather than out of the seeds. In Chapter 5, we demonstrated that the K^+:Na^+ ratio in soil was significantly different between the larger- and the smaller-seeded species. Larger-seeded species occurred in soils with smaller K^+:Na^+ ratios and larger K^+ concentrations in the cation exchange capacity than smaller-seeded species.

The proportion of boron was significantly higher in seeds of the larger-seeded *Frankenia* species. Boron is instrumental in root tip elongation. It is hypothesised that larger seeds contain more nutrients for faster root elongation to keep track of receding soil-water after rains (see Westoby *et al.* 1992; Venable *et al.* 1998; Fenner 1983, 1992; Milberg *et al.* 1996). The higher levels of boron would facilitate faster root elongation. In addition, the seedling phase is marked by the extrusion of the plumule (shoot). If a seed is buried, the plumule has to push its way to the surface, a process that expends energy from the seed reserves (Fenner & Thomson 2005). In Chapters 2 and 4 we demonstrated that the larger-seeded species were less dependent on light for germination. The larger seed reserves in the larger-seeded *Frankenia* species may be utilized in plumule extrusion from burial.

The proportion of copper was significantly higher in the smaller-seeded species. Copper is an activator of enzymes involved in oxidation and reduction. Higher concentrations of these enzymes may be necessary in soils with a high cation exchange capacity, as in the case of the smaller-seeded species of central and southern Australia (see Chapter 5).

Seeds of the two *F. magnifica* populations had nickel contents (21 mg/kg and 19 mg/kg) that were at least two-fold higher than all other populations. Sixty-seven percent of the *Frankenia* populations had a seed nickel content less than 4 mg/kg. Nickel content may reflect the soil chemistry in the region of these populations; however a *F. laxiflora* population from this same region had a seed nickel content of only 1.6 mg/kg. Nickel is an essential component of enzyme functioning in nitrogen metabolism (Raven *et al.* 1999). The overall highly variable nickel content of seeds between populations within species may be site specific and due to soil nitrogen content. The nitrogen content of soils across the range of Australian species of *Frankenia* was not investigated in this thesis.

One of the primary functions of seeds is to provide the embryo with a reserve of mineral and organic nutrients to nourish it in the initial stages of establishment. However, the measurement of the absolute amount of each mineral element per seed is not indicative of the total amount available for seedling establishment. These measurements include the mineral composition of the seed coat. The partitioning of the mineral element components of seeds into embryo development versus seed coat composition was not investigated in this thesis.

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species	K	Ca	NA	Mg	P	S	Al	Fe	Mn	B	Cu	Ni	Zn	mass	#/μg	Site	GPS co-ordinates
F. cinerea	5200	5400	3500	3500	7100	3100	760	650	56	20	10	2.1	55	95	4211	Lake King, WA	S35°05'24"E119°36'37"
F. cordata	5200	7300	3100	4000	5800	3000	600	510	64	53	11	4.3	77	391	1041	Ormiston Gorge, NT	S30°25'59"E138°22'13"
F. cordata	5800	6500	4900	3700	4300	3500	610	570	53	37	9.8	1.8	80	375	1067	Curtin Springs, NT	S25°21'01"E131°50'47"
F. eremophila	5700	4600	790	3900	7300	3900	23	104	121	15	14	2.1	88	449	906	Cactus Beach, SA	S30°04'49"E132°59'31"
F. fecunda	5400	6600	1770	3300	7400	4000	92	230	49	25	16	1	69	52	7692	Leonora, WA	S29°01'59"E121°29'13"
F. fecunda	5000	4700	3600	2600	4300	3500	330	490	39	16	11	3.9	79	82	4915	Lake Annean, WA	S26°53'15"E118°17'21"
F. fecunda	4400	5600	1050	3100	3300	3200	1730	1530	60	22	15	5.7	136	72	5611	Lake Austin, WA	S27°36'07'E117°53'31"
F. fecunda	4700	6000	1260	2700	5700	3000	490	670	49	17	11	2.2	122	72	5597	Lake Austin, WA	S27°36'07'E117°53'31"
F. foliosa	5500	6000	2400	3100	6300	4900	37	169	46	21	16	6.1	84	63	6349	Oodnadatta Track, SA	S27°28'36"E135°23'35"
F. foliosa	6000	5000	1550	3400	6500	4200	25	115	42	16	9.8	3.9	41	81	4938	Birdsville Track, SA	S29°20'13"E139°19'32"
F. foliosa	5400	6000	2900	2600	6300	4400	13	100	74	15	12	5.5	55	43	9209	Strzelecki Track, SA	S29°33'27"E139°55'08"
F. glomerata	5100	8800	1570	3700	7100	3500	46	179	38	22	11	2.1	54	832	475	Kalbarri, WA	S27°45'23"E114°08'21"
F. gracilis	4900	8200	1110	3100	6200	4000	250	370	77	20	15	6.1	77	358	1120	Roxby Downs, SA	S30°03'28"E137°04'11"
F. gracilis	4200	5700	1410	3500	7200	3700	31	300	26	48	12	0.84	137	678	600	Fords Bridge, NSW	S29°42'27"E145°28'22"
F. gracilis	4200	7300	1080	2800	5500	3700	470	500	53	20	14	2.5	113	358	1131	Roxby Downs, SA	S30°03'28"E137°04'11"
F. irregularis	5600	5500	2600	2700	5400	3900	230	590	48	24	12	2.5	92	61	6590	Kalgoorlie, WA	S30°32'03"E121°24'45"
F. irregularis	5800	13800	2500	3800	8900	5600	230	360	67	29	12	4.2	111	71	5592	Lake Grace, WA	S33°06'35"E118°24'24"
F. interioris	6700	4300	1040	3400	7400	4800	133	260	31	16	15	8.6	51	349	1166	Coolgardie, WA	S30°58'20"E121°03'11"
F. interioris	6100	8200	12700	3200	5500	3500	96	250	37	36	8.4	2.8	58	286	1406	Mundrabilla, WA	S31°54'37"E127°21'26"
F. laxiflora	6400	5000	1400	3100	7300	4500	48	182	33	17	16	9.9	41	59	6729	Ponton River, WA	S31°02'22"E123°47'04"
F. laxiflora	4300	6100	540	3300	5900	3700	158	370	47	22	15	1.6	129	72	5542	Mt Narryer, WA	S28°42'13"E115°53'24"
F. laxiflora	5200	7800	2600	3100	7300	4000	194	320	65	38	11	1	51	67	6030	Lake Annean, WA	S26°53'15"E118°17'21"
F. magnifica	5300	6300	1230	3600	7100	3500	350	950	77	26	13	21	77	119	3412	Curbur Station, WA	S26°27'45"E115°56'26"
F. magnifica	5500	5700	2300	3900	3900	3200	1330	890	47	27	14	19	91	90	4456	Gascoyne Junction, WA	S24°45'29"E115°18'53"
F. pauciflora	4000	8000	720	3000	5200	3400	400	530	52	21	14	2.4	78	40	9900	Pindar, WA	S28°28'29"E115°47'27"
F. pauciflora	4400	7700	2400	2900	6200	3600	162	270	49	18	14	1.3	52	61	6656	Shark Bay, WA	S26°01'18"E113°35'07"
F. pauciflora	6700	4500	1610	3800	7600	4200	21	120	36	15	14	3.8	69	94	4340	Goolwa, SA	S35°31'56"E138°49'37"
F. pauciflora	6000	4200	1460	3000	6600	4700	63	188	53	16	13	3.8	55	146	2767	Kingston SE, SA	S36°49'45"E139°52'13"
F. pauciflora	3900	6000	2500	2900	6100	3400	76	200	25	23	12	0	72	127	2008	Beachport, SA	S25°29'02"E139°59'59"
F. planifolia	6600	4800	3100	2700	7200	4000	6.7	122	39	18	12	4.9	68	532	761	Oodnadatta Track, SA	S27°40'38"E135°32'36"
F. serpylifolia	7500	6700	3000	3200	5800	3600	380	620	50	21	8.6	1.3	61	724	551	Oodnadatta Track, SA	S28°16'33"E135°50'16"
F. serpylifolia	5700	3800	5900	3300	6700	3100	220	380	39	21	14	3.7	111	621	646	Tibooburra, NSW	S29°06'26"E131°55'48"
F. serpylifolia	4400	5500	4300	3300	6700	3700	18	164	27	28	8.3	1.4	54	643	627	Anna Creek Station, SA	S29°40'22"E135°46'07"
F. serpylifolia	4600	10300	2200	3300	6300	3400	56	220	47	22	9.4	2.4	67	551	730	Oodnadatta Track, SA	S27°40'38"E135°32'36"
F. sessilis	6600	4400	1210	3600	7500	3900	39	127	32	15	13	3.7	70	159	2491	Fowlers Bay, SA	NR
F. sessilis	7000	4500	5600	2700	5700	5300	18	119	66	22	13	6.3	94	199	2050	Madura, WA	S31°53'59"E127°00'32"
F. subteres	6400	5500	620	4300	8700	3900	200	290	44	13	13	5.8	96	155	2574	Leigh Creek, SA	S30°25'59"E138°22'13"
F. tetrapetala	5000	5500	3400	3700	6500	3400	94	173	25	24	5	2.4	58	135	2963	Lake Newton, WA	S32°57'39"E119°36'33"
F. tetrapetala	4600	4800	6000	2900	5500	3400	900	560	48	50	11	2.5	79	122	3270	Newdegate, WA	S33°11'29"E119°12'49"
F. tetrapetala	4500	4100	5900	3400	6200	3200	680	420	84	40	8	1.2	80	185	2146	Grasspatch, WA	S33°25'09"E121°42'32"

Table 1. Species population sites (with GPS co-ordinates) and the mean mineral content per population (mg/kg). 'SA' indicates South Australia, 'WA' indicates Western Australia, 'N SW' indicates New South Wales, 'NT' indicates Northern Territory', and "NR" indicates GPS co-ordinates not recorded. 'Mass' is the mean seed weight for that population. '#/μg' is the number of seeds needed to produce 0.4 grams of material for the ICPAES analysis.

	Larger-seeded species		Smaller-seeded species	
	Mean (±se) mg/kg	**Range (mg/kg)**	**Mean (±se) mg/kg**	**Range (mg/kg)**
Potassium	5480 (±222)	4200 – 7500	5295 (±181)	3900 – 6700
Calcium	6035 (±404)	3800 – 10300	6300 (±458)	4200 – 13800
Sodium	3591 (±628)	790 – 12700	1851 (±187)	540 – 3600
Magnesium	3345 (±84)	2700 – 4000	32100 (±105)	2600 – 4300
Phosphorus	6375 (±189)	4300 – 7500	6300 (±323)	3300 – 8900
Sulfur	3685 (125)	3000 – 5300	3940 (±146)	3000 – 5600
Aluminium	272 (±66)	7 – 900	309 (±99)	13 – 1730
Iron	330 (±41)	104 – 650	428 (±80)	100 – 1530
Manganese	51 (±.2)	25 – 121	50 (±2.9)	25 – 77
Boron	27 (±2.7)	15 – 53	21 (±1.4)	13 – 38
Copper	11 (±0.6)	5 – 15	13.2 (±0.4)	9.8 – 16
Nickel	3.2 (±0.4)	0.8 – 8.6	5.2 (±1.2)	0 – 21
Zinc	76.6 (±5.1)	51 – 137	80 (±6.3)	41 – 136
Weight (μgm)	402 (±49)	95 – 832	81.4 (±7.2)	40 – 155
Number	1468 (±234)	475 – 4211	5543 (±455)	2008 – 9900

Table 2. Mean seed mass (mg/kg) for each mineral content per seed mass category, and the maximum and minimum mass values from populations within each seed mass category. ‘Weight’ denotes the mean seed mass per seed mass category. ‘Number’ indicates the number of seeds needed to attain 0.4 grams.

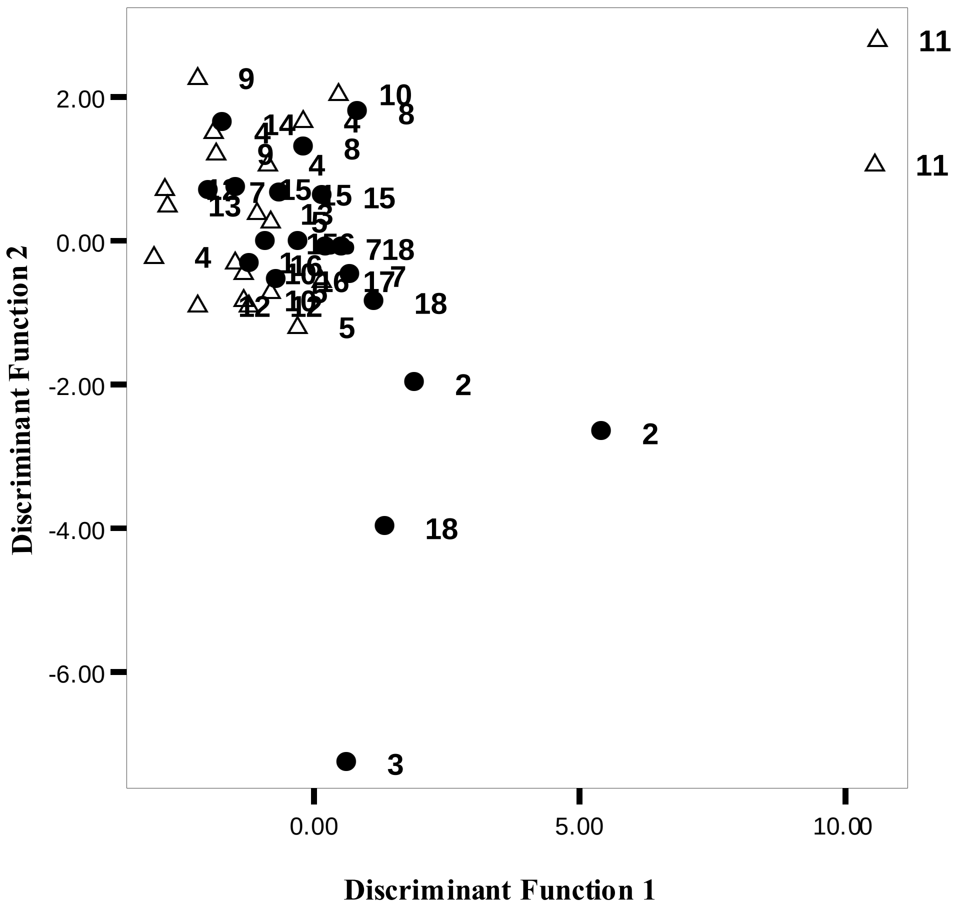

Figure 1. Scatterplot generated by the first 2 Discriminant Function scores calculated to identify the seed mineral nutrient content interactions that maximise the differences between *Frankenia* populations included in this study. Solid circles are larger-seeded species. Open triangles are smaller-seeded species. Label numbers represent species as follows: (1) *F. cinerea,* (2) *F. cordata,* (3) *F. eremophila,* (4) *F. fecunda,* (5) *F. foliosa,* (6) *F. glomerata,* (7) *F. gracilis,* (8) *F. interioris,* (9) *F. irregularis,* (10) *F. laxiflora,* (11) *F. magnifica,* (12) *F. pauciflora* var. *gunnii,* (13) *F. pauciflora* var. *pauciflora,* (14) *F. planifolia,* (15) *F. serpyllifolia,* (16) *F. sessilis,* (17) *F. subteres,* (18) *F. tetrapetala.*