Arillate seeds, with special reference to titoki (*Alectryon excelsus* Gaernt. (Sapindaceae))

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Abstract

Titoki (*Alectryon excelsus* Gaernt. (Sapindaceae)) is an endemic tree species of tropical affinity, up to 10m tall, common in New Zealand lowland forests. Development of the fruit/seed takes 12-14 months, with flowering between October-December and fruiting from October-March of the following year. The fruits are hard capsules up to 12mm, which split at maturity to reveal a lustrous black seed, a striking aspect of which is investment of the lower half by a scarlet vascularised aril with a firm texture and a surface of small tesselated lobes. The possession of an aril has been variously linked to sub-tropical/tropical rain forest species with large, non-dormant seeds, where the aril has been suggested to act either in a protective water-conserving capacity for the seed or to serve to attract animal dispersers. In *Alectryon* species also, the aril has been suggested to play a role in the splitting of the capsule. The present investigation addressed the following questions: 1) Does the aril play a role in opening the capsule? 2) Once the capsule is open does the aril buffer the seed against moisture loss? 3) Does the presence of an aril enhance/prolong viability of the seed? 4) How much moisture can the seed lose and still germinate? Observations and results suggested a function for the aril in capsule splitting, although the mechanism remains unclear. Seed moisture content (SMC) of mature arillate seeds was between 30-40 %; relative water content (RWC) was also high. While possession of an aril maintained the seed at a moisture content higher than that of bare seed, its presence did not enhance viability since SMC could drop to a low level (<8 %) without affecting germination. While the majority of viable seeds, of whatever initial SMC, germinated within 20-30 days, germination of a few was delayed for up to 90-100 days, although the total percentage germination of different samples was variable. Seeds maintained at a low SMC for up to 90 days with batches planted at intervals over this time showed a similar pattern - the first seeds germinated after around 16 days, the majority had germinated after 27 days, germination dwindled over 101 days and no seeds germinated beyond this point. Titoki seeds are non-dormant. They germinate readily but remain viable for only a relatively short period of time.

Additional key words: *aril ultrastructure, recalcitrance, relative water content, seed desiccation, seed germination*

Introduction

Arils occur spasmodically in 45 taxonomically unrelated families. Only one (Myristicaceae - the Nutmeg family) is totally arillate; six are mainly arillate. Neither is the possession of an aril a function of a genus since in some large genera only one or two species are arillate (Corner, 1949). For example in *Pithecellobium* (Leguminosae) a genus of about 100 species, seeds of *P. dulce* are entirely covered by a red aril in a fleshy pink pod, but the other species have no aril. The most notable example of an aril occurs in the durian *Durio zibethinus* (Bombaceae) where a hard prickly capsule the size of a large coconut contains seeds covered by a thick creamy aril; most of the other 14 *Durio* species have vestigial arils or none at all (Corner, 1976).

As defined by Corner (1949;1953) most arillate species are tropical trees or woody climbers. They have fruits containing large seeds described as being non-dormant and incapable of withstanding desiccation (Corner, 1949; Werker, 1997), with an implication of recalcitrance. In some species, for example *Theobroma cacao*, cocoa (Li and Sun, 1999), *Litchi chinensis*, lychee, *Euphoria longan*, longan (Xia *et al.*, 1992), *Nephelium lappaceum*, rambutan and durian (Hansen, 1984) recalcitrance is well documented. However only some of the arillate species characterised by Corner (1976) are listed as non-dormant, maybe recalcitrant, in

the extensive survey of germination data collected by Baskin and Baskin (1998). Similarly not all recalcitrant species have arils. In *Acacia*, for example, the aril is a long extension of the funicle and has been related to seed dispersal (O'Dowd and Gill, 1986).

The terms "orthodox" and "recalcitrant" have been used (Roberts, 1973) to describe the storage behaviour of seeds in relation to their viability and SMC at maturation. The SMC of recalcitrant species (30-70 %) contrasts with the lower values (15-20 %) for orthodox seeds, with the seeds of the recalcitrant type losing viability if SMC drops below some relatively high critical level (often between 20-31 %). Although found in a variety of habitats, recalcitrant species have been suggested to be more common in tropical rain forests (Chin *et al.*, 1989).

Alectryon is a genus of about 20 species of Hawaii, Pacific islands, New Guinea and Australia. Both New Zealand species are endemic. The more common *Alectryon excelsus* is a tree of lowland forests, whereas *A. grandis* (Allan, 1961) is a small tree of coastal cliffs on Great Island in the Three Kings Group (Cheeseman, 1892; 1911) found only in small numbers (Baylis, 1948) and now regarded as endangered (Given, 1981). The seeds of both species are characterised by a crimson aril arising from the raphe and funicle, supplied by numerous fine vascular bundles from the raphe (Corner, 1976). Vascularity is continuous between aril, seed, capsule wall and maternal tree. The cotyledons are spirally coiled within the seed. The aril meets the usually accepted morphological criteria of a true aril as a pulpy structure growing from the ovule or funicle after fertilisation to invest a part or the whole of the seed (Lawrence, 1960; Corner, 1976). However fertilisation is not necessary for aril development. For example, in *Durio zibethinus* unfertilised ovules may develop arils as the fruit ripens (Corner, 1976). Neither does development of the aril-seed unit proceed hand-in-hand as in *Taxus baccata*, yew, where there is an almost entire absence of a vascular supply to the aril (Sahni, 1920), and ovules develop to viable seeds after surgical removal of the aril at all stages of its development (Outred, unpublished observation).

As well as *Alectryon*, New Zealand angiosperm species with seeds associated with a true aril are the monotypic endemics *Tetrapathaea tetrandra* (Passifloraceae), *Ixerba brexioides* (Escallionaceae) (Eagle, 1975) and the endemic species *Dysoxylum spectabile* (Meliaceae) - the only member of the Mahogany family in New Zealand (Allan, 1961). Fleshy structures of various morphological derivation are also associated with the seeds of many New Zealand podocarps.

The use of the term "aril" is often confusing. A good review is given in Boesewinkel and Bouman (1984) where it is defined as a "fleshy seed appendage, often with vivid colours to attract animals" suggesting that the aril acts as a fruit flag similar to those proposed by Stiles (1982) as being important for bird dispersed species. This would agree with the function of the aril proposed by Eames (1961). In *Alectryon* the aril has also been suggested to be important for the opening of the capsule (Corner, 1976). It may possibly, also, be implicated in the water relations of the seed acting as a buffer against moisture loss, as water absorption/retention properties for arils or aril-like structures, which either prolong the viability of the seed (Fountain *et al.*, 1989) or enable them to germinate under conditions too dry for bare seeds, have been suggested (Bhojwani and Bhatnagar, 1979; Serrato-Valenti *et al.*, 1991; Bianchini and Pacini, 1996; Tiano *et al.*, 1998). Indeed, van der Pijl (1957) proposed a water storage function for arils of some members of the Sapindaceae.

On the basis of its belonging to the Sapindaceae and information in Burrows (1993), Baskin and Baskin (1998) assigned *Alectryon excelsus* to the category of physical dormancy. However Fountain *et al.* (1991) suggested the seeds to be non-dormant.

The aim of the work reported here was to examine the role of the aril in capsule splitting and in water relations of the seed and to determine the viability of seeds with low SMCs with a view to commenting on possible recalcitrance of the seeds.

Materials and Methods

For germination tests mature titoki seeds were collected from the ground beneath a single source tree in Bledisloe Park, Palmerston North (Grid Reference NZMS 260T23/452161, lat. 40° 22' S long. 175° 38' E, 50m a.s.l.). Seeds were collected either as bare seeds or with attached arils which were rubbed off before planting. The few seeds damaged by larvae of the moth *Conopomorpha cyanospila* (Burrows, 1996) were discarded. Seeds were planted *ca* 1cm deep, one per depression, in trays of fused 3cm-diameter pots, 12x12, in a potting mix of equal quantities of peat, sand and humus and germinated at ambient temperature on the bench in the glasshouse with daily automatic watering. All seeds were weighed before planting and subsamples taken for measurements of seed moisture content (SMC) and relative water content (RWC). Germination criterion was, in most cases, emergence of the plumule. Seeds which had not germinated within three months were replanted; those which remained ungerminated after eight

months were determined to have rotted. Randomly chosen samples were either sown immediately or allowed to dry under natural conditions on trays in the glasshouse before planting.

A series of developmental stages of fruits, as judged by the colour of the aril, were collected in late summer from a source tree in Kitchener Park, Feilding (Grid Reference NZMS260T23/452161, lat.40° 14'S long.175° 34' E, 50m a.s.l.). "Pivot" fruits were those which split when slight pressure was applied to the mid-region ridge of the capsule. Capsule wall, aril and seed of each fruit were treated separately. They were weighed and moisture contents and RWC values determined.

Moisture contents (FW basis) were determined by drying at 105° C for 24h. RWC measurements were obtained by weight before (FW1) and after incubation at room temperature in distilled water for 24h (FW2) and then dry weights taken (DW). RWC is expressed as FW1-DW/FW2-DW (Slatyer and Barrs, 1965).

For electron microscopy fresh aril material was dissected away from seeds and fixed in 3 % glutaraldehyde, 2 % formaldehyde in 0.1M phosphate buffer at pH 7.2 at 4° C for 24h. Samples were washed in three changes of phosphate buffer and post-fixed in 1 % osmium tetroxide in 0.1M phosphate buffer, dehydrated in a graded acetone series and embedded in Polarbed 812 epoxy resin using standard procedures. Sections 90nm thick were grid mounted, stained with uranyl acetate and lead citrate and studied using a Philips 201C Transmission electron microscope.

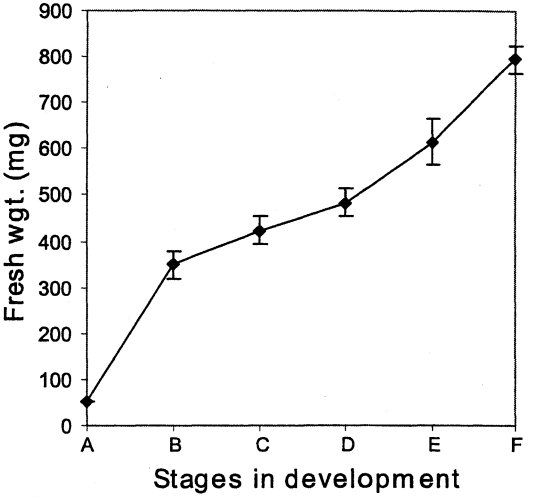

Figure 1. Fresh weights (mg) of titoki fruits, collected from a single female tree, at different stages of maturity. Stages A-E are unopened capsules (A- undifferentiated arils, B- white arils, C- pink arils, D- dark pink arils, E- "pivot" stage), and Stage F open capsules - crimson arils. Values shown are means and standard deviations for ten fruits at each stage of development.

Results

Development

The single arillate seed is enclosed in an oval capsule with a somewhat flattened crest, one side terminating in a spur. At maturity the capsule splits into two more or less equal halves at a point just below the spur and a ridge on the opposite side, causing the top half to swing back and expose the seed invested in its lower half by a crimson aril. When the capsule is mature (the "pivot" stage) a slight pressure on the mid-region of the ridge will cause it to split.

Figure 1 shows the increase in FW of the fruit in the course of development from young fruit with undifferentiated arils through to mature open capsules. FWs increased 15-fold between stages A-F with the greatest increase (seven times) between stages A-B, and thereafter a gradual weight gain.

Table 1 shows general trends in fresh and dry weights and moisture contents of fruits with white through to crimson arils (developmental stages B-F) separated into capsule wall (pericarp), seed and aril. As the fruit matured the greatest FW increase was in the aril with that of the seed varying little; the aril/seed ratio increased more than seven times (from 0.43 to 3.20). The capsule fresh weights increased slowly to the pink aril stage and then more rapidly towards maturity. Aril, seed and capsule dry weights increased more slowly. The aril moisture content increased by 12 % while that of the seed fell by 18 % to a final SMC of 40 %. The moisture content of the capsule wall showed a slight drop but results were inconclusive.

Capsule splitting

The possibility that the aril may play a role in the splitting of the capsule wall by sudden expansion creating a great enough force from the generation of matric potential was examined by measuring moisture contents and RWCs of capsules, arils, and for comparison seeds, at a series of developmental stages of

Table 1. Stages in the development of the fruit wall (capsule), seed and aril of titoki. Developing fruits were collected from a single female tree in January. Stages B-E are unopened capsules (B - white arils, C - pink arils, D - dark pink arils, E - "pivot" stage), and Stage F open capsules- crimson arils. Stage A was omitted because the components could not be separated. Mean weights were obtained by weighing six replicates of each thus no error values are given.

Developmental Stage	FW (mg)			DW (mg)			% moisture content		
	Seed	Aril	Capsule	Seed	Aril	Capsule	Seed	Aril	Capsule
B	120.3	52.7	176.2	50.3	14.5	64.8	58.0	72.5	63.2
C	110.3	123.2	188.8	51.9	31.4	123.7	58.4	74.5	65.5
D	109.2	179.4	202.2	52.3	38.3	102.4	52.1	78.6	49.4
E	111.8	184.9	317.2	60.9	30.4	127.2	45.5	83.6	59.9
F	106.7	338.2	339.6	64.0	51.6	150.2	40.0	84.8	55.8

the fruit, and by observations of immature white arils and mature arils at the "pivot" stage, using electron microscopy. The results are shown in Table 2 and in Figure 2. As in the previous set of results, the moisture content of the aril increased and that of the seed decreased in the developmental stages considered here. The possibility that differential drying of the capsule halves contributed was checked by measuring them separately. The moisture contents of capsule halves, separated along their line of dehiscence remained more or less constant. Aril moisture contents increased only slightly (72 %-82 %) between the closed and the open capsules and RWCs remained unchanged (0.66-0.65).

RWC gives an indication of water deficit. It reflects the ability to take up pure water - thus the lower the value the greater the potential to withdraw water from the surroundings. Capsules had an average moisture content of 58 % and RWC of 0.77. Seeds, with a somewhat lower moisture content, had a higher RWC until the capsule opened when the potential to take up water increased. Arils had the highest moisture content but this did not increase significantly between closed and open capsules (79 %-82 %); neither did RWC increase.

Electron microscopy

The aril appeared flat and compressed in the unopened fruit but became more swollen and granular in the open capsule. Figure 2a shows large thin-walled aril cells in the immature white aril stage. Each cell was filled with several large inclusions, which are tentatively identified as oil droplets on the basis of their staining reactions and density. Between the two stages of development the cells doubled in size (8.2 - 17.6 µm) and became highly vacuolate with indications of degradative processes (Fig. 2b).

Table 2. Moisture contents (MC) and relative water contents (RWC) of titoki capsules, arils and seeds collected in late January 1999. Stages B-E are unopened capsules (B- white arils, C- pink arils, D- dark pink arils, E- "pivot" stage), Stage F are open capsules – crimson arils. Values shown are means and standard deviations for eight replicates at each stage except for Stages E-F capsules where only duplicate samples were used.

	Capsule				Aril		Seed	
	Top half		Bottom half					
Stage	MC	RWC	MC	RWC	MC	RWC	MC	RWC
F	54.0	0.70	56.4	0.79	85.1 ± 3.4	0.72 ± 0.07	40.9 ± 3.9	0.68 ± 0.17
E	59.9	0.78	58.6	0.76	82.4 ± 2.6	0.65 ± 0.06	45.6 ± 2.1	0.85 ± 0.09
	MC		RWC					
D	56.2 ± 3.4		0.75 ± 0.08		78.9 ± 2.4	0.66 ± 0.12	52.4 ± 4.0	0.83 ± 0.05
C	61.4 ± 3.2		0.78 ± 0.03		74.2 ± 2.6	0.70 ± 0.10	53.1 ± 3.8	0.79 ± 0.12
B	59.7 ± 2.8		0.82 ± 0.03		72.5 ± 3.0	0.79 ± 0.14	58.2 ± 3.2	0.87 ± 0.14

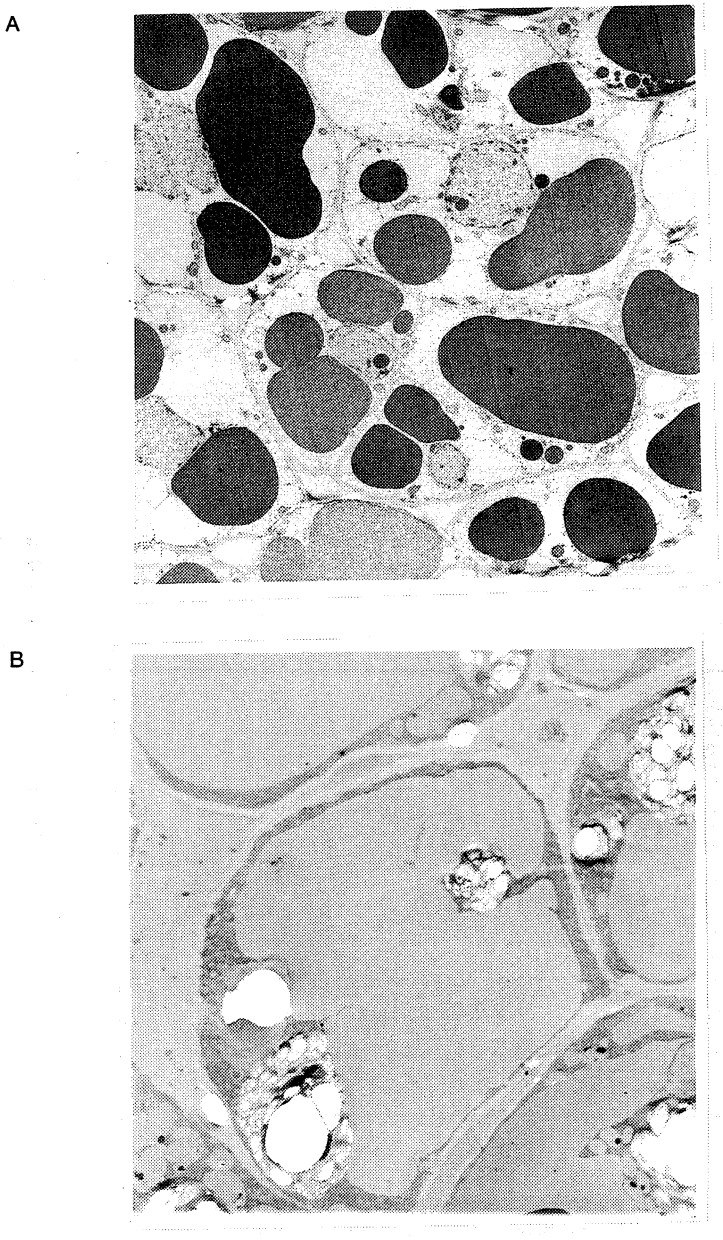

Figure 2. Titoki aril cells at the immature white aril stage (A) and the mature "pivot" stage just prior to capsule opening (B). X 3400.

Seed and aril moisture contents

Titoki seeds mature between December-March, 12-14 months post-pollination. After capsule splitting, seeds either remain on the maternal tree for several weeks, often after the aril has withered, or drop to the ground beneath the tree which becomes littered with a mixture of bare seeds and seeds with attached arils.

Table 3 shows the moisture contents and RWCs of arils and seeds collected in late March 1998, at the end of a long, dry summer. The lower moisture content of the aril-associated seeds (30 %) compared to those collected in early January 1999 (40 %) may reflect this. Here SMCs were about 30 % in open and "pivot" capsules. RWCs were also similar. Moisture contents of seeds collected bare from the ground were halved and RWCs much lower; if the arils were still attached SMCs were maintained at tree values, but those of seeds without arils on the tree dropped to 11 % SMC. In these results RWCs of both aril and seed on the tree were very similar in the open capsules but in the "pivot" capsules RWCs of the aril were lower.

Seed viability

Figure 3 shows the time course for germination of seeds collected from the ground with or without their arils and of seeds collected off the tree from capsules with dried aril remnants. Arils were rubbed off before the seeds were sown. In total 66 % of the bare seeds germinated between 13-48d, most of them by 26d. Of those removed from the ground with attached arils, 62 % germinated between 16-42d, most by 32d. The other seeds were either not viable or rotted. It was not always the smaller (< 0.1g) seeds of either batch which failed to germinate. Viability of seeds removed from aril-less capsules on the tree was low. Only 18 % germinated between 14-56d. Although three seeds germinated later (up to 56d) they showed only feeble radicle protrusion and died within a few days.

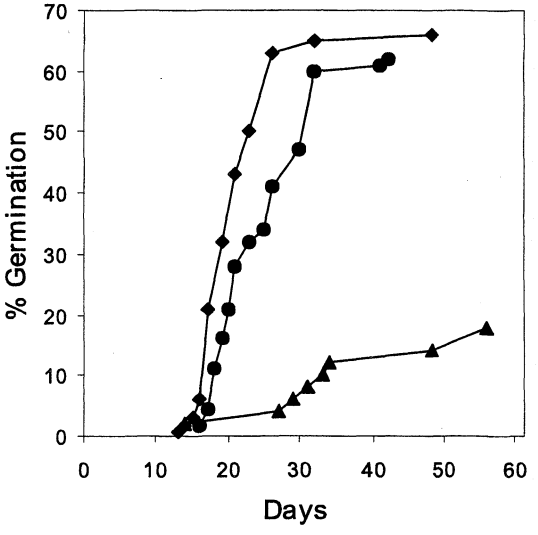

Figure 3. Percentage germination of titoki seeds collected from the ground either bare (n=124) ♦ or with attached arils (n=110) • or from tree-borne capsules with withered arils (n=50) ▲. Arils and aril remnants were removed before planting. Initial numbers of seeds are given in brackets.

Seed moisture content effects on germination

Table 4 shows germination of bare seeds collected from the ground and planted either immediately or after

Table 3. Moisture contents (MC) and relative water contents (RWC) of titoki arils and seeds in open capsules with or without arils, in "pivot" capsules, and of bare seeds with or without arils on the ground. Values shown are means and standard deviations for 20 replicate samples.

	Open capsules		Pivot		Bare seeds on ground		Seeds + arils on ground		Seeds in open capsules, dried arils	
	MC	RWC	MC	RWC	MC	RWC	MC	RWC	MC	RWC
Aril	87.2 ±2.1	0.76 ±0.05	82.6 ±4.1	0.54 ±0.09			80.4 ±3.2	0.75 ±0.08		
Seed	30.6 ±1.6	0.88 ±0.06	29.4 ±1.7	0.93 ±0.03	14.1 ±0.53	0.46 ±0.07	30.1 ±0.85	0.85 ±0.25	11.0 ±4.8	0.30 ±0.12

Table 4. Germination of titoki seeds collected bare from the ground around the maternal tree. Seeds were either planted immediately or allowed to dry further for up to 90 days on the laboratory bench. 20 seeds were planted at each time interval. SMC and RWC values were determined from replicates of five seeds. Values shown are means and standard deviations.

Seed drying time (d)	SMC %	RWC	Germination (%)	First day	Last day	Non-viable seed[1] (%)	Rotten seed[1] (%)
0	12.8 ± 0.4	0.28 ± 0.02	40	12	35	40	20
6	12.6 ± 1.6	.18 ± .02	20	14	27	50	30
12	9.1 ± 2.2	.20 ± .01	70	22	101	30	0
20	8.8 ± 0.4	.23 ± .02	20	17	17	70	10
26	8.6 ± 0.4	.23 ± .03	20	18	49	60	20
33	7.7 ± 0.2	.27 ± .02	50	17	25	40	10
40	7.5 ± 0.4	.19 ± .01	30	14	29	70	0
47	9.6 ± 2.1	.19 ± .02	40	15	25	60	0
54	8.5 ± 0.1	.17 ± .02	30	16	20	70	0
61	8.8 ± 0.1	.18 ± .02	30	18	18	70	0
90	7.7 ± 0.2	.13 ± .03	50	17	32	50	0

[1] The few seeds obviously damaged were discarded, but some may possibly have been damaged by larvae of a small unidentified Dipteran (Burrows, 1996).

further drying under natural conditions in the glasshouse for up to 90d. The already low SMCs dropped slowly and to a variable extent but never fell below 7.5 % indicating that this was the limit of natural seed dehydration. RWCs were also low. Germination occurred between 12-35d, with an outlyer at 101d. Most seeds germinated within the first 30d. Batches varied between 20 %-70 % germination but the results showed no pattern. However ten of the eleven batches had germination percentages 50 % or lower.

Discussion

Alectryon excelsus (titoki) is a species with arillate seeds endemic to New Zealand. Seeds are shed during summer and are immediately susceptible to desiccation. They are large (7x5mm) and can be found in high densities on the soil surface beneath the parent tree. Development of the fruit takes 12-14 months. During this time arils change from white, to crimson in the open capsule; all stages can be found on the same tree.

Results on the role of aril expansion in causing the capsule to split are conflicting. Corner (1976) commented that vestigial arils are found in predominantly indehiscent fruits, whereas fully developed arils occur in dehiscent fruits. Of *Alectryon* specifically, he noted that the aril cells enlarge and "burst the pericarp transversely". Enlargement of the aril cells of titoki from closed to open capsules was confirmed (Fig. 2).

In titoki, capsules always split into the same two halves, at a point below the spur and a flange on the opposite side, presumably along a line of weakness. Differential drying of the two capsule halves does not contribute to this, as moisture contents of the halves were similar (Table 2). That increased aril succulence might create a force great enough to split the capsule gained little support (Tables 2 and 3) from measurements of moisture contents and RWCs of arils immediately prior to and after this occurred.

Some observations, however, do suggest a role for the aril. At the end of summer (late February-March) unopened capsules always remain on the parent tree. All capsules examined were found to contain withered black arils but viable seeds (pers. obs.). This suggests that capsules did not open because succulent arils were lacking at the time of fruit ripening. In unopened capsules the arils are highly compressed; as they develop the cells enlarge but the aril expands more after the capsule has opened. Unopened lichen-covered capsules with rotten arils may persist on a parent tree for several years. Allan (1961) commented that some trees, even whole populations, may produce seeds with vestigial arils, but whether the capsules open or not was not commented upon. In the closely related *A. grandis*, fruits are normally joined together in pairs along the flanged edges for almost the whole length (Oliver, 1951). This might be expected to impede the dehiscence of the capsules. A titoki tree bearing many undehisced twin capsules occurs in Kitchener Park, Feilding.

Seeds have been shown to germinate from unopened sown capsules (Burrows,1996), presumably because the pericarp breaks down in the soil, but generally seeds are shed as intact seed-aril units from the open capsule.

A review of the literature suggests that the occurrence of arils is more widespread in plants with tropical affinities, is correlated with a high moisture content of mature seeds, a tendency towards lack of dormancy, and storage recalcitrance. The characteristically bright colours of arils have been attributed to flavonoids and anthocyanins, as well as to coloured oils and oil droplets (Werker, 1997), features characteristic of the bird dispersal syndrome. Eames (1961) suggested the possibility that possession of an aril seems to be related to dispersal of seed by animals, as it is in *Acacia* (O'Dowd and Gill, 1986). However much of the evidence is anecdotal. Burrows (1996) commented that New Zealand native pigeons (*Hemiphaga novaeselandiae*) eat titoki seeds (and since they are firmly attached presumably arils). They are reported to be eaten by all medium-sized native and introduced birds (Clout and Hay, 1989).

Analysis of seeds and arils has shown that both contain a cyanogenic oil (Brooker,1957). Electron microscopy showed that immature aril cells do contain abundant amounts of oil (Fig. 2a) which degrades in ripe arils (Fig. 2b). It is of interest that the arilloid juice of rambutan (*Nephelium*, Sapindaceae) is said to prevent germination in storage (Chin, 1975), and in some species (*Calathea microcephala*, Herwitz, 1981; *Prolium heptaphyllum*, Macedo, 1977) seed germination improves when the aril is removed thus breaking dormancy of the seeds. Experiments with titoki (Burrows, 1996) showed that only a few seeds sown "in fruit" germinated.

Titoki seeds fall from the parent tree in great numbers with arils intact. The possibility existed that the aril may be a protective structure related to the water relations of the seed. Such a role is not unknown, for example in the New Zealand podocarp *Dacrydium dacrydioides* (Fountain *et al.*, 1989) the succulent receptacle buffers the seed against water stress and the caruncle of *Ricinus communis* has water absorption and retention properties which enable seeds to germinate under conditions too dry for bare seeds. In titoki the aril invests the lower half of the seed like a collar. In this investigation the mature arillate tree-borne seed had a high SMC of 30-40 % and a relatively high RWC. Shed seeds desiccated rapidly to *ca* 14 % SMC with RWCs approximately halved while those which retained their arils on the ground maintained the moisture levels of those on the tree. Seeds on the tree in open capsules without their arils dried the most (Table3). These results indicate that arils do maintain SMCs at a high level. The germination success of seeds collected from the ground with or without their arils was closely similar. In contrast, seeds collected from tree-borne capsules without arils germinated poorly (Fig 3).

Whaley (1996) suggested that titoki seeds require a period of stratification as of 55 seeds caught in seed traps over summer only one germinated, and in a buried seed experiment *in situ* germination occurred only after nine months, although seeds seemed capable of germinating earlier in a glasshouse. Whaley commented that seeds appeared to remain viable on the soil surface from one fruiting season to the next. However results reported in the present investigation suggest that, under laboratory conditions at least, viability for most seeds is lost within about 50 days.

Baskin and Baskin (1998) attributed physical dormancy (testa impermeability) to titoki, on the basis of information in Burrows (1993) that germination occurs over two to five months, and that it belongs to the Sapindaceae. However testa impermeability seems unlikely since titoki seeds take up water immediately, either as liquid water, or if placed in 100 % RH containers (pers. obs.). Results from Burrows (1996) showed 48 %-56 % germination success between 2-223d. In comparison, apart from one exception, germination times reported here were between 12-58 days with no germination thereafter. Germination percentages were higher at around 65 %. Seeds desiccated to a low water status and retained often around 50 % viability. Some seeds in a population remained viable at low SMCs for at least 90 days.

Previous work on *Dacrydium dacrydioides* (Fountain *et al.*,1989) showed that the succulent receptacle protected the seed from excess drying and prolonged viability. In this case the presence of an aril-like structure was linked to recalcitrance. Seeds of the arillate New Zealand endemic *Dysoxylum spectabile* are non-dormant but very susceptible to desiccation and thus may be recalcitrant (Court and Mitchell, 1985). On the other hand many non-arillate New Zealand species, for example *Griselinia littoralis* and *Corynocarpus laevigatus*, are recalcitrant (Bannister *et al.*, 1996). In titoki (*Alectryon excelsus*), the aril maintained a high SMC but its continued presence around the seed did not enhance viability. Titoki seeds had a high SMC and germinated readily. There was no evidence of a dormancy mechanism or of recalcitrance.

Conclusion

Circumstantial evidence suggests a role for the aril in capsule opening, but results are inconclusive. The aril

buffers the seed against moisture loss in the open capsule and on the ground but does not prolong viability of the seed. Seeds can drop to low SMC and retain viability.

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