Notes S1: Seed and seedling morphologies associated with Groups A to F

Group A - Orthodox species that possibly require a mandatory dormancy period before germination

This orthodox group included species that did not germinate within the first season after shedding. Included species produced capsules containing 25 to 100 seeds per capsule and dried seeds were really light (0.03 and 0.07 mg per seed) and small (from 0.59 x 0.65 mm to 1.08 x 1.76 mm). Seeds had lignified and pigmented tegmens with an irregular surface type (clearly visible depressions and crests) and no visible hypocotyl protrusion. All of these seeds contained endosperm and mature seeds had un-pigmented embryos (Figure 3A).

Group B - Orthodox species that germinated soon after shedding

These seeds had capsules with 5 to 90 seeds per capsule and dried seeds weighed between 0.03 and 0.91 mg per seed. Seeds had lignified and pigmented tegmens with an irregular surface type ('deep grooves' or 'small bumps'). Seeds had tegmens that were relatively impermeable to water in comparison to intermediate seeds (desiccation or moisture stored conditions did not have any effect on the timing of germination). They contained endosperm, but had green-pigmented embryos (Figure 3B). The hypocotyl emerged within 4 to 22 days, root hairs developed within 5 to 23 days, cotyledons opened within 8 to 30 days and the first foliar leaf emerged within 10 to 29 days after germination. Germination sequence in this group followed the sequence typical of most angiosperms, by which the radicle develops before the plumule (Esau, 1960; Bewley and Black, 1994). These orthodox seedlings had relatively narrow hypocotyl widths that ranged from 0.34 to 0.55 mm, relatively long root lengths that ranged from 3.33 to 14.5 mm (measured after cotyledons opened) and relatively long hypocotyl lengths that ranged from 0.58 to 6.12 mm (measured after the foliar leaf matured). All species had elliptical cotyledons, with no or short cotyledon petioles (0 to 1.47 mm) and relatively high abaxial (AB) stomatal densities (11 to 51 stomata/mm^2) on cotyledons that were amphistomatic or hypostomatic.

Group C - Endospermous intermediate seeds

Species from the first sub-cluster of intermediate seeds typically produced 5 to 50 seeds per capsule and dried seeds weighed 0.03 to 0.10 mg per seed. Seeds from this cluster had lignified and pigmented tegmens with an irregular surface with small crests or smooth surface with a papery texture. Seeds had tegmens that were relatively permeable to water in comparison to orthodox seeds. All seeds contained endosperm at shedding and had green- pigmented embryos (Figure 3C). Root hairs developed within 3 to 13 days, cotyledons unfolded within 6 to 10 days and the first foliar leaf emerged within 8 to 19 days after germination. They also followed the classical angiosperm sequence

of seed germination. Seedlings had relatively short root lengths (0.54 to 5.15 mm) after the cotyledons opened, and hypocotyl widths (0.26 to 0.64 mm) and lengths (0.12 to 0.59 mm) after the first foliar leaf matured. All species had elliptical cotyledons, relatively short (0.41 to 1.99 mm) or long (2.87 to 3.67 mm) cotyledon petioles and relatively low abaxial (AB) stomatal densities (14 to 28 stomata/mm^2) on cotyledons that were all amphistomatic.

Group D - Exendospermous intermediate seeds

Species from this intermediate sub-cluster had capsules with 20 to 45 seeds per capsule and dried seed weights ranged from 0.10 to 0.12 mg per seed. All species from this group had green-pigmented and non-lignified tegmens with a velvety or smooth texture. Seeds had tegmens that were much more permeable to water in comparison to intermediate Group C seeds. At shedding, all seeds lacked endosperm and had green-pigmented embryos (Figure 3D). Root hairs developed within 2 to 6 days, cotyledons unfolded within 2 to 5 days and the first foliar leaf emerged within 3 to 18 days after germination. The root and first foliar leaf developed simultaneously. Seedlings had relatively long roots (0.42 to 12.041 mm) after the cotyledons opened, and large hypocotyl widths (0.43 to 1.04 mm) and lengths (0.17 to 0.96 mm) after the first foliar leaf matured. All species had elliptical cotyledons, relatively short (0.87 to 2.92 mm) or long (2.99 to 5.23 mm) cotyledon petioles and relatively low abaxial (AB) stomatal densities (14 to 28 stomata/mm^2) on cotyledons that were amphistomatic, except for two species (*O. phloxidiflora* and *O. stenopetala*) that had epistomatic cotyledons.

Group E - Pardales recalcitrant clade

Species produced 5 to 30 seeds per capsule, dried seeds were relatively heavy (1.78 to 3.54 mg per seed), but similar in size (from 1.27 x 1.67 mm to 1.80 x 2.72 mm) to seeds from Group F. Seeds had un-lignified tegmens with a smooth, papery texture. The majority of these seeds had semi-transparent pigmented tegmens (except *O. kamiesbergensis*, which is only very distantly related to the rest of this group (Oberlander et al., 2011) with a transparent tegmen). Seeds contained no endosperm and had green-pigmented embryos (Figure 3E). Root hairs developed within 2 to 8 days, cotyledons unfolded within 1 to 4 days and the first foliar leaf emerged within 1 to 3 days after germination. As with species from Group D, the root and first foliar leaf developed simultaneously. Seedlings had hypocotyl widths ranging from 0.43 to 1.65 mm. All species had ovate cotyledons that were either sessile or had very short (0 to 0.65 mm) petioles. Four of these species had epistomatic cotyledons, while the remainder had amphistomatic (17 to 27 stomata per mm^2 on the abaxial surface) cotyledons.

Group F - Main recalcitrant group

Species produced capsules with 5 to 25 seeds per capsule, dried seeds were relatively light (0.10 to 0.82 mg per seed), but similar in size (1.11 x 1.41 mm to 2.44 x 3.95 mm) to members of Group E.

Seeds from this cluster had un-lignified and un-pigmented tegmens with a smooth surface texture. Seeds contained no endosperm and had green-pigmented embryos (Figure 3F). The sequence of germination was inverted relative to most angiosperms, where the first foliar leaf developed before the root and hypocotyl. Seedlings had hypocotyl widths ranging from 0.52 to 1.44 mm. All species had ovate cotyledons that were either sessile or on short (0 to 1.92 mm) petioles. Fifty per cent of these species had epistomatic cotyledons, while the remainder had amphistomatic (7 to 28 stomata/mm^2 on AB surface) cotyledons.

Interpretation of morphological and phenological traits associated with germination strategies

Seed traits show distinct variation between the three germination strategies. Orthodox species produce capsules with many seeds, where each seed is very small (low seed mass). This may be a low risk strategy for orthodox species, as seeds have the ability to survive desiccation and can consequently be effectively dispersed through space and time until they encounter favourable germination conditions (Evans and Dennehy, 2005). Recalcitrant species seem to follow the exact opposite strategy, where species produce few seeds per capsule, but with high seed mass, potentially indicating relatively higher investment of resources in these seeds. Typically, large seeds reduce the rate of water loss as they have a lower surface to volume ratio (Berjak and Pammenter, 2008). This would be a beneficial trait, as recalcitrant seeds do not have tegmens or endosperm to help prevent water loss. However, recalcitrant seeds are dispersed and germinate in the wettest time of the year. Species with intermediate seeds are intermediate in number and mass between these two strategies.

Endosperm is the storage tissue that feeds the developing seed and releases hormones to cue germination (Forbis et al., 2002). Seeds that are shed with underdeveloped embryos would require endosperm, as observed among the orthodox *Oxalis* seeds that did not germinate within the first season after shedding (Group A). Unlike these seeds, all other desiccation tolerant orthodox (Group B) and intermediate (Group C) seeds that contained endosperm at shedding had green-pigmented embryos. These embryos would be metabolically active and have the potential of relatively rapid germination under favourable conditions. These seeds also have endosperm storage tissue, which can release ABA hormones to suppress germination (Koornneef et al., 2002; Finch-Savage and LeubnerMetzger, 2006). However, it may be that orthodox species (Group B) must germinate within a few days to weeks, or they will lose viability. Exendospermous intermediate (Group D) and all recalcitrant (Groups E and F) seeds were shed with well developed, green-pigmented embryos that filled the entire volume of the seeds and no visible endosperm. As these embryos are ready to germinate upon release, these species do not have to invest resources into the production of endosperm tissue.

Orthodox and endospermous intermediate seeds (Groups A to C) are capable of desiccation tolerance and are able to undergo periods of dormancy, during which they need to be protected from

unfavourable environmental conditions. These seeds typically have lignified and pigmented tegmens with an irregular surface with depressions and crests. Tegmen lignification would prevent water loss (low water permeability) and protect seeds against predators or microbial decay. Tegmen pigmentation is most likely a by-product of lignification (Kannenberg and Allard, 1964), but could also prevent UV-radiation damage to the seed. UV-light exposure could cause seeds to germinate prematurely or more rapidly than normal, which would be detrimental to developing seedlings (Noble, 2002). It is possible that the irregular tegmen surface (with crests and depressions) enlarge the seed surface area. This could aid with water uptake before germination, to break dormancy. Alternatively this could aid with rapid seed dehydration (if seeds are shed during unfavourable conditions). Often orthodox seeds are much more likely to survive long periods of desiccation if they are stored at lower seed moisture contents. Recalcitrant species are shed with metabolically active embryos, which have cotyledons that are capable of photosynthesis (pre- and post-shedding from the capsule) (Maciejewska et al., 1974; Ry¢ et al., 1980; Ruuska et al., 2004). Recalcitrant species have thin and transparent tegmens, would allow UV-light to reach the embryos while seeds are still in their capsules, allowing embryos to photosynthesise and develop rapidly. Thin and transparent tegmens with stomata have previously been described among angiosperm seeds (Macloskie, 1884; Corner, 1976; Berjak and Pammenter, 2008), which would allow gas exchange of the metabolically active seed to take place. Again, the well-developed embryos of intermediate seeds (Group D) are protected by a semi-lignified and pigmented tegmen. We found that these semi-lignified tegmens were relatively more water permeable than the lignified tegmens of Groups B and C. We would also expect to find that these tegmens (especially the `velvet' type) would allow gas exchange of the metabolically active embryo while it is still in its capsule. We also suggest that the pigmented tegmens associated with recalcitrant species from Group E would provide desiccation resistance, protection from predation and could aid in UV-protection of the developing embryo.

Orthodox and intermediate species (Groups B to D) had elliptical cotyledons. The cotyledon petioles of orthodox species' seedlings are often shorter that those of most of the intermediate seedlings. Often these species (Groups B to D) had stomata on both cotyledon surfaces, and it is possible that these cotyledons are adapted to maximize their photosynthetic capacity by ensuring that cotyledons are positioned in well-ventilated areas, where both surfaces are exposed to the atmosphere – allowing high rates of gas exchange that promotes rapid uptake of nutrients and rapid vegetative growth. Group E recalcitrant species had elliptical, sessile cotyledons. The majority of recalcitrant species (Group F) had ovate and fleshy cotyledons with stomata on the adaxial (AD) surface only. It seems as if a relatively large proportion of seed resources had been invested to `build' such large cotyledons and we suspect that these cotyledons are capable of more rapid photosynthetic rates (especially with AD located stomata for recalcitrant species that are growing in the wet winter months). Higher photosynthetic rates would enable more rapid seedling establishment and growth. Cotyledon petioles

of recalcitrant seedlings are either short or absent. Often species with sessile cotyledons have AD located stomata, which would allow sufficient exposure of the photosynthetic surface (AB located stomata would be too close to the soil surface to allow efficient gas exchange). Brink (2017) suggested that cotyledon shape aided with the shedding of the tegmen. It is also possible that the cotyledons shape is non-adaptive, so a developmental artefact determined by the embryo structure. Embryos of orthodox *Oxalis* seeds have a larger proportion of root tissue relative to the undeveloped cotyledons, while probably 90% of the recalcitrant seed volumes are filled with cotyledon tissue. The constraints formed by the tegmen and testa during seed development would then force ovate-shaped cotyledons.

Orthodox species (Group B) have seedlings that germinate with their hypocotyl emerging from the seed, followed by substantial root growth and then the development of root-hairs. These species form long roots with a long and thin hypocotyl. Cotyledons only unfold once the root and root-hairs are well-established. The first foliar leaf develops and matures at a much later stage. This sequence of development is similar to the classical sequence of development documented among the majority of angiosperm species (Esau, 1960). Intermediate species (Groups C and D) display various sequences of development where either the hypocotyl or root hairs emerge from the seed. The cotyledons and foliar leaves of species from Group D unfold more rapidly than in members from Group C. Overall, species from Group C follow a very similar pattern of germination to Group B, except that seedlings reach maturity much sooner. Species from Group D seem to display a simultaneous sequence of development where the roots and foliar leaves develop at the same rate. These species have relatively shorter hypocotyls and roots than orthodox species. Group E recalcitrant species display root-first germination. The hypocotyl and root hairs emerge and develop, followed by cotyledons unfolding and the development and maturation of the first foliar leaf. The majority of recalcitrant species (Group F) display a strategy of inverse germination, where cotyledons and the first foliar leaf develop rapidly and appear to sustain rapid growth of the seedling, until the hypocotyl, root-hairs and roots subsequently emerge. This is a remarkable phenomenon where seedlings are capable of rapid growth and development without well-established roots to supply the seedling with nutrients. Many of these recalcitrant species produce large amounts of mucilage upon germination. Preliminary investigation of microbes within the mucilage (under sterile control and various experimental conditions) revealed the presence of both bacteria and fungi. Subsequent research is aimed at investigating potential associations between recalcitrant *Oxalis* species and mucilage-dwelling microbes.

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