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Seed behaviour in *Phoenix reclinata* Jacquin, the wild date palm

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Abstract

Despite the importance of the palm family, *Arecaceae*, little has been systematically documented about the seed behaviour of the many species. The post-harvest seed behaviour of *Phoenix reclinata*, the highly utilized wild date palm species distributed along the eastern seaboard of Africa, is investigated in the present study. While both embryo and endosperm water concentration declined as the seeds of *Phoenix reclinata* matured, they remained relatively high: this is a characteristic of (but not confined to) non-orthodox seeds. The ultrastructure of embryo cells, and the finding that negligible water uptake was required for the initiation of germination, were in keeping with the possible non-orthodox nature of the seeds. A developmental study revealed that between the acquisition of full germinability and complete pre-shedding maturity, germination performance appeared to be constrained, suggesting the presence of an inhibitor. Pre-treatment by soaking, mechanical or acid scarification had no significant promotory effect on either rate or totality of germination of mature *P. reclinata* seeds, while use of water transiently at 100°C was highly deleterious. However, germination of partially dehydrated seeds was initiated sooner if they had been soaked or scarified. Mature *P. reclinata* seeds tolerated dehydration to a mean embryo water concentration of 0.40 g g^{-1} (dry mass basis; dmb), but at 0.14 g g^{-1}, both rate and totality of germination were adversely affected. However, viability of seeds dehydrated to the mean embryo water concentration 0.40 g g^{-1} declined during storage for 16 weeks. It is concluded that *P. reclinata* seeds are non-orthodox, and are best categorized as showing intermediate post-harvest behaviour.

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Introduction

There are around 200 genera of palms worldwide (Uhl and Dransfield, 1987), of which only 19 are native to Africa and five to South Africa (Tuley, 1995). Wherever palms occur, they are very heavily utilized, leading to the estimation that half the species could face global extinction within the next 50–100 years (Smith *et al*., 1993), and consequently to the need for establishment of extensive conservation projects (Maunder *et al*., 2001). However, such projects will require knowledge of palm seed storage behaviour and germination characteristics, which is presently lacking (Davies and Pritchard, 1998a).

Seeds are categorized as orthodox or non-orthodox in post-harvest behaviour, based upon the degree of desiccation they will tolerate. Additionally, there are various species with seeds that are relatively desiccation tolerant, although less so than orthodox types. Such seeds, which may be chilling sensitive, especially after dehydration, have been described as exhibiting intermediate storage behaviour (Hong and Ellis, 1996). Although this categorization of seed types is considered an over-simplification (Pammenter and Berjak, 1999), it will be used here for convenience.

It is generally recommended (e.g. Wicht, 1969; Donselman, 1982; Meerow, 1991) that palm seeds should be planted fresh, as viability is lost within a relatively short time. According to Broschat (1994) seeds of many palm species lose viability within 3–6 weeks of harvest, due to the deleterious effects of desiccation.

Various procedures promote palm seed germination, including removal of the fruit tissue (Rauch *et*

al., 1982; Broschat and Donselman, 1986, 1987; Meerow, 1991; Rauch, 1994; Ehara *et al*., 2001), soaking, hot-water scarification, use of growth regulators and mechanical scarification. However, the outcomes of soaking trials have been equivocal. Increases in germination rate and extent have been recorded for *Archontophoenix alexandrae* (Nagao and Sakai, 1979; Nagao *et al*., 1980; Odetola, 1987), *Chrysalidocarpus lutescens* (Odetola, 1987; Maciel de Sousa, 1995), *Phoenix dactylifera* (Odetola, 1987), *Hyphaene thebaica* (Davies and Pritchard, 1998b; Moussa *et al*., 1998), *H. petersiana* and *Medemia argun* (Davies and Pritchard, 1998b), *Rhapidophyllum hystrix* (Carpenter *et al*., 1994), *Chamaedorea seifrizii* (Rauch, 1994) and *Roystonea oleraceae* (Maciel, 2001). In other instances, seed soaking has been ineffective, e.g. *Arecastrum romanzoffianum* and *Roystonea regia* (Broschat and Donselman, 1987), *Dictyosperma aureum* and *Verschaffeltia splendida* (Odetola, 1987). Loomis (1958) found that hot-water scarification (100°C, 3 min), followed by soaking for 2–3 weeks, was beneficial to the germination of *Acrocomia sclerocarpa* and *Astrocaryum mexicanum*.

Mechanical scarification promotes germination of a variety of palms, especially where the seed coat is hard. Success has been recorded for *Rhapidophyllum hystrix* (Carpenter *et al*., 1994), *Phoenix roebelenii* (Doughty *et al*., 1986), *Archontophoenix alexandrae* and *Ptychosperma macarthurii* (Nagao *et al*., 1980), and other species, including *Hyphaene schatan*, *Phoenix acaulis* and *Sabal palmetto* (Odetola, 1987).

In general, mature palm seeds exhibit the best overall germination performance (Rauch *et al*., 1982; Broschat and Donselman, 1987; Broschat, 1994; Maciel de Sousa, 1995; Silva *et al*., 1999). However, in some species, germination rates are higher for pre-mature seeds, but the overall germination percentages were superior once the seeds were mature (Broschat and Donselman, 1987; Maciel, 2001). These authors suggested that this may be due to an inhibitor in the mature fruit tissue. Alternatively in such cases, increased hardening of the seed coat with maturity may be a contributing factor.

Phoenix seeds are considered as orthodox (*P. dactylifera*) or probably orthodox [*P. canariensis*, *P. rupicola*, *P. sylvestris* and *P. reclinata* (Tweddle *et al*., 2003)]. The uncertainty about palm seed categorization generally reflects gaps in the information about seed water concentrations at shedding, storage parameters and seed survival in storage, as well as germination characteristics and conditions.

Phoenix reclinata Jacquin was chosen for the present study, the first investigation of the post-harvest seed behaviour of any South African palm species. *P. reclinata* occurs naturally along the eastern seaboard of Africa, extending into Egypt (Pooley, 1993). It is mainly riverine in distribution, where the root system plays an important part in bank stabilization, and occurs also in the brackish-water regions adjacent to mangrove forests (Wicht, 1969; the authors' personal observations), but it also grows in open savannah. The species is heavily utilized throughout Africa, and the fruits are eaten by a wide range of animals (Wicht, 1969; Pooley, 1993). Although not presently endangered, the demands made on the species are such that this may not always be the case. Although Hong and Ellis (1996), and comments made by Mbuya *et al*. (1994), suggest the seeds to be orthodox, this may not be the case, as confirmatory data are not available. The present contribution reports on germinability of seeds of differing maturity status, the effects of various pre-treatments on germination, seed responses to dehydration and survival in storage at various water concentrations.

Materials and methods

Fruits and seeds

The ripening fruits of *P. reclinata* pass from green through green–yellow to yellow, orange and brown when fully ripe. Fruits at these developmental stages were collected in the vicinity of Durban, enclosed in plastic bags and immediately brought to the laboratory, where they were stored at 16°C for no longer than 1 week. Immediately before use, seeds were extracted manually and cleaned of all fruit pulp. The coats of seeds from orange and brown fruits were darker and harder than those from fruits in the green through to yellow maturity stages, although all were of a similar seed and embryo size. For convenience, developmental (or maturity) status of seeds is described in relation to fruit colour as 1 (green), 2 (green–yellow), 3 (yellow), 4 (orange) and 5 (brown, mature).

Initial seed lot characteristics

Water concentration was determined gravimetrically for individual embryos excised from 20 seeds per assessment, for endosperm segments from fresh seeds and immediately after dehydration to individual target moisture contents (see below). Wet and dry mass was determined after oven-drying to constant weight at 80°C. Data are recorded as g H_2O (g dry mass)$^{-1}$ (g g^{-1}).

Fifteen seeds per fruit maturity stage, or 20 seeds that had been dehydrated to each of a series of water concentrations, were surface sterilized by immersion in 1% sodium hypochlorite for 10 min, and set to germinate on 1% water agar in sterile Petri dishes, at 29°C with a 14 h photoperiod in a controlled

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environment cabinet. Seeds were monitored daily for 50 d, and germination scored as positive upon radicle emergence.

Germination pre-treatments

Batches of 20 fresh, mature seeds (from brown fruits) and 20 that had been dehydrated to an embryo water concentration of 0.21 g g^{-1} were subjected to one of the following pre-treatments: soaking in aerated water at ambient temperature (~25°C) for 3 d; scarification with water briefly at 100°C, which was left to cool to ambient temperature, followed by soaking (in the same water) for 3 d; mechanical scarification; acid scarification using 0.1 M HCl for 10 h and an untreated control. Immediately after the various pre-treatments, seeds were surface-sterilized and set to germinate as described above.

Desiccation

Batches of 320 weighed mature seeds were thoroughly mixed with an equal weight of activated silica gel within sealed, heavy-duty, polythene bags that were maintained at ambient temperature. The silica gel was exchanged in all the bags at the first sign of a change of the indicator colour. Equivalent seed batches were mixed with dry vermiculite and similarly maintained as the control material. Individual seed batches subjected to desiccation were weighed at intervals until a collective mass, predetermined by the target moisture content (TMC) equation (IPGRI/DFSC, 1999), was achieved. Seeds were removed for experimentation or storage at each of a declining series of TMCs, prior to which the actual water concentration of individual embryos and endosperm segments was determined and germination performance assessed.

Storage

Experimental and control seed batches were dusted with a fungicide (Benomyl 500 WP, Dow AgroSciences, Pretoria, South Africa) and stored in air-tight containers at 16°C for various time intervals. A sub-set of seeds at the initial water concentration was stored at 6°C. Seeds were sampled periodically over 22 or 16 weeks (control and variously dehydrated samples, respectively) for water content determination, rate of imbibition and assessment of germination performance.

Electron microscopy

After immersion in water for 15 min, embryos were excised from non-dehydrated seeds, processed routinely through phosphate-buffered glutaraldehyde, aqueous osmium tetroxide and a graded acetone series, after which they were embedded in a low-viscosity, epoxy resin. Ultrathin sections were post-stained with uranyl acetate and lead citrate, and examined with a JEOL JEM 1010 transmission electron microscope (JOEL Ltd, Tokyo, Japan).

Statistical analysis

Water concentration data were analysed by one-way analysis of variance, using the SPSS statistical analysis programme (version 9.0.1, SPSS Inc., Chicago, Illinois, USA); as the data were normally distributed, they were not transformed prior to analysis. In cases where analysis of variance indicated a significant treatment effect, Tukey's multiple range test was used to identify homogeneous groups (Sokal and Rohlf, 1981). Where appropriate, germination data were subjected to χ^2 tests.

Results and discussion

Initial seed-lot characteristics

The mean water concentration of the embryos remained essentially constant as seeds matured to stage 3, but declined significantly by stage 4 ($P < 0.05$). In contrast, endosperm water concentration was similar at stages 1 and 2, declined by stage 3 ($P < 0.05$) and thereafter did not decline significantly (Fig. 1). A differential between embryo and endosperm water concentrations was a consistent feature during seed development in *P. reclinata*, and even at maturity, the embryo tissues remained considerably more hydrated, at a mean of 1.5 g g^{-1}, than the endosperm (*c.* 0.5 g g^{-1}). The proportional decline in water concentration from stages 1 to 5 of the two tissues was essentially the same (embryos, 34.7%; endosperm, 32.4%).

The fruits of *P. reclinata* are naturally shed once the exocarp has browned, and the pulp is still hydrated and fleshy. Hence, seeds at stage 5, presently removed from hand-harvested fruits in this condition, are assumed to have completed maturation. While some seed dehydration may occur after fruit abscission, embryo and endosperm water concentrations of stage 5 seeds are consistent with the seeds being non-orthodox. This is supported by the ultrastructure of axis cells, which, although showing a degree of intracellular dedifferentiation relative to stage 2, (compare Figs 2a and 2b, c) did not present typical features of the mature, orthodox condition (e.g. Klein and Pollock, 1968).

Seeds of developmental stages 2–5 initiated germination within 10 d, the lag period being the shortest (7 d) for stages 2 and 3 (Fig. 3). Stage 1 seeds,

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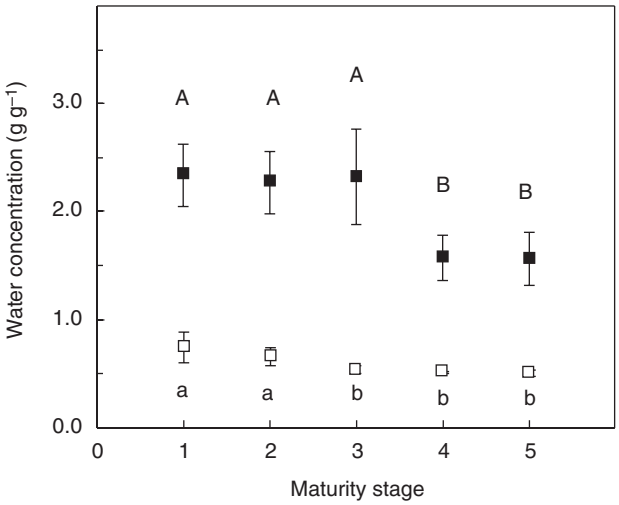

Figure 1. Water concentrations in embryos (closed symbols) and endosperm (open symbols) of *Phoenix reclinata* seeds of different maturity stages. Error bars show 95% confidence intervals. Letters indicate homogeneous groups in embryo (upper case) and endosperm (lower case) water concentrations (ANOVA, $F_{4–101} = 36.26$, $P < 0.05$ for embryos, and $F_{4–67} = 26.69$, $P < 0.05$ for endosperm; homogeneous groups from Tukey's multiple range test).

extracted from green fruits, were clearly immature, with only 27% germination and 31 d elapsing before first radicle protrusion. While seeds of developmental stages 2 and 5 germinated at essentially the same rate (T_{50} = 12 and 14 d, respectively) and achieved the same final germination (87%), those harvested in developmental stages 3 and 4 germinated less rapidly, with stage 3 seeds showing only 60% total germination. This trend was confirmed in trials with seeds harvested the following year (data not shown).

While it is presently not possible to account for these observations, a possible explanation may be that a temporary physiological block develops between the time that the seeds acquire full germinability (stage 2) and when they are fully mature (stage 5). This view is supported by the indication that germination rate is also adversely affected at stage 4, although the overall effect on germination is not as extreme as for stage 3 seeds. As the seeds were presently cleaned of all fruit tissue, this cannot be ascribed to immediate inhibitory effects of factors in the fruit pulp in *P. reclinata*, as has been suggested for other palm species by a variety of authors (Rauch *et al.*, 1982; Broschat and Donselman, 1986, 1987; Meerow, 1991; Rauch, 1994; Ehara *et al.*, 2001). Furthermore, it is difficult to argue that the seed coat imposes this postulated block, as germination rate and totality were essentially similar for stage 5 seeds, where the testa had become harder and had browned, and for stage 2 seeds, with a softer coat. This leaves the embryo itself, the endosperm, or the interaction of

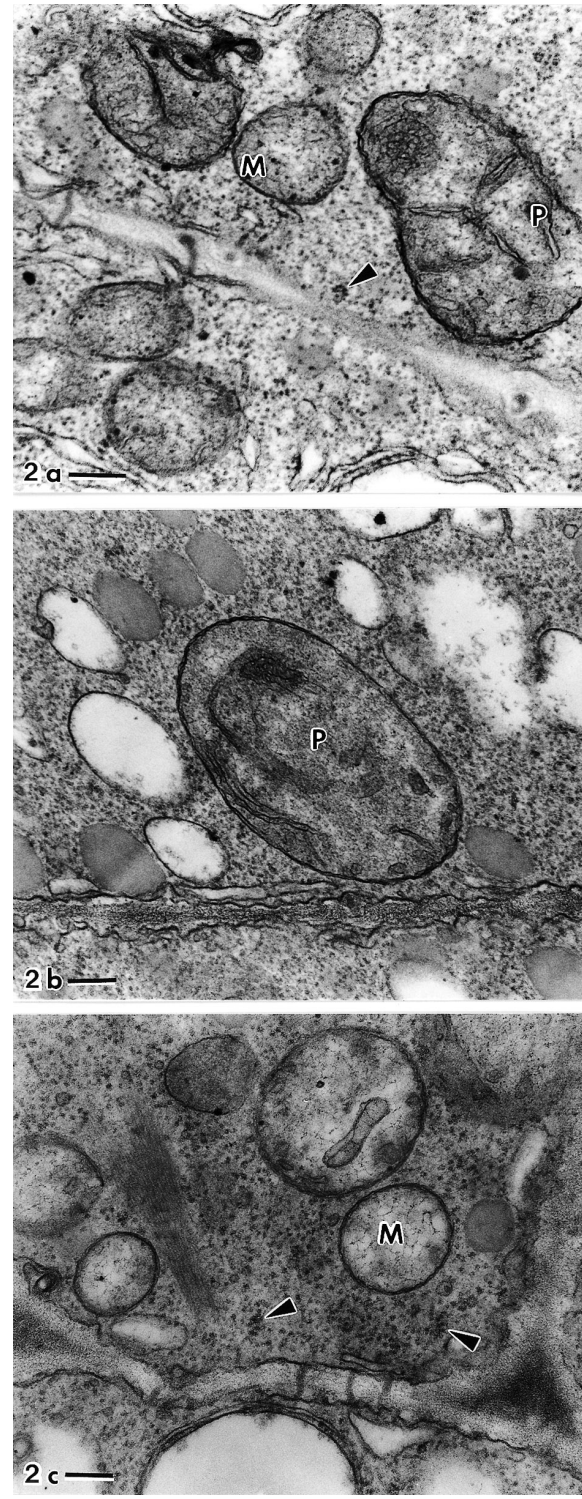

Figure 2. Ultrastructure of the radicle meristem cells of *Phoenix reclinata* seeds at (a) developmental stage 2, and (b and c) developmental stage 5. Plastids (P), in particular, had not dedifferentiated significantly at stage 5 relative to stage 2. Polysomes (arrowheads) are also evident at both stage 2 and stage 5. Bars, 0.2 µm.

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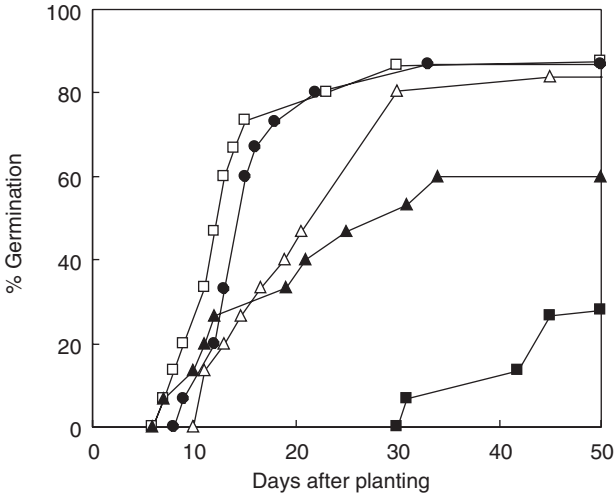

Figure 3. Time course of germination of *Phoenix reclinata* at different maturity stages: ■, stage 1; □, stage 2; ▲, stage 3; △, stage 4; ●, stage 5.

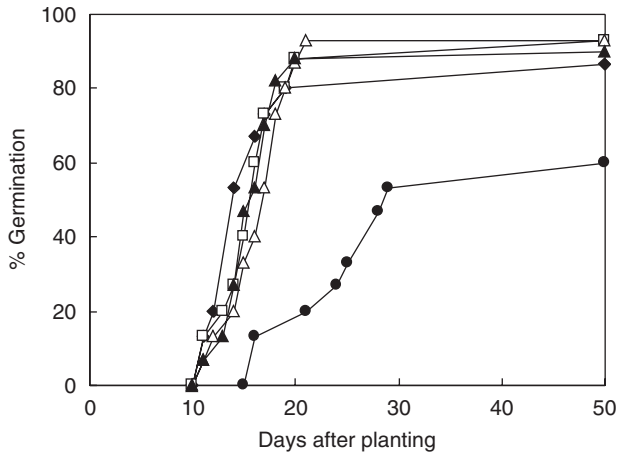

Figure 4. Time course of germination of seeds of *Phoenix reclinata* at the initial shedding water concentration after a variety of pre-treatments: ◆, no treatment; □, soak; △, HCl; ●, boil; ▲, scarification.

the cotyledon with the endosperm as possible locations where the block might be sought. The ultrastructure of the axis of stage 3 seeds was that of highly metabolically active cells (data not shown), and so provides no explanation of the differences in germination performance of the earlier and later developmental states of the seeds.

Pre-treatments

Except where indicated, all pre-treatments were applied to hydrated, stage 5 seeds. At the initial mean embryo water concentration of 1.58 g g^{-1}, the time to first radicle protrusion, germination rate and totality were not significantly different for untreated seeds, or those that were mechanically or acid scarified, or soaked for 3 d at ambient temperature (soaking time was included in the germination time) (Fig. 4). Application of water transiently at 100°C, followed by soaking the seeds for 3 d in the same water after cooling, had markedly deleterious effects in terms of the lag phase, and rate and totality of germination. Additionally, fungal proliferation, emanating from within the seed tissues, was a common feature of seeds subjected to this treatment. While association of fungi was generally noted during germination assessment of the *P. reclinata* seeds, whether pre-treated or not, in no other case did the mycoflora proliferate extensively. Both vigorous germinating orthodox seeds (Berjak, 1996) and non-orthodox seeds have mechanisms to counteract the proliferation of fungi, which fail when the seeds become debilitated (Anguelova-Merhar *et al*., 2003), and there can be little doubt that treatment with near-boiling water did debilitate the *P. reclinata* seeds.

The germination data for *P. reclinata* seeds, dehydrated to a mean embryo water concentration of 0.21 g g^{-1} prior to the various pre-treatments, are shown in Fig. 5. Immersion in water at 100°C was considerably more deleterious after desiccation, than when the seeds had not been dehydrated. While no differences in germination parameters were apparent for dehydrated seeds that received no pre-treatment and those that were soaked (3 d) or acid scarified, those that had been mechanically scarified initiated germination more rapidly.

Successful hot-water scarification, as reported by Loomis (1958) for *Acrocomia sclerocarpa* and

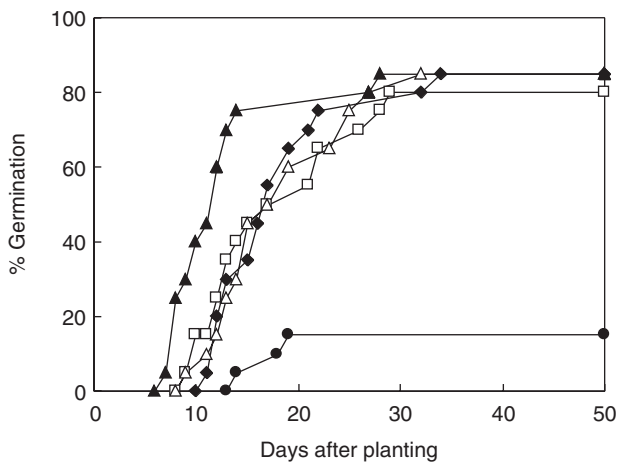

Figure 5. The effects of various pre-treatments on the germination time course of *Phoenix reclinata* seeds that had been previously dehydrated to a water concentration of 0.21 g g^{-1}. ◆, no treatment; □, soak; △, HCl; ●, boil; ▲, scarification.

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Astrocaryum mexicanum, may not be deleterious if the palm seeds are thick-coated and are orthodox. The embryos in newly harvested non-orthodox seeds at high embryo water concentration are highly likely to be active metabolically, and the ultrastructure (Fig. 2) suggested this to be the case for *P. reclinata* seeds. Embryos would be highly vulnerable to high temperatures in this condition.

Phoenix reclinata seeds at the initial water concentration (embryo, 1.58 g g^{-1}; endosperm, ~0.5 g g^{-1}) took up only 3% of their initial mass in water during imbibition over 10 d, and only after dehydration to a mean embryo water concentration of 0.21 g g^{-1} was water uptake increased by *c.* 35% during this period (data not shown). This is a further indicator that these seeds are non-orthodox. The fact that neither mechanical, nor acid, scarification had any significant promotive effects on the germination of the stage 5 *P. reclinata* seeds at the initial water concentration, argues that the seed coat presents no barrier to radicle protrusion in this species. The slightly beneficial effects of mechanical scarification of the seeds after they had been dehydrated suggests that, as it dries down, the coat does slow the ingress of water and/or present a slightly more challenging barrier for radicle protrusion. However, even without any pre-treatment, seeds dehydrated to an embryo water concentration of 0.21 g g^{-1} germinated readily, reinforcing the idea that the coat is not a major impediment for germination in *P. reclinata* seeds.

Desiccation

Mature (stage 5) seeds of *P. reclinata* were dehydrated by burial in silica gel for a total of 16 d. The decline in embryo water concentration was rapid over the first 2 d, declining gradually by the twelfth day, and remaining relatively constant thereafter. Endosperm water concentration declined to about half the initial value in the first 24 h, and then very gradually to day 16. Seeds were sampled at four TWCs, corresponding to embryo water concentrations of 1.14, 0.51, 0.40 and 0.14 g g^{-1}. When seeds were immediately planted after dehydration, the impact of drying was reflected in the germination rate, which was slower in all cases relative to the rate at which seeds germinated at the initial water concentration (Fig. 6). Nevertheless, total germination was essentially similar for seeds at the initial water concentration and those dehydrated to the range 1.14–0.40 g g^{-1}. The reduction in germination rate may have been a consequence of desiccation damage or because the partially dried seeds required longer to imbibe. However, there was a significant decline in germinability ($P < 0.01$; χ^2 test) and an increased germination lag of the seeds dried to 0.14 g g^{-1} (Fig. 6).

It took 12 d for water concentrations in both the embryo and endosperm to decline to 0.14 g g^{-1}. Were the seeds of *P. reclinata* orthodox, the marked decline in vigour and viability accompanying this dehydration regime would not be expected. These responses of *P. reclinata* seeds suggest that they are intermediate, *sensu* Hong and Ellis (1996).

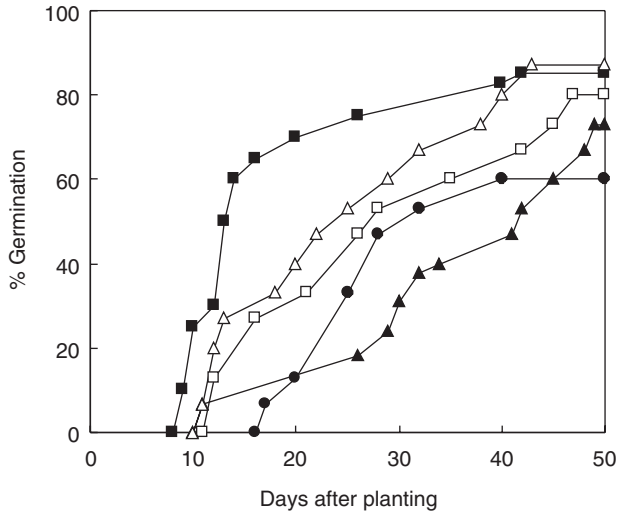

Figure 6. Germination time course of seeds of *Phoenix reclinata* that had been dried to a range of water concentrations: ■, 1.58 g g^{-1}; □, 1.14 g g^{-1}; ▲, 0.51 g g^{-1}; △, 0.40 g g^{-1}; ●, 0.14 g g^{-1}. Total germination percentages at the end of the experiment differed among dehydration treatments ($\chi^2 = 19.05$, df = 4, $P < 0.01$).

Seed storage

Seeds at the initial embryo water concentration were stored at 16°C for a total of 22 weeks and those dehydrated to the levels indicated above for 16 weeks, there being insufficient material for longer storage trials (Fig. 7). The trends reported for viability immediately after dehydration from embryo water concentrations of 1.58 to 0.51 g g^{-1} were retained throughout the storage period. However, viability of seeds stored at an embryo water concentration of 0.40 g g^{-1} declined significantly, compared with values immediately after dehydration ($P < 0.01$, χ^2 test), despite their unimpaired germination totality when set out on water agar immediately after dehydration. The condition of seeds dehydrated to the embryo water concentration of 0.14 g g^{-1} declined steadily and significantly ($P < 0.01$, χ^2 test) (Fig. 7). Cold storage had adverse effects on *P. reclinata* seeds; viability of seeds stored at 4°C for 12 weeks (58%) was significantly lower ($P < 0.01$, χ^2 test) than that of seeds stored at 16°C for the same period (86%). Shortage of material precluded assessment of the effects of low temperature on seeds after dehydration.

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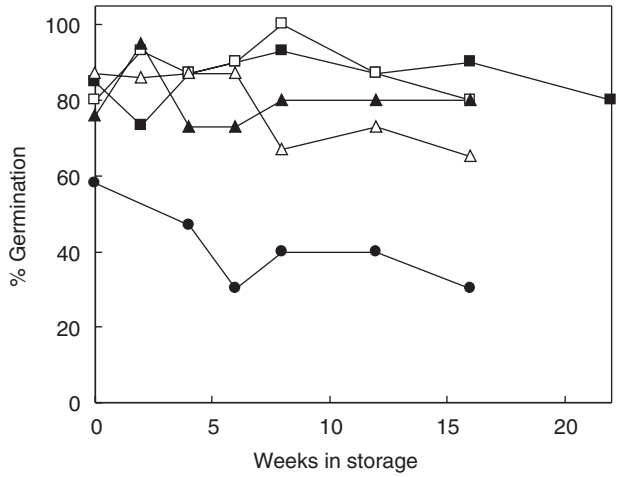

Figure 7. Total germination percentage of seeds of *Phoenix reclinata* stored at 16°C after initial drying to a range of water concentrations: ■, 1.58 g g^{-1}; □, 1.14 g g^{-1}; ▲, 0.51 g g^{-1}; △, 0.40 g g^{-1}; ●, 0.14 g g^{-1}. There was a significant difference in germination between the start and end of the storage period for seeds at a water concentration of 0.40 g g^{-1} (χ^2 = 13.27, df = 1, P < 0.01) and of 0.14 g g^{-1} (χ^2 = 9.52, df = 1, P < 0.01).

The present results indicate that seeds of *P. reclinata* are neither orthodox nor recalcitrant, but show intermediate post-harvest behaviour, as defined by Hong and Ellis (1996). Although surviving with unabated vigour and viability for 22 weeks when stored at 16°C at the original (shedding) water concentration, dehydration to embryo water concentrations below 0.4 g g^{-1} adversely affects these seeds. For plants occurring in the riparian zone, this degree of desiccation sensitivity may be unimportant in terms of seed survival and germination. However, unless seed shed coincides with the wet season, the lack of desiccation tolerance may impose constraints on reproduction via seed in open savannahs.

These findings further illustrate that there is a diverse range of post-harvest seed behaviour in the palm family, as the data compiled by Tweddle *et al.* (2003) indicate, highlighting the need for further investigations into this highly utilized family.

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