Water Concentration Considerations in Recalcitrant / Non-orthodox Seeds

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Introduction

Seeds categorised as recalcitrant are shed at high water concentrations (g H_2O g^{-1} dry mass) and cannot withstand the loss of more than a small proportion of water without deleterious – or even lethal – consequences: such seeds are desiccation-sensitive. Hence, as originally recorded by Roberts (1973), recalcitrant seeds cannot be stored at low water concentrations ('moisture contents'), i.e. under low relative humidity (RH) conditions, as are ideal for desiccation-tolerant orthodox seeds. In fact, storage quality and lifespan of recalcitrant seeds of several species have been found to be diminished by even a slight degree of dehydration (Corbineau and Côme, 1988; Drew *et al.*, 2000; Eggers *et al.*, 2006). While seed recalcitrance is generally perceived to be a characteristic of tree species, the phenomenon is certainly not restricted to woody plants. For example, many species of amaryllids, which are herbaceous geophytes, produce recalcitrant seeds (Figure 1 [Sershen Naidoo, 2006]), as do *Zizania* spp., and other members of the Poaceae (Probert and Longley, 1989; Kovach and Bradford, 1992; Vertucci *et al.*, 1995). Furthermore, although seed recalcitrance is more common in tropical tree species (e.g. Sacandé *et al.*, 2004), there are a number of tree species of temperate provenance such as *Quercus* spp. (e.g. Finch-Savage and Blake, 1994; Connor and Bonner, 1996) and *Aesculus hippocastanum* (e.g. Tompsett and Pritchard, 1993; 1998) that also produce recalcitrant seeds. Other non-orthodox seeds, broadly categorised as showing intermediate post-harvest behaviour, are those that will withstand considerable dehydration, but cannot be dried down to the low water concentrations tolerated by orthodox types. Such seeds are generally relatively short-lived, and those of tropical provenance may be intolerant of chilling temperatures (Hong and Ellis, 1996).

Figure 1. Fruit and seeds of Amaryllis belladonna. The variation in size of seeds from a single harvest is clearly indicated.

As an aside, the amount of water in an orthodox seed is frequently expressed as a percentage calculated on a fresh mass basis (that is, the proportion of hydrated or partially dehydrated seed that is water), although the amount of water present can also be expressed on a dry mass basis. At the low water concentration suitable for storage of orthodox seeds it makes very little difference if data are expressed on a fresh or dry mass, but in the case of recalcitrant seeds that contain considerable amounts of water, there are marked differences in values when expressed on a fresh or dry mass basis. We prefer data to be expressed relative to dry mass. In this case the basis to which values are being normalised does not change as the amount of water changes, and the proportional change in 'water content' reflects the proportional change in the amount of water in the tissue; if the water concentration changes from 1.0 to 0.5 g water g^{-1} dry mass, the tissue has lost half its water. If the data are expressed on fresh mass basis, for tissue at 1.0 g water per gram dry mass that loses half its water, water content on a fresh mass basis changes from 50% to 33.3%. However, since the deleterious processes occurring in recalcitrant seeds as they dry are influenced by the free energy of the tissue water, ideally the water status of recalcitrant seeds should be expressed in terms of their water potential.

Desiccation sensitivity of recalcitrant seeds is the outcome of two major, but inter-related features: firstly, the suite of mechanisms and processes that collectively confer the property of desiccation tolerance in orthodox seeds may be absent, or incompletely expressed, in recalcitrant types; and secondly, the seeds remain actively metabolic, grading virtually imperceptibly from development into germination (Pammenter and Berjak, 1999; Berjak and Pammenter, 2004). This second feature is at least partly the outcome of the non-occurrence of two processes of the suite of events conferring desiccation tolerance, viz. intracellular dedifferentiation and metabolic 'switch-off' (e.g. Farrant *et al.*, 1997). The expression of recalcitrant traits, however, may well also be influenced by the degree of seed development at shedding (Finch-Savage and Blake, 1994; Daws *et al.*, 2004b; 2005).

Variability is a key feature among recalcitrant seeds

Recalcitrance is not an all-or-nothing situation (Berjak and Pammenter, 1994). From a perusal of the literature up to 1988, Farrant and co-workers had already loosely categorised desiccation-sensitive seeds as being minimally, medially and maximally recalcitrant in terms of the proportion of water loss tolerated, responses to chilling (above zero) temperatures and storability. Since then, however, it has become apparent that variability among recalcitrant seeds of different species – and within the same species – is far more complex.

Rate of dehydration

Drying rate has been shown to be an important factor in the degree of dehydration that recalcitrant seeds or excised axes will withstand. Although there is the occasional recorded exception (e.g. for the relatively large axes of *Theobroma cacao* [Liang and Sun, 2000]), in general, the more rapidly dehydration is achieved, the greater the water loss that will be tolerated without irreversible injury (Normah *et al.*, 1986; Pammenter *et al.*, 1991; 1998; Pritchard, 1991; Kundu and Karachi, 2000; Potts and Lumpkin, 2000). Additionally, seeds of different species will lose water at different rates under the same