INVITED REVIEW

A review of recalcitrant seed physiology in relation to desiccation-tolerance mechanisms

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Abstract

A suite of mechanisms or processes that together have been implicated in the acquisition and maintenance of desiccation tolerance in orthodox seeds is discussed in the context of the behaviour of desiccation-sensitive seeds, and where appropriate, parallels are drawn with the situation in vegetative plant tissues that tolerate dehydration. Factors included are: physical characteristics of cells and intracellular constituents; insoluble reserve accumulation; intracellular de-differentiation; metabolic 'switching off'; presence, and efficient operation, of antioxidant systems; accumulation of putatively protective substances including LEAs, sucrose and other oligosaccharides, as well as amphipathic molecules; the presence and role of oleosins; and the presence and operation of repair systems during rehydration. The variable response to dehydration shown by desiccation-sensitive seeds is considered in terms of the absence or incomplete expression of this suite of mechanisms or processes.

Three categories of damage are envisaged: (i) reduction in cell volume which can lead to mechanical damage; (ii) aqueous-based degradative processes, probably consequent upon deranged metabolism at intermediate water contents. This is termed 'metabolism-induced damage' and its extent will depend upon the metabolic rate and the rate of dehydration; and (iii) the removal of water intimately associated with macromolecular surfaces leading to denaturation: this is referred to as desiccation damage *sensu stricto*. The effects of drying rate and the maturity status of seeds are considered in relation to the responses to dehydration, leading to the conclusion that the concept of critical water contents on a species basis is inappropriate. Viewing seed postharvest physiology in terms of a continuum of behaviour is considered to be more realistic than attempting precise categorization.

Rapid dehydration of excised embryonic axes (or other explants) from desiccation-sensitive seeds permits retention of viability (in the short term) to water contents approaching the level of non-freezable water. This opens up the possibility of long-term conservation, by cryopreservation techniques, of the genetic resources of species producing non-orthodox seeds.

Keywords: dehydration rate, desiccation-sensitivity, desiccation-tolerance, developmental status, intermediate, orthodox, recalcitrant, resurrection plant, seed

Introduction

Seeds that are tolerant of relatively extreme desiccation and will survive in the dehydrated state for periods that are predictable depending on storage conditions are said to show orthodox storage behaviour. At the other extreme, recalcitrant seeds are damaged by dehydration, may also be chilling-sensitive, and generally cannot be stored effectively for useful periods (Roberts, 1973; Chin and Roberts, 1980). Seeds categorized as showing intermediate postharvest behaviour are relatively desiccation-tolerant, but will not withstand removal of water to levels as low as orthodox seeds. Such seeds, particularly if they are of tropical origin, may also be chilling-sensitive, even in the dehydrated state (Ellis *et al.*, 1990; Hong and Ellis, 1996).

This categorization was originally based on the seeds of a narrow spectrum of mostly economically-important crop species. However, with further studies on an increasingly wide range of species, especially those from the tropics and sub-tropics, it has become apparent that there is a wide range in the postharvest responses of seeds, suggesting an open-endedness to the three categories such that postharvest physiology may be considered as constituting a continuum across species. Even within the recalcitrant category, there are marked differences in the responses of seeds of individual species, which led some 10 years ago to the

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