HANDBOOKS FOR GENEBANKS. NO. 4

Seed Storage Behaviour: a Compendium

T.D. Hong, S. Linington and R.H. Ellis

International Plant Genetic Resources Institute
IPGRI

ISBN 92-9043-280-2

Handbooks for Genebanks: No. 4

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International Plant Genetic Resources Institute

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Citation:
Hong, T.D., S. Linington and R.H. Ellis. 1996. Seed Storage Behaviour: a Compendium. Handbooks for Genebanks: No. 4. International Plant Genetic Resources Institute, Rome.

Cover illustration by Maddine Insalaco

ISBN 92-9043-280-2

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Part II. Compendium

Note to the reader:
The information contained in the Compendium is now available through the online searchable database 'IPGRI Species Compendium' on IPGRI's web site at

http://www.ipgri.cgiar.org/themes/exsitu/IPGRIspeciescompendium

Preface

This handbook provides an introduction to seed storage physiology for those responsible for plant genetic conservation and a selective summary of the literature on seed survival in storage, and thus on seed storage behaviour, for over 7000 species from 251 families.

Part IA summarizes progress in our understanding of seed physiology in relation to seed storage for genetic conservation in the past 17 years since the publication of *The Storage of Recalcitrant Seeds: Achievements and Possible Approaches* by King and Roberts (1979), and particularly the various problems that may result in the misclassification of seed storage behaviour.

Part IB provides a compendium of information on seed survival during storage and attempts to classify plant species into the several categories of seed storage behaviour.

Classification of seed storage behaviour is an essential step in devising a suitable method of conservation for each species. This is because long-term seed storage for genetic conservation under the conditions recommended by IPGRI (formerly IBPGR) is possible for species which show ‘orthodox’ seed storage behaviour. Medium-term storage under well-defined storage conditions is possible for species which show ‘intermediate’ seed storage behaviour. Such storage underwrites *in situ* conservation activities against the threats of epidemics, fire, human pressures, etc. and against similar losses at field genebanks. It also facilitates utilization. However, for species with ‘recalcitrant’ seeds, seed conservation is inappropriate (other than as a very short-term measure) and field genebanks, tissue culture techniques and/or *in situ* conservation will need to be adopted. Knowing where seed conservation can be applied is thus essential to those planning conservation strategies and this handbook attempts to address this issue. Finally, information in this volume is required by seed collectors devising appropriate methods of handling and storing seeds over the short term.

This handbook is the fourth in the series. The first handbook in this series covered the design of long-term seed stores for genetic conservation (Cromarty *et al.* 1982). The second and third were concerned with approaches to germinate the seeds withdrawn from these stores (Ellis et al., 1985a, 1985b). This handbook complements the earlier handbooks, which made only passing reference to the survival of seeds in storage and to the variation in seed storage behaviour among contrasting species; this handbook updates (and expands considerably) parts of those previous handbooks.

In preparing this compendium we have relied heavily on publications, seed lists, reports, handbooks and other material published in different languages from many parts of the world. We are therefore very grateful to the staff of the Library of The University of Reading for their help in obtaining such publications. Many institutes were contacted and we are most grateful to (in alphabetical order) Dr D. Astley (Genetic Resources Unit, Horticulture Research International, UK), Dr J.S. Brouard (Project Manager, SADC Tree Seed Centre Network, Zimbabwe), Professors D. Côme and F. Corbineau (Université Pierre et Marie Curie, Paris, France), Dr I.D. Kossmann Ferraz (Instituto Nacional de Pesquisas da Amazonia, Manaus, Brazil), Dr B. Krishnapillay (Seed Technology Centre, Malaysia), Mr O. Leveron (Escuela Nacional de Ciencias Forestales, Honduras), Mr. C. Marunda (Seed Centre, Zimbabwe), Mr L. Motoma (Forestry Association of Botswana), Mr H.P. Msanga (DANIDA/ Tanzania Tree Seed Programme), Professor A.R. Nautiyal (Garhwal University, India), Dr Doai Van Nguyen (National Forest Seed Company, Vietnam), Mr W. Omondi (Kenya Forestry Seed Centre), Mr P. Pukittayacamee (ASEAN-Canada Forest Tree Seed Centre, Thailand), Dr K. Poulsen (DANIDA Forest Seed Centre, Denmark), Dr G.S. Richmond (Curtin University of Technology, Perth, Australia), Mr I.M. Shehaghilo (Tanzania Forestry Research

Institute), Professor G.M. Simpson (University of Saskatchewan, Canada), Mr. Enrique Trujillo N. (Banco Latinoamericano de Semillas Forestales, CATIE, Costa Rica), and to Professor C. Vazquez-Yanes (Universidad Nacional Autonoma de Mexico, Mexico) for providing reprints, documents, seed lists, etc.; to Professor E.H. Roberts (The University of Reading, UK), Drs H.W. Pritchard, R.J. Probert, and Mr R.D. Smith (RBG Kew, Wakehurst, UK) for their many helpful comments and suggestions, and to the following staff from the Herbarium RBG Kew, UK for their checking of scientific names used in certain plant families: Ms S. Bidgood (Scrophulariaceae), Dr R.K. Brummitt (certain problem genera), Dr T.A. Cope (Gramineae - general), Dr P.J. Cribb (Orchidaceae), Dr J. Dransfield (Palmae), Dr I.K. Ferguson (Scrophulariaceae), Dr D.J.N. Hind (Compositae, Dipsacaceae and Valerianaceae), Mr G.P. Lewis (Leguminosae), Dr A.J. Paton (Labiatae), Dr L. Rico-Arce (Leguminosae), Dr C. Stapleton (Gramineae - bamboos), and Mr N.P. Taylor (certain Rosaceae).

Glossary of Terms

Achene. A dry indehiscent one-seeded pericarp (e.g. lettuce).
Acorn. The fruit of the oak (*Quercus* spp.) and comprised of a nut and its cup or cupule.
Aril. An appendage or an outer covering of a seed, growing out from the hilum or funiculus; it sometimes appears as a pulpy covering.
Berry. Pulpy indehiscent few- or many-seeded fruit; technically the pulpy fruit resulting from a single pistil, containing one or more seeds (e.g. tomato) but no true stone.
Calyx. The outer circle of floral envelopes, comprised of the sepals; the latter may be distinct or connate in a single structure.
Capsule. Compound pod; a dry fruit of more than one carpel, usually opening at maturity by one or more lines of dehiscence (e.g. poppy).
Caruncle. A fleshy, sometimes coloured, appendage of the outer integuments for some seeds.
Caryopsis. An achene with pericarp and seed testa inseparably fused (e.g. Gramineae)
Catkin. A scaly-bract usually flexuous spike or spike-like raceme with diclinous flowers (e.g. willow).
Cone. A dense and usually elongated collection of flowers or fruits that are borne beneath scales, the whole with scales and axis forming a detachable homogenous fruit-like body (e.g. pine).
Cotyledon (s). The primary leaf (or leaves) in the embryo.
Deciduous. A plant whose leaves are shed at a specific season or growth stage.
Dehiscence. The method or process of opening of a seed-pod; **loculicidally** dehiscent when the split opens into a cavity or locule; **septicidally** dehiscent when splitting along septum of the ovary; **circumscissally** dehiscent when the top valve comes off as a lid.
Dormancy. The condition of a live seed which prevents germination when it is supplied with the conditions normally considered to be suitable for germination, viz. adequate moisture, a suitable temperature and adequate aeration.
Drupe. A fleshy one-seeded indehiscent fruit with seed enclosed in a stony endocarp (stone-fruit) (e.g. *Aleurites*).
Drupelet. One drupe in a fruit made up of aggregate drupes (e.g. raspberry).
Embryo. The rudimentary plant within a seed, which arises from the zygote or sometimes from an unfertilized egg cell. It consists of an axis bearing an apical meristem or a plumule, a radicle, and one or more cotyledons.
Endocarp. The inner layer of the pericarp.
Endosperm. Triploid tissue which develops from the fusion of a sperm nucleus with the two polar nuclei of the embryo sac. It supplies nutrients to the embryo and may be entirely used up during seed formation, or part of it may remain and sustain the seed during germination.
Follicle. Dry dehiscent fruit opening only on the front suture and the product of a simple pistil (e.g. *Delphinium*).
Germination. Ultimately the production of a seedling from a seed; the emergence of the radicle from the seed is normally the first visible sign that germination has commenced, but germination begins from the first metabolic process during imbibition.
Germination test. A laboratory test to estimate the proportion of seeds within an accession capable of germinating.
Herb. Plant naturally dying to the ground, without persistent stem above ground, and lacking definite woody firm structure.
Hermetic storage. Storage in an air-tight, moisture-proof container.
Intermediate seed storage behaviour. A category of seed storage behaviour

intermediate between those defined as orthodox and recalcitrant. For a detailed definition see Part IA, Section 5. Mature whole seeds are able to tolerate desiccation to seed moisture contents in equilibrium at 20°C with about 40-50% relative humidity but further desiccation often reduces viability and always results in more rapid deterioration in subsequent hermetic storage the more the seeds are dried below this value.

Long-term storage. The storage of seed accession for long-term periods (a decade at a minimum, but many such stores expect satisfactory storage for 50-100 years or more). Stores operated at subzero temperatures are generally classed as long-term seed stores, but the storage conditions recommended by IPGRI (formerly IBPGR) for long-term seed conservation are –18°C or less in air-tight containers at a seed moisture content of 5 ± 1%. (w.b.) (Cromarty *et al.* 1982).

Longevity. Life span. In seeds, it is the length of time that they remain viable. The life span depends on the species and the environmental conditions under which the seeds are stored. The duration is often qualified by the percentage of seed viability at the end of the period because seedlots are populations in which some seeds die sooner than others (e.g. 85% viability in order to ensure that the majority of individuals in the seed population are viable and in good condition at the end of this period).

Medium-term storage. The storage of seed for medium-term periods as is often used for active collections in genebanks or by plant breeders and seedsmen. Under the same conditions of storage, the seeds of different species will have different periods of longevity. Thus it is difficult to define precisely the period envisaged by ‘medium-term’. A period of 2-10 years or so is generally assumed. As a guide, stores which are run at temperatures between 0 and 10°C have been listed as medium-term stores.

Nut. An indehiscent, one-seeded, hard and bony fruit, even if resulting from a compound ovary (e.g. chestnut).

Nutlet. A small nut.

Open storage. Storage conditions where seeds are exposed directly or indirectly to ambient relative humidity (and sometimes also temperature); for example, in a paper bag, cloth bag, or a similar material which permits seed moisture content to be influenced by ambient relative humidity.

Orthodox seed storage behaviour. Mature whole seeds not only survive considerable desiccation (to at least 5% moisture content) but their longevity in air-dry storage is increased in a predictable way by reduction in seed storage moisture content and temperature (e.g. to those values employed in long-term seed stores). See Part IA, Section 3 for further information.

Perianth. The collective term for the calyx and corolla. It is made up of one or more whorls of floral leaves (petals and sepals).

Pericarp. The fruit wall which has developed from the ovary wall. The pericarp comprises the endo-, meso- and exocarps. There are various forms such as dry, fleshy and woody pericarps.

Pome. A fruit in which the multiseeded core is surrounded by a papery endocarp which, in turn, is fused to the fleshy receptacle (e.g. apple).

Preferred storage conditions. The storage conditions recommended by FAO and IPGRI (formerly IBPGR) for long-term seed conservation, viz. storage at –18°C or less in air-tight containers at a seed moisture content of 3-7% (w.b.) (Engels and Tao 1994).

Pod. A dehiscent dry pericarp.

Pyrene. The stone of a small drupe.

Recalcitrant seed storage behaviour. Mature whole seeds are unable to tolerate more than a limited amount of desiccation, for example to moisture contents in equilibrium at 20°C with about 96-98% relative humidity or a seed water potential of around –1.5 to –5MPa. See Part IA, Section 4 for more information.

Samara. Indehiscent winged fruit (e.g. *Acer*).

Schizocarp. A dry dehiscent fruit that splits into two halves, each half a mericarp (e.g. Umbelliferae).

Shrub. A woody plant that remains low and produces shoots or trunks from the base.

Siliqua. The long fruit of certain Cruciferae.

Tree. A woody plant that produces one main trunk and a more or less distinct and elevated head.

Utricle. A bladdery one-seeded and usually indehiscent fruit (e.g. *Basella*).

Viability. The possession in a seed of those processes essential for a seed to germinate. Thus a viable seed is alive; but this does not ensure that the seed will germinate (for example, if the seed is dormant). Within an accession, percentage viability is the proportion of seeds which are viable; it is estimated from the result of a viability test.

Viability test. A test on a sample of seeds withdrawn from the accession designed to estimate the percentage viability of the accession. A germination test can only function as a viability test either if all the seeds are non-dormant, or if special treatments are applied to remove dormancy. An alternative viability test procedure which does not require special treatments to remove dormancy is the tetrazolium test; in forest tree seed testing the term viability test is often synonymous with a tetrazolium test.

Acronyms and Abbreviations

AVRDC	Asian Vegetable Research and Development Center, Taiwan
BLSF	Banco Latinoamericano de Semillas Forestales, *Catalogo de Semillas Forestales* 1994; Centro Agronomico Tropical De Investigation y Enseñanza, Proyecto de Semillas Forestales (PROSEFOR)
CIAT	Centro Internacional de Agricultura Tropical, Cali, Colombia
CIMMYT	Centro Internacional de Mejoramiento de Maiz y Trigo, El Batan, Mexico
CNSF	Centre National de Semences Forestières, Ouagadougou, Burkina Faso, Catalogue 1995-1996
C_w	Coefficient indicating the response of seed longevity to moisture content (from the viability equation). See Part IA, Section 3.2
D	Dicotyledons
DFSC	Danida Forest Seed Centre, *Seed List 1993*
ELSMC	Lowest safe embryo moisture content (%, w.b.), below which viability of excised embryos (or embryonic axes) is reduced
EMCS	Embryo moisture content (%, w.b.) at shedding, harvest, maturity
ESNACIFOR	Escuela Nacional de Ciencias Forestales, Banco de Semillas, Siguatepeque, Honduras
FSB/Argentina	Forest Seed Bank, Santiago del Estero, Argentina
G	Gymnosperm
HBSTGB	Handbook of Seed Technology for Genebanks. Volume II. (Ellis et al., 1985b)
ICARDA	International Center for Agricultural Research in the Dry Areas, Aleppo, Syria
ICRISAT	International Crops Research Institute for the Semi-Arid Tropics, Hyderabad, India
IITA	International Institute of Tropical Agriculture, Ibadan, Nigeria
IPGRI	International Plant Genetic Resources Institute, Rome, Italy
ISTA	International Seed Testing Association; ISTA (1993a, 1993b)
LMCL	Low-moisture-content limit (%, w.b.) to the viability equation, see Part IA, Section 3.3
LSMC	Lowest safe moisture content, also termed “critical moisture content” (%, w.b.), below which viability is significantly reduced by further desiccation
M	Monocotyledons
mc	Moisture content (%, w.b.)
MCS	Whole seed moisture content (%, w.b.) determined at shedding, harvest, maturity
NSSL	National Seed Storage Laboratory, Fort Collins, USA
Orthodox p	Orthodox probable. See Part IB, Introduction
pers. comm.	Personal communication
p_{50}	Half-viability period, i.e., time taken for 50% of the seeds to lose viability
PGRC/Ethiopia	Plant Genetic Resources Centre, Ethiopia
RGB Kew, WP	Seed Bank, Royal Botanic Gardens Kew, Wakehurst Place, UK
r.h.	Relative humidity
RSS	Recommended seed storage conditions
SSLR	Results of unpublished research, Seed Science Laboratory, Department of Agriculture, The University of Reading
TSW	Thousand-seed weight (g) (because information is collated from many different sources, TSW will have been determined at different seed moisture contents)
ULMC	Upper moisture content limit (%, w.b.) to the viability equation. See Part IA, Section 3.3
VGB	Vegetable Genebank, Wellesbourne, UK
w.b.	Wet weight basis or fresh weight basis, when referring to seed moisture content
*	Before species name = taxonomic difficulty with species listed.

Part IA. An Introduction to Seed Storage Behaviour

1. Introduction

Conservation of plant genetic resources comprises two types of approach; *in situ* and *ex situ* conservation. *In situ* conservation has been defined as the conservation of whole ecosystems and natural habitats where wild or cultivated species are maintained and may continue to evolve. *Ex situ* conservation maintains germplasm outside its original habitats, in the form of whole plants in botanical gardens and field genebanks, seeds as in seed genebanks, or certain other parts of the plant such as roots, dormant buds, pollen, explants as *in vitro* genebanks, or possibly as DNA. Knowledge of the seed storage behaviour of a target species is required in order to determine whether or not seed storage is suitable as a method of genetic conservation, and how to handle seeds during collection and germplasm exchange. If it is feasible, long-term seed storage is generally considered the safest, most inexpensive and most convenient method of genetic conservation. Most plant genetic resources are conserved by this means.

The importance of seed storage has been recognized ever since humans began to domesticate plants. The duration of storage depends upon the objectives of the particular conservation effort and the species concerned. Farmers need to maintain viable seeds from one growing season to the next while seed producers may also wish to maintain ‘carry-over stock’ for several years. In contrast, the goal of genebanks is essentially the maintenance of seed viability in a very wide range of species for indefinite but considerable periods, a much harder task which requires both specific facilities and information.

This **Compendium of Information on Seed Storage Behaviour** should be read in conjunction with the earlier **IBPGR Handbooks for Genebanks** which cover the design and construction of long-term seed stores (Cromarty *et al.*, 1982) and the germination and dormancy of seed accessions (Ellis et al., 1985a), (Ellis et al., 1985b). In particular, readers are referred to Appendix 3 of Cromarty *et al.* (Cromarty *et al.*, 1982) for information on seed moisture content, relations between seed moisture content and relative humidity, and the effect of temperature and seed composition on these relations. Throughout this document, seed moisture content is expressed on the fresh weight basis (also described as wet basis, and often abbreviated to w.b.).

2. Classification of seed storage behaviour

Classification of the variation in seed storage behaviour among species is required before choosing appropriate methods of storage. Seed survival in storage has long fascinated humans. The first publication referring to seed storage behaviour appeared in 535 AD in China; Ssu-Hsieh Chia published a handbook in which he recognized two methods of seed storage. For example, for cereals he advised “not to store in warm and damp environments”, whereas with (chinese) chestnut “the fresh seeds should be stored in damp soil placed in the house, and during transport the seeds should be packed in a leather bag, because chestnut seeds will die when exposed to sun and wind” (Ssu-Hsieh Chia, 535). Thus it was recognized one and a half millenia ago that seeds of different species showed two contrasting types of seed storage behaviour.

Ewart (Ewart, 1908) divided seeds into three biological classes according to their life span under ordinary storage conditions:

- microbiotic, i.e. seeds with life spans not exceeding 3 years;
- mesobiotic, i.e. seeds with life spans from 3 to 15 years;
- macrobiotic, i.e. seeds with life spans from 15 to 100 or more years.

In this classification, the effect of the seed storage environment was not taken into account.

Elliott 1912, cited by (Baldwin, 1942) similarly divided (forest tree) seeds into three classes but his classification was based on the response of seeds to desiccation:

- those which can withstand drying, such as most conifers and birch (*Betula* spp.);
- those which can survive partial drying, such as *Fraxinus* spp., *Tilia americana*;
- those which can rarely be dried at all, such as *Quercus* spp. and *Fagus* spp.

In addition to Elliott’s classes of seed storage behaviour, Tillotson (Tillotson, 1921), cited by (Baldwin, 1942) added a fourth class of species whose seeds cannot be stored at all, such as *Acer saccharinum*, red maple (*Acer rubrum*), poplars (*Populus* spp.), willows (*Salix* spp.), elms (*Ulmus* spp.) and hornbeams (*Carpinus* spp.). Although Ewart's system of classification has been well cited, Elliott's classification has unfortunately been largely ignored.

Forest tree seed nurseries are concerned with short-term storage and the pretreatment of seeds before or after storage. For these activities, Holmes and Buszewicz (Holmes & Buszewicz, 1958) divided temperate tree species into five groups:

- seeds with short life spans under ordinary storage conditions (open storage at ambient temperature), but whose longevity can be improved considerably by lowering seed moisture content and storage temperature (e.g. *Salix, Populus, Ulmus, Betula, Alnus* – note the contrast with Tillotson's comments above);
- seeds which can be stored moist for short periods or dry for long periods (e.g. *Acer, Carpinus, Crataegus, Euonymus, Fraxinus, Liriodendron, Nothofagus, Prunus, Pyrus, Sorbus* and *Tilia*);
- large desiccation-sensitive seeds requiring moist storage (e.g. *Aesculus, Castanea, Carya, Corylus, Fagus, Juglans* and *Quercus*);
- species which show hard impermeable seed coats and have long life spans in open storage (e.g. Leguminosae);
- species whose seeds tolerate desiccation to low moisture content and can be stored hermetically at cool, near-zero or subzero temperatures (e.g. conifers).

However, it will be shown in the next paragraph that, in fact, these five groups can be represented by just two categories of seed storage behaviour.

Roberts (Roberts, 1973) introduced a classification based not on longevity *per se*, but on contrasting physiological responses of seed survival during storage to moisture content and temperature. He introduced the terms “orthodox” and “recalcitrant” for the two categories of seed storage behaviour he identified. According to Roberts (Roberts, 1973), orthodox seeds can be dried to low moisture contents (2-5%) without damage. In addition, their longevity increases with decreases in seed storage moisture content and temperature in a quantifiable and predictable way over a wide range of storage environments. In contrast, recalcitrant seeds cannot survive desiccation below a comparatively high (between 12 and 31%) moisture content (Roberts, 1973).

Roberts’ terminology has been widely adopted, and there has since been a considerable emphasis on research activities on recalcitrant seed physiology over the last decade or so. Alternatives to Roberts’ terminology have been suggested from time to time. For example, it has been argued that the term “poikilohydric” should replace “orthodox” to describe seeds that can be maintained in equilibrium with ambient relative humidity for long periods, and that “homoiohydric” should replace “recalcitrant” to describe those that do not tolerate desiccation (Berjak *et al.*, 1990a) (Berjak *et al*., 1990b). It has also been suggested that species with recalcitrant seeds can be further categorized into three subgroups – minimally, moderately and highly recalcitrant (Farrant *et al.*, 1988). Minimally recalcitrant seeds can withstand desiccation to relatively low levels of moisture content, at which germination is slow; they are also able to tolerate cooler storage temperatures, e.g. *Quercus* spp., *Auracaria hunsteinii* and *Podocarpus henkelii.* In contrast, highly recalcitrant seeds are extremely sensitive to desiccation and cool temperatures, e.g. *Syzygium* spp. and *Avicennia marina.* Moderately recalcitrant seeds show a level of desiccation sensitivity between those of the above two groups, e.g. *Theobroma cacao* and *Hevea brasiliensis* (Farrant *et al*., 1988). Although these authors divided recalcitrant seed storage behaviour into three subgroups, they suggested that the categories are not discrete. Rather, they suggested that there is a continuum of recalcitrant seed types, varying from less recalcitrant to highly recalcitrant, depending on the natural habitat to which they are adapted; the highly recalcitrant species tending to be adapted to tropical regions and wetlands, the moderately recalcitrant species to tropical regions, and the minimally recalcitrant species to temperate or subtropical regions (Farrant *et al*., 1988). Thus, this classification provides four groups (orthodox, minimally recalcitrant, moderately recalcitrant and highly recalcitrant) which take into account both the effects of storage environment and adaptation to natural habitats.

Bonner (Bonner, 1990) also suggested a classification based on storage conditions and adaptation to natural habitats. He divided tree species into four classes; the two main categories of orthodox and recalcitrant seed storage behaviour defined by Roberts (Roberts, 1973) were each divided further into two subcategories:

- “true orthodox” seeds can be stored for relatively long periods at subfreezing temperatures with <10% moisture content (e.g. *Abies* spp., *Araucaria cunninghamii, Pinus* spp., *Tectona grandis,* etc.);
- “suborthodox” seeds are those that can be stored under the same conditions as true orthodox seeds, but only for shorter periods (e.g. some *Carya* spp., *Citrus* spp., *Fagus* spp., *Gmelina arborea, Juglans* spp., *Populus* spp., *Salix* spp.);
- “temperate-recalcitrant” seeds that cannot be dried without damage, but can be stored for several years at near-freezing temperatures (e.g. *Aesculus, Quercus* spp.);
- “tropical-recalcitrant” seeds that are sensitive to damage from both desiccation and exposure to cool temperatures of 10-15°C or less (e.g. *Hopea* spp., *Shorea* spp. and *Theobroma cacao*).

In addition to the two categories of seed storage behaviour defined by Roberts (Roberts, 1973), a third category of seed storage behaviour has recently been identified and termed “intermediate” (Ellis et al., 1990a) because a group of species has been identified which shows seed storage behaviour intermediate between the orthodox and recalcitrant categories (Ellis et al., 1990a), (Ellis et al., 1991a), (Ellis et al., 1991b), (Ellis et al., 1991d), (Hong & Ellis, 1992c), (Hong & Ellis, 1995). Essentially, seeds from this group of species are able to withstand desiccation to the higher band of air-dry seed storage moisture content – e.g. to the band between about 7-10% to 20% moisture content – (and within this range of air-dry seed storage moisture contents longevity improves with reduction in seed storage moisture content) but they are damaged by desiccation to moisture contents below this band. The evidence of a third category of seed storage behaviour began to accumulate once it was recognized that the two categories of seed storage behaviour identified by Roberts (Roberts, 1973) did not account satisfactorily for all observations on seed storage behaviour. For example, in an extensive programme of research on *Araucaria* spp. Tompsett (Tompsett, 1984a) concluded that, in addition to orthodox and recalcitrant species, the "New Caledonian species (*A. columnaris, A. nemorosa, A. scopulorum*, and *A. rulei*) would appear to be more difficult to categorize, since they can be dried with safety to about 12% moisture content only; on further desiccation to near 7% moisture content, half their germination is lost". Accordingly, Farrant *et al.* (Farrant *et al.*, 1988) indicated that seeds of *Araucaria columnaris*, *Citrus* spp., and *Coffea arabica* should be viewed as intermediate between recalcitrant and orthodox species. Similarly, Hofmann and Steiner (Hofmann & Steiner, 1989) noted a group of species which show some of the characteristics of both orthodox and recalcitrant seeds, such as *Bixa orellana* and arabica coffee.

Thus, species can be classified into three main categories of seed storage behaviour: orthodox, recalcitrant and intermediate. In order to accommodate the subgroups defined by Farrant *et al.* (Farrant *et al.*, 1988) and Bonner (Bonner, 1990), Hong and Ellis (Hong & Ellis, 1995) (Hong & Ellis, 1996) have divided the latter two categories of seed storage behaviour (recalcitrant and intermediate) as follows: recalcitrant of tropical origin, recalcitrant of temperate origin; intermediate of tropical origin, intermediate of temperate origin. The categories "true orthodox", "temperate recalcitrant", and "tropical recalcitrant" defined by Bonner (Bonner, 1990) are similar to "orthodox", "recalcitrant of temperate origin", and "recalcitrant of tropical origin", respectively in this handbook. However, certain "suborthodox" species defined by Bonner (Bonner, 1990) are classified here as "orthodox" (e.g. *Populus* spp., *Salix* spp.) or "intermediate" (e.g. certain *Citrus* spp.) in our system of classification, depending upon the ability to tolerate desiccation to low (?5%) moisture contents. It is possible that certain species in the "minimally recalcitrant" category defined by Farrant *et al.* (Farrant *et al.*, 1988) may show intermediate seed storage behaviour as defined here.

Figure 1 summarizes an experimental protocol to distinguish between orthodox, recalcitrant and intermediate seed storage behaviour provided by Hong and Ellis (Hong & Ellis, 1996).

The following sections attempt to summarize progress in seed physiology in relation to seed storage for genetic conservation in the past two decades or so, and provide definitions of and further details on the categories of seed storage behaviour outlined above.

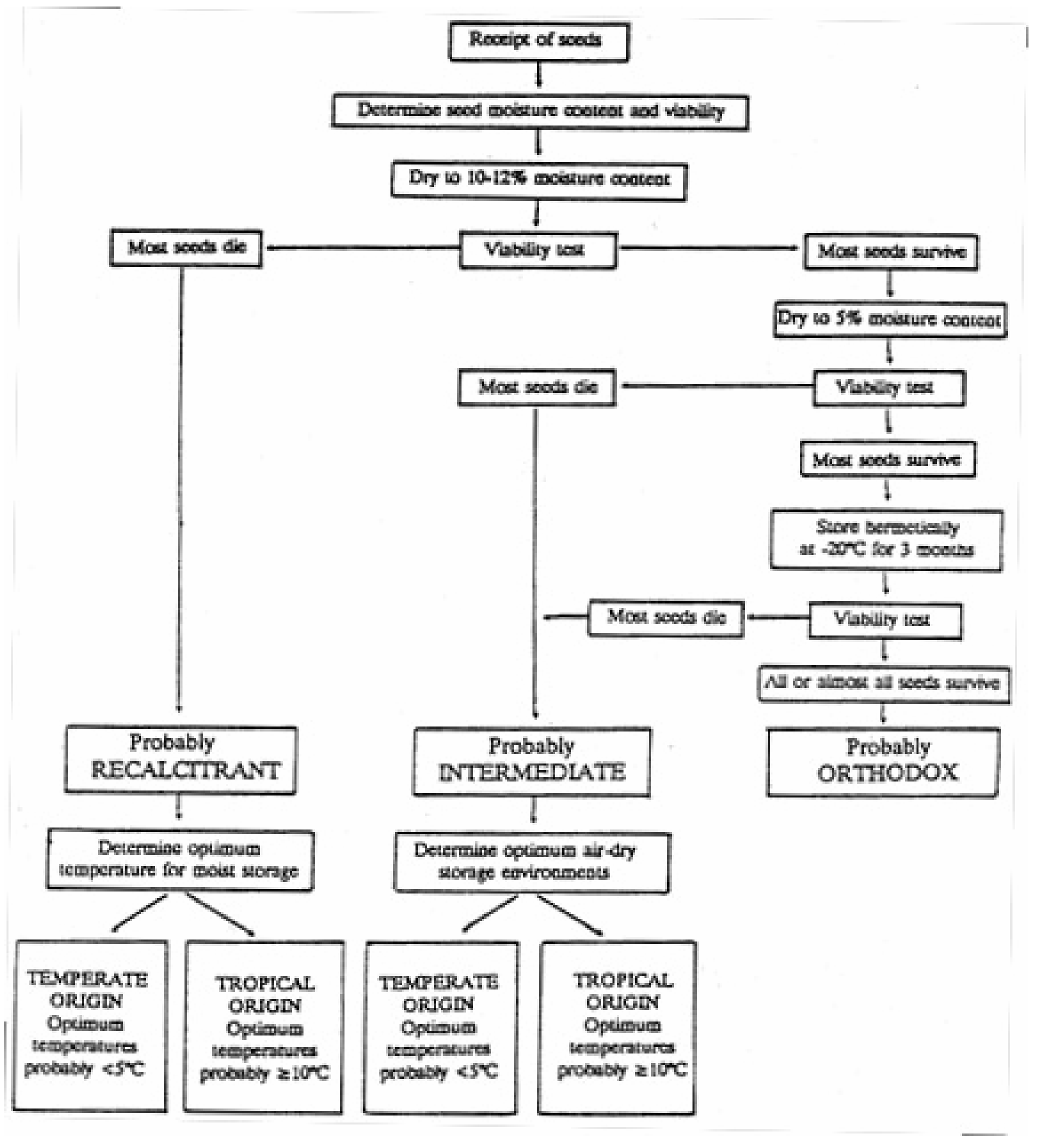

Fig. 1. Simplified outline of a protocol to determine seed storage behaviour. From (Hong & Ellis, 1996).

3. Characteristics of orthodox seeds

3.1 Definition

Orthodox seeds can be dried without damage to low moisture content and, over a wide range of environments, their longevity increases with decreases in seed storage moisture content and temperature in a quantifiable and predictable way (Roberts, 1973). The latter is defined by the improved seed viability equation (Ellis & Roberts, 1980a). In essence, in order for seed storage behaviour to be defined as orthodox, two conditions must be satisfied:

Mature seeds survive desiccation to low moisture contents, at least to 2-6% (w.b.) depending on the species. Above this value (but within the air-dry range) there is a negative logarithmic relation between seed moisture content and longevity (Ellis & Roberts, 1980a), (Ellis & Roberts, 1980b); (Ellis, 1988).

With regard to the effect of temperature on longevity, there is a negative relation between temperature (at least between –20 and 90°C) and seed longevity at a constant moisture content (Roberts, 1973). The precise form of this relation is a negative semilogarithmic relation modified by a quadratic term such that the relative benefit to longevity of a reduction in temperature declines the cooler the temperature (Ellis & Roberts, 1980a); (Ellis, 1988); (Dickie *et al*., 1990).

3.2 Viability equations

Relations between (orthodox) seed survival and storage duration, temperature and moisture content have been quantified by the equation

$$v = K_i - p \;/\; 10^{K_E - C_W \log_{10} m - C_H t - C_Q t^2} \qquad (1)$$

where *v* is probit percentage viability after *p* days in storage at m% moisture content (w.b.) and t°C temperature, K_i is a constant specific to the seed lot, and K_E, C_W, C_H and C_Q are species viability constants (Ellis & Roberts, 1980a). The power term of equation (1) is ?, the standard deviation of life spans of individual seeds in a population, under the storage conditions indicated (Ellis & Roberts, 1980a), so that:

$$\log_{10} ? = K_E - C_W \log_{10} m - C_H t - C_Q t^2 \qquad (2)$$

Equation (1) can therefore be rewritten:

$$v = K_i - p / ? \qquad (3)$$

where ? is a measure of the longevity of seeds, since it is the period in days during which percentage viability is reduced by one probit; e.g. from 84.1 to 50% viability. These equations describe the (considerable) extent to which the period of survival of orthodox seeds can be manipulated by altering the environment in which they are stored, and the constants and coefficients therein reflect the effects of key variables in successful seed genebank operation.

The constant K_i is the seed lot constant. The value of this constant indicates the initial quality of the seed accession when placed in the store. The frequency distribution of the life spans of seeds stored in constant environments (i.e. at a constant moisture content and storage temperature) is normal (Roberts, 1972b). As a consequence, the seed survival curve (percentage germination plotted against time) is a sigmoid curve of distinct form, a cumulative normal distribution of negative slope (Fig. 2a). A convenient way of dealing with data which fit a cumulative normal distribution is to plot percentage germination on a probability scale against time, which results in a straight line (Fig. 2b). The intercept of this line at zero time (i.e. just before storage, because from equation (3) when p = 0, K_i = v) is the value of

K_i. K_i is thus an indicator of "potential longevity". The higher the value the better the quality of the seed lot. K_i can be accurately determined from a rapid ageing test in constant conditions (e.g. hermetic storage at 40°C with seeds at 15% moisture content, sampling twice a week for a total duration of 20-40 days, depending on species and initial germination percentage, in order to obtain a complete survival curve), or estimated very roughly from a single large-scale germination test by transforming percentage initial viability to the equivalent probit value (e.g. using the nomograph described by (Ellis, 1984a)).

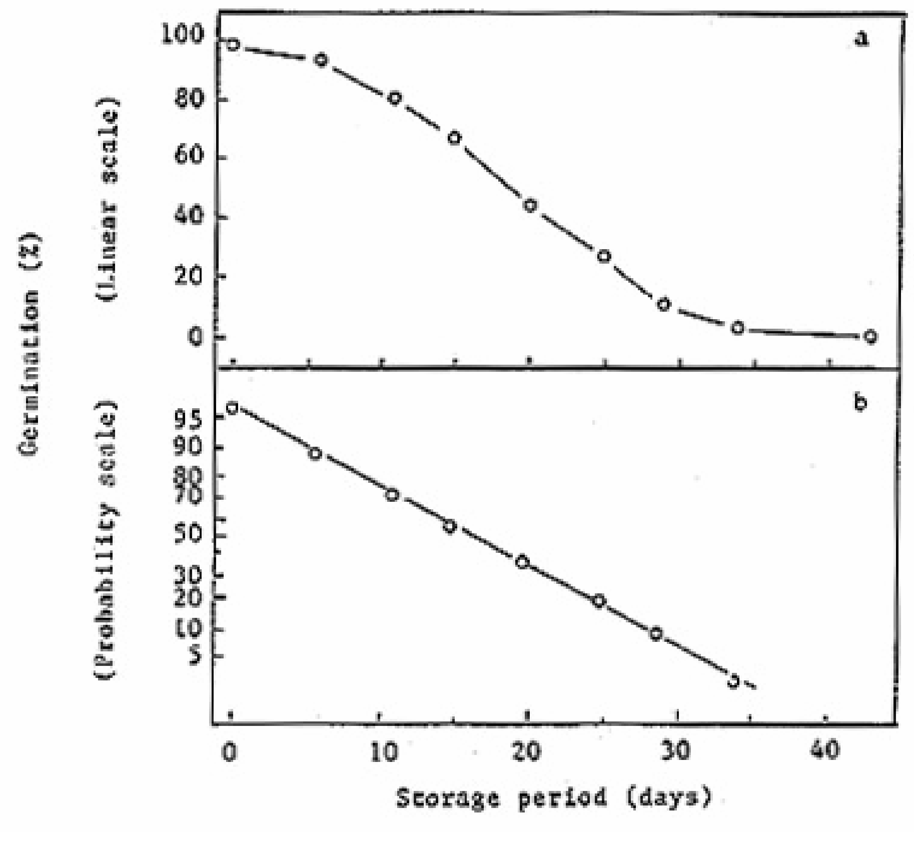

Fig. 2. The results of serial germination tests (o) of seeds of finger millet (*Eleusine coracana*) plotted against the period of hermetic storage at 40°C with 15% moisture content show the typical sigmoidal pattern of seed survival curves (a). When the percentage germination is plotted on the probability scale, the cumulative negative normal distribution results in a straight line (b). Data from (Ellis, 1984a).

The combined effects of the constants C_H and C_Q describe the response of seed longevity to temperature. A comparison of contrasting species found that the values of the temperature terms C_H and C_Q did not differ significantly among species (Dickie *et al.*, 1990). This suggests that the seed longevity of all orthodox species may well show a similar quantitative response to storage temperature. The best estimate available to date for this response is provided by the following values: $C_H = 0.0329$ and $C_Q = 0.000478$.

The constant K_E denotes the extrapolated value of $\log_{10}?$ at 1% moisture content (because $\log_{10}1 = 0$) and 0°C (though this does not imply that seeds can or should be stored at 1% moisture content; this value is below the range of moisture content over which the equation applies, as is explained later on).

The gradient of the negative logarithmic relation between seed moisture content (m) and longevity (?) provides the value of C_W. This value describes the relative effect of moisture content on longevity. Although invariant within a species, the value of C_w differs considerably between species. In cereals C_w has a high value (close to 6), but in oily seeds the value of this constant is much lower (e.g. between 3.5 and 4 for onion (*Allium cepa*) and soyabean (*Glycine max*)). Tree species tend to have lower values for C_w, for example 0.98 for *Pinus elliottii* (Bonner, 1994), 2.15 for *Terminalia brassii* (Tompsett, 1986b) and 4.23 for Norway maple (*Acer platanoides*) (Dickie *et al*., 1991) with a mean value of 2.8 for forest tree species compared with the mean value of 4.72 for herbaceous species (Tompsett, 1994). This means that to obtain the same relative increase in longevity it is necessary to dry oily seeds more than starchy seeds from a given moisture content. This also has implications for the relative advantage of ultra-dry seed storage (to be discussed later) for species with oily seeds compared with those with starchy seeds.

The great differences in the values of C_w among orthodox species appear to result from differences in seed composition and, hence, differences in equilibrium relative humidity, and thus in seed water potential, at the same moisture content (Roberts & Ellis, 1989).

Therefore, a tentative development of the viability equation based on water potential or equilibrium relative humidity was proposed by Roberts and Ellis (Roberts & Ellis, 1989)

$$\log_{10} ? = K_E - C_M\, r - C_H t - C_Q t^2 \qquad (4)$$

where r is equilibrium relative humidity (%), t is temperature (°C), and K_E, C_M, C_H and C_Q are constants (with values different from those of equations (1) or (2)). Once equilibrium relative humidity is used in place of seed moisture content, C_M values become invariant, at least for the 23 species of the different families investigated so far (Roberts & Ellis, 1989); (Ellis et al., 1988), (Ellis et al., 1989), (Ellis et al., 1990b), (Ellis et al., 1990d). That value, $C_M = 0.0346$, is equivalent to a doubling of longevity for each 8.7% reduction in equilibrium relative humidity, or an increase in longevity by a factor of 2.22 for each 10% reduction in equilibrium relative humidity (Ellis et al., 1990d); (Zanakis *et al*., 1993).

Differences among species in absolute seed longevity at the same temperature and moisture content also appear to be largely the result of differences in seed water potential brought about by differences in seed composition. For example, seed longevity in the cereal tef (*Eragrostis tef*) was 11- to 12-fold greater than that of the oilseed niger (*Guizotia abyssinica*) when both were stored at the same temperature and similar moisture contents, but longevity in niger was no less than that of tef when they were stored at the same temperature and similar equilibrium relative humidities (Zewdie & Ellis, 1991a).

3.3 Limits to the viability equations

There are two limits to the negative logarithmic relation between seed moisture content and seed longevity (Roberts & Ellis, 1989): an upper limit, beyond which seed longevity in hermetic storage is no longer reduced with further increases in moisture, and beyond which seed longevity in aerated storage increases with further increase in moisture content (Roberts & Ellis, 1982); and a lower limit below which further reduction in moisture content no longer increases longevity in hermetic storage ((Ellis et al., 1988), (Ellis et al., 1989), (Ellis et al., 1990b), (Ellis et al., 1990d), (Ellis et al., 1992). Figure 3 shows the contiguous relations between seed longevity and moisture content over a very wide range of moisture contents, from very dry to very wet seeds of lettuce (*Lactuca sativa*).

The upper moisture content limit is about 15% in lettuce (Ibrahim & Roberts, 1983), about 18% in onion (Ellis & Roberts, 1977), 22% in elm (*Ulmus carpinifolia*) (Tompsett, 1986b), 22% in niger (Zewdie & Ellis, 1991c), 24-28% in tef (Zewdie & Ellis, 1991c), and about 26% in durum wheat (*Triticum durum*) (Petruzzelli, 1986). Despite wide variation among species in terms of moisture content, these values coincide with a seed water potential of about –14 MPa (Roberts & Ellis, 1989); (Zewdie & Ellis, 1991c), i.e. the upper moisture content limit to the viability equation occurs at seed moisture content levels in equilibrium with about 90% r.h. at 20°C.

The lower moisture content limit to the seed viability equation is more difficult to determine. This is because the longevity of very dry seeds is considerable. Consequently, much of this research has been carried out at high temperatures. Results from hermetic storage at 65°C have shown that the lower moisture content limit to the seed viability equation at this temperature varies substantially between species, e.g. about 6% for pea (*Pisum sativum*) and mung bean (*Vigna radiata*), 4.5% for rice (*Oryza sativa*) and tef, 2% for sunflower (*Helianthus annuus*) (Ellis et al., 1988), (Ellis et al., 1989), (Ellis et al., 1992). However, these variant levels of moisture content coincide with 10-12% equilibrium relative humidity at 20°C (Ellis et al., 1988), (Ellis et al., 1989), (Ellis et al., 1992), this being the temperature at which seeds were dried and then sealed into the hermetic containers, or with a seed water potential of about –350 MPa at this seed-drying and packaging temperature (Roberts & Ellis, 1989). This lower moisture content limit is close to the value to which genebanks were previously recommended to dry seed accessions to (e.g. (Cromarty *et al.*, 1982) recommended a drying regime of 10-15% relative humidity at 15°C).

However, the lower moisture content limit to the seed viability equation may vary with temperature (Ellis et al., 1989); (Vertucci & Roos, 1990), not least because the equilibrium relative humidity of seeds at a given moisture content varies with temperature, see (Cromarty *et al.*, 1982). Accordingly, there is some uncertainty concerning the lowest moisture content to which seeds should first be dried in order to maximize longevity in hermetic storage at cool temperatures (see 3.8).

3.4 Longevity of moist orthodox seeds

Above the upper moisture content limit to the application of the viability equation in orthodox seeds, the trend of seed longevity in relation to moisture is reversed in aerated storage whereby longevity increases with further increase in moisture content (Fig. 3) (Roberts & Ellis, 1982), (Roberts & Ellis, 1989); (Ibrahim *et al.*, 1983). When orthodox seeds are fully hydrated, they tend to germinate, but if this can be prevented by maintaining the seeds in a dormant condition they can often remain viable for many years (Villiers, 1974), (Villiers, 1975). Barton (Barton, 1961b) reported that 25 and 37% of seeds of *Amaranthus retroflexus* and *Rumex obtusifolius* which were stored on moist glass wool at constant temperatures of 20 and 30°C, respectively, germinated during moist storage over a period of 8 years, while the remaining seeds were viable and germinated when transferred to suitable environments. It has also been known that many orthodox seeds can survive many years or decades in the soil (soil seedbank) under conditions where they must be fully or intermittently hydrated for much of the time (Roberts & Ellis, 1982). Aerobic conditions are essential for the successful moist storage of orthodox seeds (Roberts & Ellis, 1989). The longevity of moist seeds will be maximal if the supply of oxygen is unhindered and the seeds are kept fully or almost fully imbibed. In contrast, seeds stored at moisture contents close to the upper moisture content limit of the seed viability equation will show the maximum rate of deterioration at a given temperature.

3.5 Freezing injury in cold storage of orthodox seeds

In general, free water in seeds is frozen at subzero temperatures and death of the seed occurs because of ice crystallization. For example, soyabean seeds at 26% moisture content will be killed when exposed to –65°C, but seeds at 20% moisture content will survive at least a brief exposure to this temperature (Leopold & Vertucci, 1989).

In some circumstances, seeds at comparatively high moisture contents can withstand lower temperatures without freezing injury. For this to occur the water in the cell has to vitrify, instead of crystallizing. This is why it has been possible for lettuce seed rapidly cooled at 18% moisture content in liquid nitrogen (–196°C) and then stored for 30 days at this temperature to survive without injury, whereas seeds at 16% moisture content cooled at a slower rate to –70°C showed low viability (Roos

& Stanwood, 1981). The rate of cooling (Roos & Stanwood, 1981), the addition of cryoprotectant and the presence of trehalose might contribute to the formation of the glassy (vitrified) state in seeds (Williams & Leopold, 1989).

In theory, the water present within seeds would not be expected to freeze when they are cooled to –20°C if seed moisture content is in equilibrium with <85% r.h. (Roberts & Ellis, 1989). In practice, small losses in viability have sometimes been detected in orthodox seeds in equilibrium with 70% r.h., and consequently it has been suggested that it would be prudent to first dry seeds at 20°C until moisture contents have been reduced to values in equilibrium with ?65% relative humidity before beginning hermetic storage at –20°C in order to avoid any possibility of freezing damage (Zewdie & Ellis, 1991b). Safe seed moisture contents (i.e. those at which freezing damage is avoided) for storage at –20°C are about 12.5-13.5% for cereals but lower moisture contents are necessary for species with oily seeds.

Orthodox seeds have been stored in liquid nitrogen (–196°C). However, cryopreservation in liquid nitrogen is not always an easy method of seed storage, particularly in developing countries. First, optimum (safe) moisture content levels must be determined for each orthodox species, particularly those with oily seeds. In general, 5-18% moisture content is said to be safe for liquid nitrogen storage (Stanwood & Roos, 1979). Pretreatment with cryoprotectants sometimes improves survival in liquid nitrogen, but in some circumstances can be damaging (Touchell & Dixon, 1993). Wang *et al.* (Wang et al., 1994) collated information on the cryopreservation of orthodox tree seeds, which suggests that moisture content levels between 3.8 and 11% are safe for at least short periods of time (4 days to 3 years). However, in other studies storage at low levels of moisture content (2-8%) showed considerable damage by reducing seed viability and by increasing abnormal germination (Sakai & Noshiro, 1975); (Stanwood & Bass, 1981); (Stanwood, 1987); (Vertucci, 1989); (Zewdie & Ellis, 1991b). A loss in viability of about 10% following 14 days of storage in liquid nitrogen at 6-8% moisture content was reported in certain tree seeds (Wang *et al.*, 1994). One possible cause of problems with liquid nitrogen storage is the requirement to optimize the rate of cooling and warming (thawing). This must be determined empirically (Meryman & Williams, 1981). But even when this is done, legume seeds nevertheless tend to be damaged by cryopreservation (Saunders, 1981); (Boyce, 1987); (Pritchard *et al.*, 1988). Furthermore, despite suggestions of infinite seed longevity by cryostorage in liquid nitrogen, Tompsett (Tompsett, 1986b) found similar longevity for *Ulmus carpinifolia* seed stored at –13 and –75°C, and has questioned whether reducing seed storage temperatures much below –13°C does result further significant benefits to longevity (Tompsett, 1994). Accordingly, we do not consider the cryopreservation of orthodox seeds further here. Our main concern is the identification of those species in which hermetic storage at –18°C at low moisture content is feasible; i.e., the identification of those species whose seeds can be stored successfully for considerable periods under the IPGRI preferred conditions for long-term seed storage.

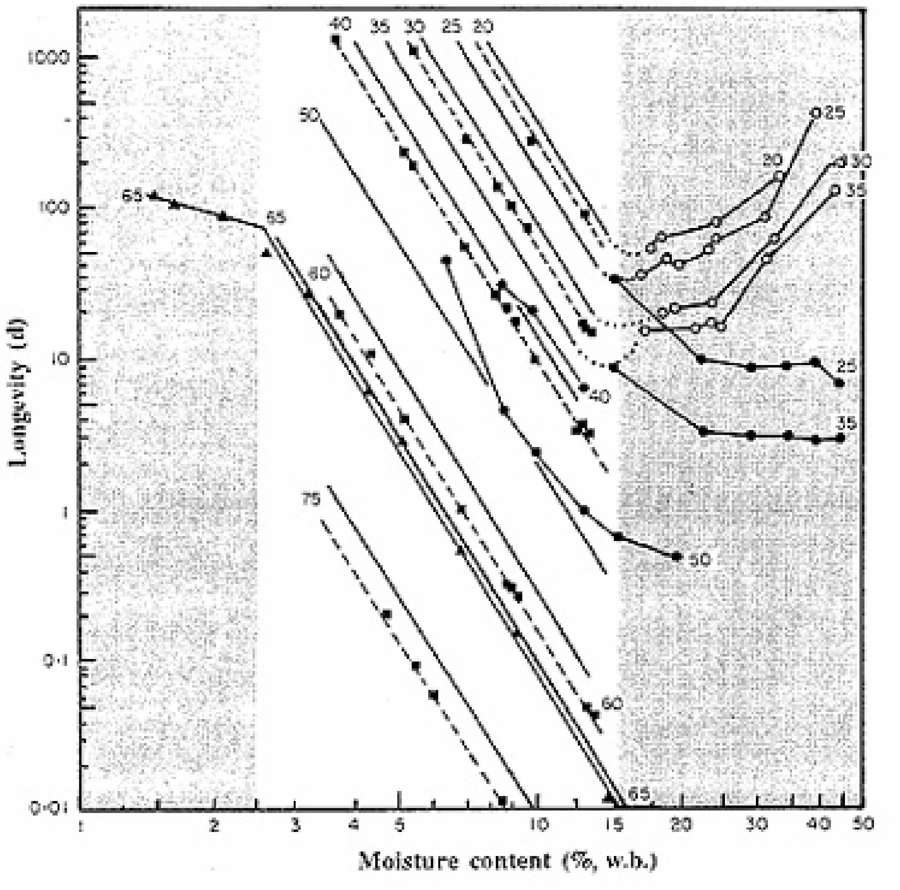

Fig. 3. The relationship between moisture content, temperature and seed longevity (p_{50}, half-viability period) in lettuce. The central unshaded region shows the range of seed moisture contents where the viability equation (1) applies. The shaded region on the left is where change in moisture has little effect; the shaded region on the right is where longevity improves with increase in moisture content in the presence of oxygen. Different symbols refer to results from different investigations: squares (Wageningen), other symbols (Reading); open circles (with air), closed circles (with nitrogen). Although the boundaries to the application of the viability equation are shown as vertical, there is only direct evidence for this for the upper moisture content boundary. From (Roberts & Ellis, 1989).

3.6 Imbibition injury

Water can also influence orthodox seed survival during imbibition: the rapid uptake of water by dry seeds can result in imbibition injury (Powell & Matthews, 1978). Although the phenomenon is particularly pronounced if seeds are immersed (soaked) in water, it can also occur in standard laboratory germination tests (Ellis et al., 1982), (Ellis et al., 1990c). Seeds are more likely to be damaged, the lower their initial moisture content (Ellis et al., 1990c) and the cooler the temperature (Pollock, 1969); (Powell & Matthews, 1978). Imbibition injury is pronounced in Leguminosae and Malvaceae (Ellis et al., 1985b), but it is now clear that the problem can also occur in other species. For example, imbibition injury was reported in *Populus alba*, particularly in seeds at less than 8% moisture content (Polya, 1961). Imbibition injury can be avoided by conditioning (humidifying) the seeds in a moist atmosphere (close to 100% r.h.) in order to raise seed moisture contents to 16-18% before the seeds are set to germinate in contact with liquid water (Ellis et al., 1985a). This conditioning takes about 24 hours or more depending on initial moisture content (Ellis et al., 1990c) and species (Ellis, 1987). It is suggested that seeds at 8%

moisture content and below, irrespective of species, should routinely either be humidified before germination tests or germinated on 1% water agar, a technique used by the Kew Seed Bank.

3.7 Seed development, desiccation tolerance and the potential longevity of orthodox seeds

There is now considerable evidence that developing and maturing orthodox seeds do not attain maximum potential longevity until some time after the end of the seed-filling phase (Kameswara Rao *et al*., 1991); (Ellis & Pieta Filho, 1992); (Demir & Ellis, 1992a), (Demir & Ellis, 1992b); (Zanakis *et al*., 1994); (Ellis et al., 1993a). Provided seeds have reached the stage in development at which potential longevity is maximal then desiccation tolerance to low moisture contents (below 5%) will also be maximal (Ellis & Hong, 1994).

3.8 Ultra-dry seed storage

As a consequence of the research at high temperatures to determine the low moisture content limit to the seed viability equation (see 3.3), it was suggested that the maximum longevity of orthodox seeds can be achieved if seeds are dried to moisture content in equilibrium with 10-12% relative humidity at 20°C and subsequently stored, preferably at –18°C, hermetically at this moisture content (Ellis et al., 1989). The effect of desiccation to very low moisture contents was first examined carefully in sesame (*Sesamum indicum*) seed stored hermetically at 50°C, in which it was shown that reducing the seed moisture content from 5 to 2% increased longevity 40-fold; this effect on longevity in sesame is equivalent to that of reducing the storage temperature from +20 to –20°C (Ellis et al., 1986). As a consequence, it was proposed that in order to provide maximum longevity of orthodox seeds in genebanks where refrigeration to –18°C cannot be provided, seeds should be dried to moisture contents in equilibrium with 10-12% r.h. at 20°C and subsequently be stored hermetically at ambient or (preferably) cooler temperatures (Ellis et al., 1989). This low-technology approach to genebanking has been described by some as “ultra-dry” seed storage (IBPGR, 1992).

This proposal was questioned by Vertucci and Roos (Vertucci & Roos, 1990). They published evidence and theoretical arguments to suggest that ultra-dry seed storage could be dangerous, and proposed that moisture content levels in equilibrium with 19-27% r.h. are optimal for seed longevity. The main experimental results they presented initially were results of vigour (not longevity) of seeds of five orthodox species after 2 or 3 months of storage at 35°C (Vertucci & Roos, 1990).

Both groups of researchers have since published further results and arguments in support of their respective views: ultra-dry seed storage is either viewed as potentially damaging (Vertucci & Roos, 1991), (Vertucci & Roos, 1993a), (Vertucci & Roos, 1993b); (Vertucci *et al.*, 1994a), or a useful approach in circumstances where refrigeration is unavailable (Ellis *et al.*, 1991c), (Ellis *et al.*, 1993b), (Ellis *et al.*, 1995), (Ellis *et al.*, 1996). There are also a few publications on ultra-dry seed storage which are independent of these two research groups (Cheng *et al.*, 1990); (Smith, 1992); (Steiner & Ruckenbauer, 1995) to which the reader is also referred. The discussions in all these papers emphasise that we do not know the most suitable moisture content(s) for seed storage (i.e. that at which longevity is maximal) at cool temperatures, or the extent to which these values might vary with temperature. Nevertheless experience shows that the longevity of orthodox seeds stored under IBPGR preferred conditions for long-term storage is considerable. Evidence is also beginning to emerge that the ultra-dry storage of cereals (at least) at ambient temperatures results in considerable longevity: Steiner and Ruckenbauer (Steiner & Ruckenbauer, 1995) reported 90% germination of barley (*Hordeum vulgare*) seeds after 110 years of ultra-dry storage at 10-15°C.

3.9 Factors influencing desiccation tolerance in orthodox seeds

Desiccation tolerance to very low levels of moisture content, at least to those in equilibrium with about 10-12% r.h., is one of several criteria which enable species with orthodox seed storage behaviour to be identified. Disregarding factors which influence desiccation tolerance could therefore result in the mistaken classification of seed storage behaviour.

3.9.1 Effect of maturation drying

Orthodox seeds do not tolerate desiccation at all stages of their development and maturation. For example, the change from desiccation intolerance to desiccation tolerance has been reported to occur about halfway through seed development in *Phaseolus vulgaris* (Dasgupta *et al.*, 1982) and *Sinapis alba* (Fischer *et al.*, 1988). In six grain legumes, the onset of desiccation tolerance to about 10% moisture content occurred when maturation drying had reduced seed moisture content on the mother plant to about 60% (Ellis et al., 1987); this coincided more or less with the end of the seed-filling phase, defined as physiological maturity by Shaw and Loomis (Shaw & Loomis, 1950), but now termed mass maturity (Ellis & Pieta Filho, 1992).

Immature seeds of Norway maple (a species which shows orthodox seed storage behaviour) harvested at 68% moisture content, i.e. before mass maturity, are damaged by desiccation, particularly below 20% moisture content (Fig. 4). Seeds harvested at mass maturity (54% moisture content, 24 September) tolerated desiccation to 12-15% moisture content, but further desiccation reduced viability. The developing seeds did not attain desiccation tolerance to very low moisture content (3%) until 3-4 weeks after mass maturity (31 October) when maturation drying had reduced seed moisture content on the mother plant to about 27-30% (Hong & Ellis, 1990), (Hong & Ellis, 1992a). Similarly, the achievement of maximum desiccation tolerance to low (4%) moisture content in a japonica rice (*Oryza sativa*) did not occur until some 2-3 weeks after mass maturity, when maturation drying on the mother plant had naturally reduced seed moisture content to levels below 32% (Ellis & Hong, 1994).

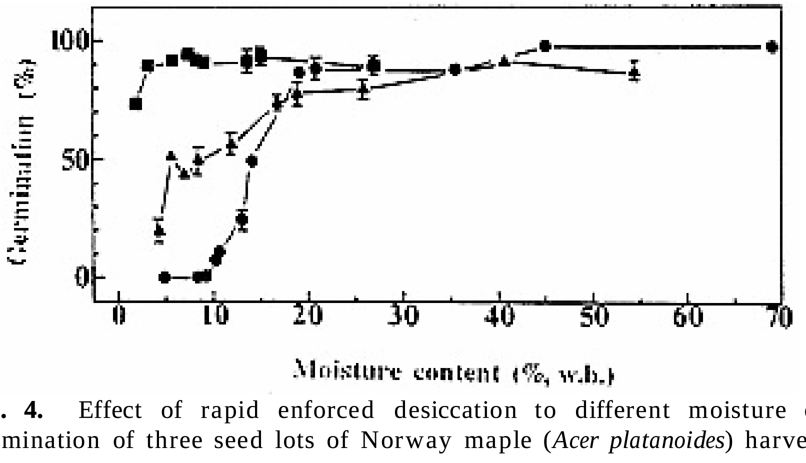

Fig. 4. Effect of rapid enforced desiccation to different moisture contents on the germination of three seed lots of Norway maple (*Acer platanoides*) harvested at different stages of development in 1991. Seeds were harvested on 3 September (†), 24 September (?) and 31 October (†). From (Hong & Ellis, 1992a).

These instances, however, should not be regarded as a generalization. The development of ability to tolerate desiccation to very low moisture content may occur at different developmental stages in different species, and may also be influenced by the seed-production environment. One important difference among species may be that of seed moisture content at seed or fruit shedding or harvest maturity. For example, seeds of the tomato (*Lycopersicon esculentum*) and sweet pepper (*Capsicum annuum*), both of which show orthodox seed storage behaviour, attain desiccation tolerance when seed moisture is reduced naturally during maturation drying to 52-55%; their fruits are ripe when seed moisture content is about 42-48% (Demir & Ellis, 1992a), (Demir & Ellis, 1992b). An example where an effect of seed production environment on the development of desiccation tolerance to low moisture contents has been detected is rice (Ellis & Hong, 1994); seeds of a *japonica* rice produced in a cool environment of 28/20°C (day/night temperatures) showed consistently greater desiccation tolerance at each stage of maturation drying than those produced at 32/24°C.

3.9.2 Desiccation sensitivity of germinating orthodox seeds

It is widely believed that once orthodox seeds begin to germinate, they then begin to lose desiccation tolerance and become more sensitive to desiccation if germination is allowed to progress (Nemmer & Luyet, 1954); (Sun, 1958); (Akalehiywot & Bewley, 1980); (McKersie & Stinson, 1980); (McKersie & Tomes, 1980); (Dasgupta *et al.*, 1982); (Senaratna & McKersie, 1983); (Koster & Leopold, 1988). However, it is also important to note that both desiccation tolerance to very low moisture contents and potential longevity can be reduced by short-duration imbibition treatments, including sometimes those which do not result in visible germination (i.e. radicle emergence) (Hong & Ellis, 1992b).

3.9.3 Reduction of desiccation tolerance by seed treatments

From the evidence presented above, there is some possibility that any treatment to seeds involving high seed moisture content before storage may reduce desiccation tolerance. Presoaking, even for as few as 3 hours, has deleterious effects on the ultrastructure of rye (*Secale cereale*) embryos when dehydrated to their initial moisture content (Sargent *et al.*, 1981). Similarly, mung bean which had been imbibed for 8 hours lost 5% viability when dried back to between 4.3 and 6.4% moisture content, despite no seeds germinating during this imbibition treatment (Hong & Ellis, 1992b).

Cold moist storage (stratification) methods have commonly been practised as a method for short-term storage when dealing with very dormant seeds of trees and shrubs. For example, the benefit of moist storage at low temperatures of 3-5°C for orthodox seeds of temperate species (e.g. *Fagus*, *Fraxinus*, *Liriodendron*, *Magnolia*, *Prunus*) (Schopmeyer, 1974a); (Young & Young, 1992) is that the seeds are ready to germinate immediately after storage, while seeds stored air-dry require a long duration of prechilling before germination will occur. There have been several reports that reduction in desiccation tolerance and subsequent longevity results from drying orthodox seeds which have been stored in a moist condition. Haut (Haut, 1932) reported a deleterious effect of drying after a prechill treatment on the germination of *Prunus* seeds, whereas drying before prechilling was not deleterious. Seeds of beech (*Fagus sylvatica*) were less tolerant of desiccation if first prechilled than those which had not been prechilled (Muller & Bonnet-Masimbert, 1989). Similarly, seeds of barley stored moist at 15°C for 14 days lost 20% viability when dried to 3.6% moisture content (Hong & Ellis, 1992b).

Seed priming (also known as osmotic priming, and osmo-conditioning), which aims to promote faster, more uniform seedling emergence (Heydecker, 1977) and may also prolong longevity in certain species at least (Probert *et al.*, 1991), can also reduce desiccation tolerance when seeds are dried to low moisture content. For example, Carpenter and Boucher (Carpenter & Boucher, 1991) reported that reducing the moisture content of unprimed seed of the orthodox pansy (*Viola* x *wittrockiana*) from 10.5 to 5.8% caused no damage to germination. On the contrary, germination of primed seed was decreased when dried to moisture content levels below 10%, and even more so when dried to 5.8% moisture content.

The intermittent hydration-drying method, which is commonly believed to prolong the longevity of orthodox seeds (Basu & Pal, 1980), can result in loss in viability rather than its maintenance (Giorgis, 1993).

This summary shows that pretreatments to seeds which involve exposure to high seed moisture contents run the risk of reducing desiccation tolerance and subsequent longevity. It is suggested, therefore, that for long-term storage, i.e. at low moisture contents and cool temperatures, dormancy-breaking and priming treatments should not be used before storage unless they have been proven not to damage desiccation tolerance to low moisture contents and subsequent longevity.

4. Characteristics of recalcitrant seeds

Recalcitrant seeds cannot be dried without damage and so they cannot conform to the viability equation which describes relations between longevity and air-dry seed storage environments (Roberts, 1973). When fresh recalcitrant seeds begin to dry, viability is first slightly reduced as moisture is lost, but then begins to decline considerably at a certain moisture content termed the "critical moisture content" (King & Roberts, 1979), (King & Roberts, 1980a) or "lowest safe moisture content" (Tompsett, 1984b). If drying continues further, viability is eventually reduced to zero. Hence, the relationship between ability to germinate when tested following desiccation (and rehydration) and moisture content is typically S-shaped (Fig. 5). If germination percentage is plotted on a probability scale, such curves may become linear (Tompsett, 1986a); (Probert & Longley, 1989); (Pritchard, 1991); (Finch-Savage, 1992b).

Critical levels of moisture content vary greatly among species (King & Roberts, 1979); (Chin, 1988), and even among cultivars and seed lots (King & Roberts, 1979); (Chin, 1988). They may also vary with method of drying (Farrant *et al*., 1985); (Pritchard & Prendergast, 1986); (Pritchard, 1991). The values of the "lowest safe moisture content" vary between extremes of 23% for cocoa (*Theobroma cacao*) (Mumford & Brett, 1982) and 61.5% for *Avicennia marina* (Farrant *et al*., 1986). Despite great variation in the lowest safe moisture content value among species, these moisture contents are equivalent to relative humidities of 96-98%, or a seed water potential of about –1.5 to -5 MPa (Roberts & Ellis, 1989); (Probert & Longley, 1989); (Pritchard, 1991); (Dickie *et al*., 1991); (Poulsen & Eriksen, 1992); (Tompsett & Pritchard, 1993), but note that Vertucci and Farrant (Vertucci & Farrant, 1995) have recently suggested a rather drier value of –11 MPa.

4.1 Factors influencing desiccation sensitivity in recalcitrant seeds

4.1.1 Maturation drying and desiccation tolerance

Desiccation tolerance in recalcitrant seeds increases during seed development on the mother plant (Fig. 5); however, unlike orthodox seeds, maturation drying to low moisture contents does not occur (Hong & Ellis, 1990); (Finch-Savage, 1992a); (Berjak *et al*., 1993), and fresh recalcitrant seeds have high levels of moisture content at maturity/shedding, between for example 36% for rubber (*Hevea brasiliensis*) (Chin *et al*., 1981) and 90% for choyote (*Sechium edule*) (Ellis, 1991).

4.1.2 Desiccation tolerance of excised embryos

Considerable differences in moisture content can be detected among tissues within a particular recalcitrant seed. For example, Grabe (Grabe, 1989) reported that, with the exception of durian (*Durio zibethinus*) and jackfruit (*Artocarpus heterophyllus*), storage tissues of recalcitrant seeds are always at a lower moisture content than the embryonic axis. Desiccation of excised embryos or embryonic axes has considerable practical potential for *in vitro* conservation of recalcitrant embryos, since embryos are able to survive desiccation to lower moisture contents than whole seeds (Chin, 1988). For example, fresh seeds (36% mc) of *Hevea brasiliensis* tolerated desiccation to 20% mc but no seeds survived further desiccation to 15% mc (Chin *et al*., 1981). However, 50-80% of their excised embryos (55% mc) survived desiccation to 14% moisture content when cultured *in vitro* (Normah *et al*., 1986). Reports of the survival of excised embryonic axes following exposure to a lower moisture content than that which the intact seeds can tolerate are several, e.g. (Finch-Savage, 1992b); (Chandel *et al*., 1995).

4.1.3 Effect of methods of drying

While there are several reports that fast drying allows intact recalcitrant seeds to survive desiccation to lower moisture contents than slow drying (Farrant *et al*., 1985); (Pritchard, 1991), Finch-Savage (Finch-Savage, 1992b) showed that drying rate does not affect the desiccation sensitivity of whole seeds of *Quercus robur*. However, fast drying allowed excised embryos of *Araucaria hunsteinii*, *Hevea brasiliensis*, *Landolphia kirkii*, *Quercus robur* and *Quercus rubra* to survive desiccation to lower moisture contents than similar embryos dried more slowly within intact seeds (Normah *et al.*, 1986); (Pritchard & Prendergast, 1986); (Pritchard, 1991); (Pammenter *et al.*, 1991); (Finch-Savage, 1992b). Fu *et al.* (Fu *et al.*, 1993) reported that drying excised embryonic axes by silica gel or an aseptic air current allowed excised embryonic axes to survive desiccation to a lower value than that achieved by the vacuum method. For example, although the vacuum drying method provided more rapid drying, no excised embyonic axes of *Artocarpus heterophyllus* survived desiccation to 44% moisture content, while the excised embryonic axes dried with an aseptic air flow and silica gel tolerated desiccation to 26% and 16% moisture content, respectively (Fu *et al.*, 1993).

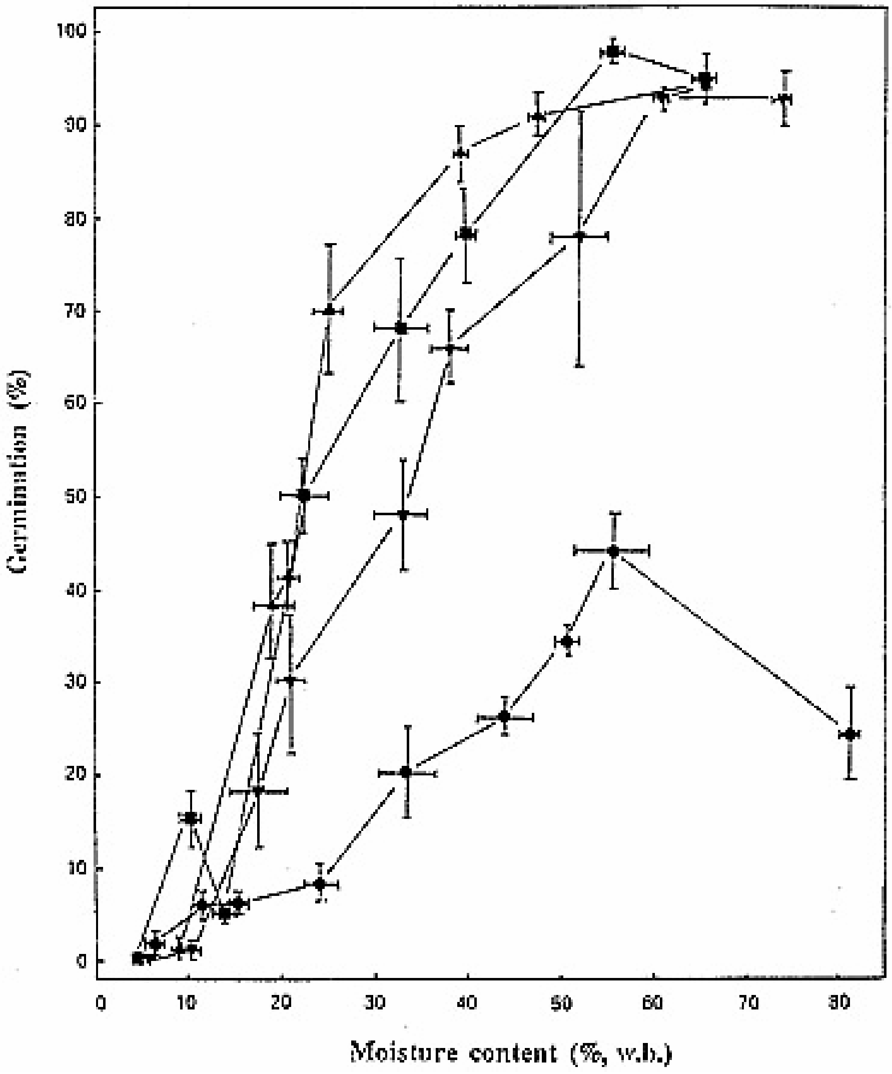

Fig. 5. Relations between germination (%) and moisture content for sycamore (*Acer pseudoplatanus*) seeds harvested on 12 July (†), 16 August (?), 20 September (†) or 18 October 1988 (?), dried to the moisture contents shown. From (Hong & Ellis, 1990).

4.2 Longevity of recalcitrant seeds in moist storage

There is no satisfactory method for maintaining the viability of intact recalcitrant seeds over the long term. This is because they cannot be dried; neither can they be stored at subzero temperatures because they would be then killed by freezing injury resulting from ice formation. In addition, some tropical recalcitrant seeds are also damaged by chilling injury at temperatures of 10-15°C and below. The longevity of recalcitrant seeds is short, particularly for species adapted to tropical environments, from a few weeks to a few months (King & Roberts, 1979), (King & Roberts, 1980a). However, the longevity of seeds of species adapted to temperate environments can be maintained for much longer periods, e.g. more than 3 years for oak (*Quercus* spp.) seeds stored moist at –3°C (Suszka, 1971-1974).

In practical terms, species with recalcitrant seeds can therefore be subdivided into those of tropical origin, and those adapted to temperate climates (temperate latitudes, or high altitudes in the tropics); the latter can be stored at cooler temperatures and for longer. This subdivision tallies with the classification of Bonner (Bonner, 1990).

The principle of successful moist seed storage for recalcitrant seeds is to maintain seeds at moisture content levels close to that at which they are shed with continuous access to oxygen, because under these circumstances seed deterioration is minimized since repair mechanisms operate (Villiers, 1975). Clearly, it is also essential that the conditions should prevent or at least delay germination. The use of germination inhibitors (Goldbach, 1979b); (Edwards & Mumford, 1983) or cool temperatures (provided the seeds are not damaged by chilling) can be effective.

In general, the viability of recalcitrant seeds can be maintained (albeit only for limited periods in aerated conditions) at moisture contents just less than fully imbibed, i.e. at (or perhaps just below) that value at which the seeds are shed, or in equilibrium with 98-99% r.h., at optimum storage temperatures which vary from about 7 to 17°C among species of tropical origin, and between about –3 and 5°C among those adapted to temperate climates.

Maintaining recalcitrant seeds fully imbibed or subimbibed, with continuous aeration and at the same time preventing germination and fungal contamination is difficult. Aeration can result in loss in seed moisture and respiration can quickly deplete oxygen. The storage medium is therefore very important for recalcitrant seeds. The storage medium should fulfil two functions: first, maintain seed moisture constant at high values; second, allow diffusion of sufficient oxygen to the moist seeds. The storage of moist recalcitrant seeds in damp charcoal, sawdust, or moist sand is generally reported to be more efficient than storage in polyethylene bags (Schaefer, 1990a).

4.3 Cryopreservation of excised embryos

Cryopreservation of somatic and zygotic embryos has been reported to be successful for many species which show orthodox, intermediate and recalcitrant seed storage behaviour (Engelmann *et al.*, 1995b).

For successful cryopreservation, excised embryos must survive desiccation below the threshold freezable moisture content (Hor *et al.*, 1990) of about 18-33% (Table 1), below which value there is no freezable water for ice formation by ultra-low temperatures. For example, embryonic axes of *Aesculus hippocastanum* survived desiccation to 12% moisture content and subsequent cryostorage in liquid nitrogen (Pence, 1992). Similarly, 40% of excised embryonic axes of longan (*Dimocarpus longan*) survived both desiccation to 18% moisture content and subsequent storage for 24 hours in liquid nitrogen (Fu *et al.*, 1993).

Unfortunately, embryos of many recalcitrant seeds are damaged by desiccation before seed moisture content is reduced to those values at which ice crystallization occurs (Table 1). Thus, the cryopreservation of excised embryos of these species results in death, either due to ice formation at moisture content levels above the threshold freezable level or by desiccation to moisture content levels below the threshold freezable moisture content (Hor *et al.*, 1990). Method of drying, rate of drying (see 4.1.3) and the pretreatment of embryos with cryoprotectants, such as DMSO, proline, sucrose, and glycerol (Chin, 1989); (Pence, 1991b); (Assy-Bah & Engelmann, 1992) are important factors influencing the survival of excised embryos (or embryonic axes) in liquid nitrogen.

Table 1. Comparison of the threshold embryo (or * embryonic axis) moisture contents above which ice crystallization occurs at ultra-low temperatures, and below which loss in viability occurs.

	Threshold embryo moisture content (%, w.b.) for:		
Species	**ice crystallization**	**desiccation damage**	**Reference**
Acer saccharinum	32	40	(Becwar *et al*., 1983)
	21*	30*	(Pammenter *et al*., 1993)
Aesculus hippocastanum	24*	31*	(Pammenter *et al*., 1993)
		12-22*	(Pence, 1992)
Artocarpus heterophyllus	33	43	(Hor *et al*. 1990
	18*	28*	(Pammenter *et al*., 1993)
Avicennia marina	21*	29*	(Pammenter *et al*., 1993)
Castanospermum australe	23*	50*	(Pammenter *et al*., 1993)
Durio zibethinus	32	54	(Hor *et al*., 1990)
Landolphia kirkii	22-27*	25 (fast drying), 52 (slow drying)*	(Pammenter *et al*., 1991)
Litchi chinensis	23*	42*	(Pammenter *et al*., 1991)
Nephelium lappaceum	30	39	(Hor *et al*., 1990)
Welfia sp.	22*	64*	(Pammenter *et al*., 1993)

Results reported for the following species have shown the feasibility of the cryopreservation of excised embryos or embryonic axes of recalcitrant seeds: *Aesculus* spp. (Pence, 1990), (Pence, 1992), *Araucaria hunsteinii* (Pritchard & Prendergast, 1986), *Artocarpus heterophyllus* Krishnapillay (Krishnapillay, 1989) cited by (Engelmann *et al*., 1995b), (Chandel *et al*., 1995), *Castanea sativa* (Pence, 1990), (Pence, 1992), *Coffea liberica* (Normah & Vengadasalam, 1992); (Hor *et al*., 1993), *Cocos nucifera* (Chin *et al*., 1988); (Assy-Bah & Engelmann, 1992), *Dimocarpus longan* (Fu *et al*., 1990); (Fu *et al*., 1993), *Hevea brasiliensis* (Normah *et al*., 1986), *Landolphia kirkii* (Vertucci *et al*., 1991), *Quercus* spp. (Pence, 1990), (Pence, 1992); (Jorgensen, 1990); (Gonzalez-Benito & Perez-Ruiz, 1992) and *Theobroma cacao* (Pence, 1991b). However, these approaches remain 'experimental' and genebanks wishing to apply such approaches should contact IPGRI for advice.

5. Characteristics of intermediate seeds

For the majority of species, it used to be a comparatively simple matter to classify seed storage behaviour as either orthodox or recalcitrant in accordance with Roberts' definitions, and it was also convenient because long-term seed storage for plant genetic conservation was feasible for the former category only. Of course, mistakes in classification occurred on occasion, but gradually evidence also began to accumulate that these two categories did not account satisfactorily for all observations on seed storage behaviour. For example, Teng and Hor (Teng & Hor, 1976) showed that seeds of both star fruit (*Averrhoa carambola*) and papaya (*Carica papaya*) withstood desiccation to around 10-12% moisture content and could be stored successfully in hermetic containers at these moisture content levels. However, in contrast to orthodox seeds, they lost viability much more rapidly in air-dry storage at 0°C than at warmer temperatures of 12-21°C. Thereafter, Tompsett (Tompsett, 1984a), (Tompsett, 1984b) showed that the longevity of seeds of *Araucaria columnaris* was increased in air-dry storage by reduction in storage temperature or moisture content, but only within limited ranges, because viability was reduced with desiccation below about 12% moisture content. In both these cases, then, it was clear that the seeds could be stored in certain air-dry environments successfully but their behaviour did not satisfy the definition of orthodox seed storage behaviour provided by Roberts (Roberts, 1973).

This topic has now been investigated extensively, initially with seeds of arabica coffee (*Coffea arabica*), using a factorial combination of several storage temperatures and moisture content levels. The research has shown that seeds of arabica coffee (Ellis et al., 1990a), (Ellis et al., 1991a); (Hong & Ellis, 1992c), robusta coffee (*Coffea canephora*) (Hong & Ellis, 1995), oil palm (*Elaeis guineensis*) (Ellis et al., 1991d), papaya (*Carica papaya*) (Ellis et al., 1991b) and several *Citrus* species (Hong & Ellis, 1995) show a type of seed storage behaviour intermediate between the orthodox and recalcitrant categories defined by Roberts (Roberts, 1973). The essential feature of intermediate seed storage behaviour is that the negative relation between seed longevity in air-dry storage and moisture content is reversed (i.e., the relation becomes positive) at values below those in equilibrium (at 20°C) with about 40-50% r.h. This type of seed storage behaviour is also found in many other species.

The main feature of intermediate seed storage behaviour described above is often (but not always) also associated with damage immediately after desiccation to a relatively low moisture content, about 7-12% moisture content depending on species (Fig. 6). The critical levels of moisture content of intermediate seeds below which more rapid loss in viability occurs during hermetic storage and/or viability is lost immediately after desiccation, varies considerably with species, degree of maturity and the method of seed extraction or handling. In general, seeds which are extracted at maturity tolerate desiccation to moisture contents in equilibrium with about 40-50% r.h., i.e., about 10% moisture content for arabica coffee and 7% moisture content for *Citrus* spp. Another feature of intermediate seeds of tropical origin is the fact that the longevity of dry seeds (7-10% moisture content) is reduced with reduction in storage temperature below about 10°C (Ellis et al., 1990a), (Ellis et al., 1991a), (Ellis et al., 1991b), (Ellis et al., 1991d); (Hong & Ellis, 1992c). In such cases, then, there is an optimum air-dry storage environment for the maintenance of seed viability. In arabica coffee this is about 10°C with 10-11% moisture content (Hong & Ellis, 1992c). Moreover, although increase in seed storage moisture content and temperature above these values reduces longevity, it is by no means certain that these relations conform to the seed viability equation for orthodox seeds (Hong & Ellis,, unpublished).

From the point of view of optimum air-dry seed storage environments, it may be helpful to distinguish between species with intermediate seed storage behaviour adapted to tropical environments and those adapted to temperate environments (including high altitudes in the tropics). For example, intermediate seeds of tropical origin such as arabica coffee (Wellman & Toole, 1960); (Bendana, 1962) and papaya (Bass, 1975) can be stored at moisture contents in equilibrium with 50% r.h. (9-10% moisture content) and 10°C for up to 5 and 6 years, respectively, without loss in viability. The viability of intermediate seeds of temperate origin is also maintained well at moisture contents in equilibrium with about 50% r.h. but at cooler temperatures of 5 to –20°C. For example, wild rice (*Zizania palustris*) seeds can be maintained in hermetic storage at –2 or 3°C with 9-11.5% moisture content for 9-12 months without loss in viability (Oelke & Stanwood, 1988); (Oelke *et al.*, 1990), or at -18°C with 5.4-6.8% moisture content for 15-16 months for embryonic axes, with loss in viability limited to about 11-15% (Berjak *et al.*, 1994).

Seed maturity also affects desiccation tolerance in intermediate seeds. For example, seeds of arabica and robusta coffee extracted from fruits of intermediate maturity (yellow) were able to tolerate greater desiccation than those from either ripe (red) or immature (green fruits) (Ellis et al., 1991a); (Hong & Ellis, 1995) (Fig. 6). The method of seed extraction and handling may also influence desiccation tolerance. For example, seeds of arabica coffee imbibed at 30°C for 3-10 days showed greater sensitivity to desiccation (Ellis et al., 1991a). It is suggested that seed-processing methods involving high seed moisture contents, e.g. soaking, fermentation, moist storage and storage in cold water (e.g. *Zizania*), will tend to reduce subsequent desiccation tolerance and seed longevity in intermediate seeds (Hong & Ellis, 1992c).

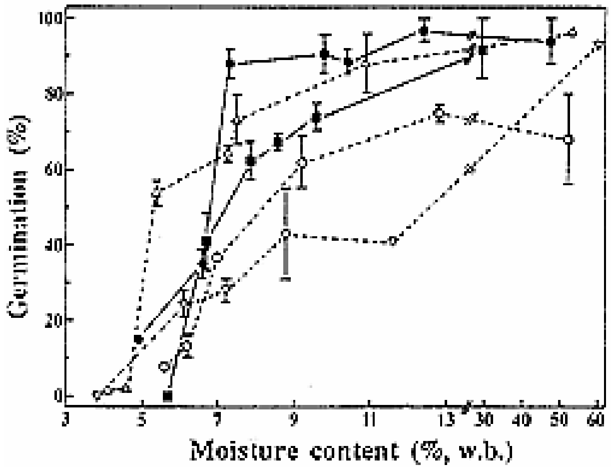

Fig. 6. Desiccation sensitivity (normal germination, %, versus moisture content, %) in seed lots of arabica coffee (*Coffea arabica*) cv. SL28 from Kenya (†) and South Africa (†) extracted from ripe (red) fruits, and seeds extracted at Reading from green (?), yellow (?), or red fruits (?) from South Africa. From (Ellis et al., 1991a).

Intermediate seeds of species of tropical origin die more rapidly with lowering of the temperature below about 10°C; in some cases temperatures just below 0°C kill whole seeds immediately (Ellis et al., 1990a), (Ellis et al., 1991a), (Ellis et al., 1991b), (Ellis et al., 1991d). Nevertheless, there is some possibility that the cryopreservation of seeds with intermediate seed storage behaviour may be feasible with more research. Despite reports of the immediate death of (whole) seeds following cryostorage in liquid nitrogen, e.g. *Coffea arabica* (Becwar *et al.*, 1983), *Corylus avellana* (Normah *et al.*, 1994), *Corylus cornuta* (Stanwood & Bass, 1981), *Elaeis guineensis* (Grout *et al.*, 1983) and *Roystonea regia* (Ellis et al., 1991c), there have been several reports of the survival of seeds of species with intermediate seed storage behaviour following immersion in liquid nitrogen, e.g. *Camellia sinensis* (Hu *et al*., 1993), (Hu *et al*., 1994), *Carica papaya* (Becwar *et al*., 1983); (Chin & Krishnapillay, 1989), *Elettaria cardamomum* (Chaudhury & Chandel, 1995), *Musa violascens* (Chin & Krishnapillay, 1989), *Passiflora edulis* (Becwar *et al*., 1983), and *Piper nigrum* (Chaudhury & Chandel, 1994).

Since the whole seeds of species which show intermediate seed storage behaviour tolerate desiccation to relatively low moisture contents (7-10%), excised embryos may have a greater chance to survive cryostorage in liquid nitrogen than the recalcitrant seeds. For example, oil palm shows intermediate seed storage behaviour (Ellis et al., 1991c) but excised embryos of oil palm which had been dried to 10.4% moisture content showed no loss in viability during 8 months of storage in liquid nitrogen whereas intact seeds were killed (Grout et al., 1983). Similar results for excised embryos of oil palm have been reported by others (Hor *et al*., 1992); (Engelmann *et al*., 1995a), (Engelmann *et al*., 1995b).

Reports of successful cryostorage of excised embryos of *Camellia sinensis* (Chaudhury *et al*., 1990), (Chaudhury *et al*., 1991); (Wesley-Smith *et al*., 1992); (Chandel *et al*., 1993), (Chandel *et al*., 1995), *Citrus sinensis* (Radhamani & Chandel, 1994), *Coffea arabica* (Abdelnour-Esquivel et al., 1992b), *Corylus avellana* (Pence, 1990); Gonzalez-Benito & Perez, 1994); (Normah *et al*., 1994); (Reed *et al*., 1994), *Howea forsteriana* (Chin *et al*., 1988); (Chin & Krishnapillay, 1989), *Musa* spp. (Abdelnour-Esquivel *et al*., 1992a), *Poncirus trifoliata* (Radhamani & Chandel, 1992) and *Veitchia merrilli* (Chin *et al*., 1988); (Chin & Krishnapillay, 1989) have shown some potential for long-term storage under such conditions.

These comments on the possibility of the cryopreservation of seeds (or embryos) of species with intermediate seed storage behaviour are indicative of our suspicion that a concerted future programme of research may enable advice to be developed for the long-term storage of seeds/embryos for these species. Until then, however, medium-term storage is likely to be the best that can be achieved, and even then only in carefully defined and controlled environments.

6. Factors leading to the misinterpretation of seed storage behaviour

Roberts *et al.* (Roberts *et al.*, 1984) recognized at least nine identifiable ways in which experimental results might be misinterpreted or confounded with other factors so that orthodox seeds might be wrongly classified as recalcitrant. We list below ten possible reasons for the misinterpretation of seed storage behaviour.

6.1 Investigations with immature seeds

Immature seeds, e.g. with moisture contents above 60%, can be very sensitive to damage from desiccation even though the mature seeds show orthodox (Dasgupta *et al.*, 1982); (Ellis et al., 1987); (Fischer *et al.*, 1988); (Hong & Ellis, 1990); (Hong & Ellis, 1992a); (Ellis et al., 1993a) or intermediate seed storage behaviour (Ellis et al., 1991a); (Hong & Ellis, 1995). Similarly, at later stages of seed development such as at the end of the seed-filling phase, orthodox species may still show damage upon desiccation to very low levels of moisture content (Fig. 4) (Hong & Ellis, 1992a); (Ellis et al., 1993a); (Ellis & Hong, 1994). Thus, tests on immature seeds of a species with orthodox seed storage behaviour could, therefore, result in erroneous classification as intermediate or recalcitrant. Similarly, the desiccation of immature seeds of a species with intermediate seed storage behaviour (Fig. 6) may result in the erroneous classification as recalcitrant. This is a potential problem in tree species where losses of ripe seeds by wind, insects, animals and pests are common, or in species in which hardseededness occurs during ripening, and in which losses are traditionally avoided by premature harvesting (Willan, 1985).

6.2 Delayed harvesting

Delaying harvests beyond harvest maturity may also render seeds sensitive to damage from desiccation to very low moisture contents. For example, delaying the harvest of seeds of a *japonica* rice grown in a hot (stressful) seed production environment resulted in reduced desiccation tolerance, compared with those harvested at harvest maturity (Ellis & Hong, 1994). The seeds produced in a hot environment (i.e. those which aged on the mother plant when harvesting was delayed in the hot environment) showed certain characteristics similar to those of intermediate seeds (Ellis & Hong, 1994).

6.3 Seed processing methods

Methods of seed extraction from fruits may also influence desiccation tolerance. Any method involving long durations of exposure to high seed moisture content at temperatures at which some progress towards germination (not necessarily visible) is possible, can increase desiccation sensitivity. Such treatments include prolonged soaking, fermentation of fleshy fruits, and prolonged durations of temporary storage of moist or freshly extracted seeds (Hong & Ellis, 1992c).

6.4 Pretreated seeds

In temperate region in particular, seeds of species which exhibit strong dormancy (such as tree seeds) are commonly stored moist and cool in order to break dormancy (prechilling) prior to sowing. Such treatments may result in loss in desiccation tolerance (because germination *sensu strictu* may occur). Such effects may explain certain reports of **considerable** desiccation sensitivity in wild rice (*Zizania palustris*), since it is a common practice to store seeds of this species in water at 3°C.

6.5 Improper drying methods

Since the rate of loss of viability in orthodox seeds is a function of time, temperature, and moisture content (Roberts *et al.*, 1984), inappropriate drying regimes – e.g. the use of high temperatures, particularly in seeds harvested / shed at high moisture contents – may result in considerable loss in viability during seed drying.

6.6 Desiccation tolerance

Despite the fact that the terms orthodox, intermediate and recalcitrant refer to seed storage behaviour as a whole, there have been many attempts to categorize seed storage behaviour from results for desiccation tolerance alone. More often than not, such approaches provide the correct conclusion, but it is possible for such studies to misclassify seed storage behaviour. The first example of misclassification concerns the question “How dry is dry?” The second highlights the dificulties already covered in sections 6.1-6.4.

It is comparatively easy in many climates to dry seeds to 10-15% moisture content using ambient relative humidity. However, tolerance of desiccation to such moisture content levels does not necessarily mean that the seeds are orthodox. For example, seeds of arabica coffee, papaya and oil palm show intermediate seed storage behaviour and are able to tolerate desiccation to 10-12% moisture content. This also implies that current catalogues of orthodox seeds which have been derived from reports of longevity in open storage may include species with intermediate seed storage behaviour.

Figure 7 provides examples of several patterns of desiccation tolerance. Determining desiccation tolerance in this way (i.e. drying subsamples of seeds to several different levels of moisture content and then determining seed moisture content and viability) is far less likely to result in misclassification of seed storage behaviour than simply drying one subsample down to a single moisture content. Indeed this sort of approach has been advocated as a preliminary step in a protocol to determine seed storage behaviour (Hong & Ellis, 1996).

Interpretation of the patterns of response to desiccation shown in Figure 7 by curves **a**, **c** and **e** is relatively easy: these samples are likely to show orthodox, intermediate, and recalcitrant seed storage behaviour, respectively. However, interpretation of the other two curves (**b** and **d**) is more likely to result in the misclassification of seed storage behaviour. Pattern **b** is found, for example, both in species with orthodox seed storage behaviour where the seed lot has been harvested slightly prematurely or has been pretreated (e.g. prechilled), and in some of the best seed lots of species with intermediate seed storage behaviour. Pattern **d** is found, for example, in species with intermediate seed storage behaviour where the seed lot has been harvested prematurely or has been exposed to high moisture contents for long periods (e.g. soaking, fermentation, moist storage, prechilling). In other words, conclusions based on desiccation tolerance alone (particularly if investigations are limited to a single seed lot) can sometimes be erroneous.

6.7 Short duration viability tests

Fresh seeds of many tropical trees germinate readily during 14-day germination tests. However, other species’ seeds require much longer to germinate. For example, seeds of *Persoonia comata* require one year or more (Fox *et al.*, 1987) and seeds of *Acrocomia sclerocarpa* require 2.5 years to germinate (Ellis et al., 1985b). Furthermore, although fresh seeds may germinate readily, once dried they may be more difficult to germinate because of hardseededness. This is often observed with seeds of Leguminosae, Malvaceae, Cannaceae, Rhamnaceae and Tiliaceae (Ellis et al., 1985b). Unless the hardseededness is overcome, seeds which do not germinate due to hardseedness could be confounded with dead seeds.

Apart from hardseededness, dormancy is sometimes induced by drying. Specific treatments are required to remove this dormancy, and the seeds require more time to germinate. For example, dry seeds of *Corylus avellana* (Bradbeer, 1968); (Jarvis, 1975), *Citrus* sp. ,, several genera of the Rosaceae (e.g. *Malus, Pyrus, Prunus*) (Ellis et al., 1985b) and *Fagus sylvatica* (Poulsen, 1993) are much more difficult to germinate than the fresh seeds, and this has sometimes led to mistaken classification as recalcitrant.

Young and Young (Young & Young, 1992) collated information of seed germination of about 386 genera of woody plants in North America, and they observed that only 40% of these genera contain species whose seeds will germinate readily without pretreatment. The remaining genera (60%) require specific pretreatments, such as prechilling, warm stratification followed by prechilling, and scarification. In most cases prolonged durations of germination testing are required (Young & Young, 1992). Of 7057 wild plant seed collections germinated by the Kew Seed Bank, 46% required either scarification, stratification or some treatment other than manipulation of the germination temperature and provision of fluorescent light for 12 hours/day. According to Soepadmo (Soepadmo, 1989), about 3-10% of the tree species native to Malaysia possess seeds which require a period of more than 26 weeks to attain even 50% germination, among which seeds of *Anisophyllea griffithii*, *Hydnocarpus woodii*, and *Barringtonia macrostachya* require 95, 83 and 65 weeks, respectively, to attain 50% germination. Seeds of about 70% of the tree species native to Malaysia germinate within 10 weeks; only in the few remaining species is less than 2 weeks required to achieve 50% germination (Soepadmo, 1989).

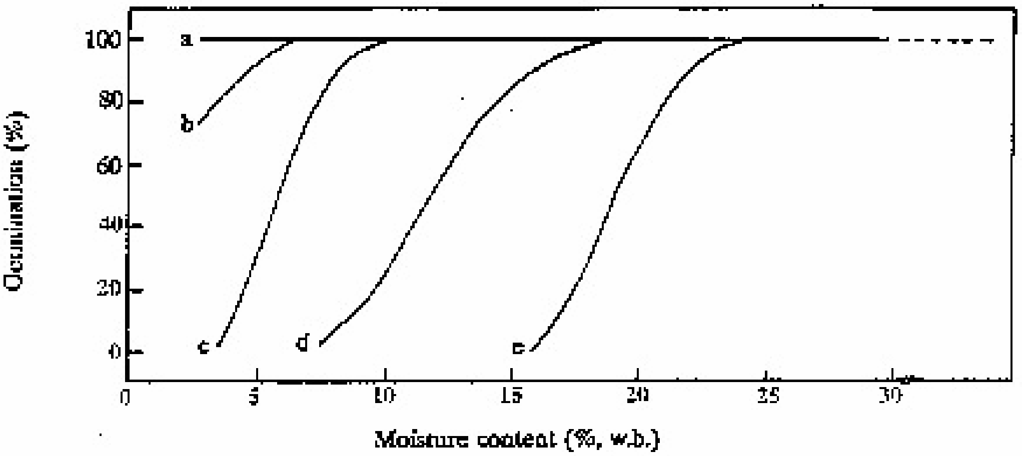

Fig. 7. Three typical patterns of desiccation tolerance (normal germination, %, plotted against moisture content, % w.b.) are shown for species with orthodox (**a**), intermediate (**c**) and recalcitrant (**e**) seed storage behaviour. Two further patterns (**b** and **d**) are also shown which may be found in species with orthodox and intermediate seed storage behaviour, respectively, where the seed lot has been harvested prematurely or too late, or has been wrongly pretreated (see sections 3.9, 5 and 6.1-6.5). Seeds of some species with recalcitrant seed behaviour are more intolerant of desiccation than those shown by pattern **e**. From (Hong & Ellis, 1996).

6.8. Rapid loss of viability during storage under ambient conditions

Rapid loss in viability during storage under ambient environments does not necessarily mean that seeds are recalcitrant. For example, seeds of *Salix* spp. were reported to lose viability during 2 days of open storage (Campbell, 1980). However, seeds of 24 species of *Salix* have been maintained without loss in viability during 3 years in hermetic storage at –19°C with 6-10% moisture content (Zasada & Densmore, 1977), or 5 years stored over a desiccant at –8°C (Sato, 1955).

6.9. Quick tests in liquid nitrogen

Dry orthodox seeds at 2-18% moisture content often survive exposure to liquid nitrogen. A quick method for identifying orthodox seeds, used to some extent, has been through the determination of survival following short-duration exposures to liquid nitrogen (from 1 hour to 6 days). However, this method is not always reliable since both the moisture content and the rate of cooling and rewarming need to be optimized for survival in each species separately. For example, whole seeds of *Juglans*, *Prunus* and *Populus* (with orthodox seed storage behaviour) were reported to be damaged by exposure to temperatures cooler than –40°C (Wang *et al.*, 1994). Moreover, such quick tests cannot distinguish between orthodox and intermediate seeds. For example, papaya seeds at 9-10% moisture content survived during 24 hours of exposure to liquid nitrogen (Becwar *et al.*, 1983); (Chin & Krishnapillay, 1989) but papaya shows intermediate seed storage behaviour and seeds stored hermetically at –20°C with 7.6-9.4% moisture content for 365 days showed 80-90% loss in viability (Ellis et al., 1991b).

6.10. Imbibition damage to dry seeds

This phenomenon may also be the cause of reports of apparent desiccation sensitivity in very dry seeds. Imbibition damage is particularly likely when seeds are soaked in water, as often occurs in tree seedling nurseries for example, but can also occur in standard laboratory tests (Ellis et al., 1990c). Hence, the desirability of preconditioning dry seeds at 100% r.h. before germination tests, as recommended in section 3.6.

7. Approaches to predict seed storage behaviour

In this section, we describe certain approaches to predict seed storage behaviour in species for which experimental results are not available.

7.1. Association between plant ecology and seed storage behaviour

Roberts and King (Roberts & King, 1980) suggested that there is an association between plant ecology and seed storage behaviour. According to this hypothesis, orthodox species originate from environments subjected to occasional or seasonal drought in which desiccation tolerance of the seeds is essential for seed survival which ensures the regeneration of the species. On the other hand, recalcitrant species tend to originate from moist or aquatic ecosystems in which seeds are subjected to high humidity during seed development, maturation and after shedding.

In accordance with this hypothesis, all 115 shrub species of 29 families native to the Mojave Desert show orthodox seed storage behaviour (Kay *et al*., 1988), while seeds of those species of the genus *Dipterocarpus*, which are native to dry habitats, show some desiccation tolerance but those species inhabiting moist evergreen areas tend to be intolerant of desiccation (Tompsett, 1987), (Tompsett, 1992). Similarly, arabica coffee shows intermediate seed storage behaviour and is native to the dry and cool regions of Ethiopia, while liberica coffee shows recalcitrant seed storage behaviour and is native to the hotter and more humid regions of Liberia (Hong & Ellis, 1995). Dickie *et al*. (Dickie *et al*., 1992) also observed that those species within the Palmae which show orthodox seed storage behaviour are native to dry habitats whereas those species which show recalcitrant seed storage behaviour are native to relatively moist habitats. Moreover, although seeds of most oak (*Quercus*) species show recalcitrant seed storage behaviour (King & Roberts, 1979), seeds of *Q. emoryi*, which is native to savanna, are not recalcitrant (Nyandiga & McPherson, 1992).

From the information on seed storage behaviour that has now been collated for over 7000 species of 251 families (Part II), it is evident that species which show recalcitrant seed storage behaviour do not occur naturally in arid habitats, desert and savanna. In these environments, the majority of plant species show orthodox seed storage behaviour, while a few may show intermediate seed storage behaviour. It is clear, however, that further generalizations are not possible. In particular, not all species native to moist habitats, rain forests, flooded forests or aquatic environments show recalcitrant seed storage behaviour. Species native to moist environments produce all three categories of seed storage behaviour. There is perhaps, however, a greater likelihood of recalcitrant behaviour in species associated with climax vegetation.

While all orthodox seeds, whether tropical or temperate, store best at subzero temperatures, this is clearly not true of species showing intermediate or recalcitrant seed storage behaviour, and information on their geographical distribution and ecology also helps in the determination of optimum storage temperatures. Table 2 shows that there may be an association between the optimum seed storage temperature and the minimum air temperature at which the plants can survive without chilling injury. From this observation it appears that the cool temperatures that cause chilling injury to the growing plants also reduce seed longevity and in some cases result in almost immediate seed death. In general, fresh (or moist) seeds of species with intermediate or recalcitrant seed storage behaviour which are adapted to tropical lowlands tend to show chilling injury at 10-15°C, while seeds of those adapted to high latitudes or high altitudes are able to tolerate exposure to cooler temperatures. For example, Sasaki (Sasaki, 1980a) divided *Shorea* species into two groups in relation to the effect of storage temperature on seed longevity; seeds of the Yellow Meranti Group tolerate 4°C, while seeds of the White Meranti, Red Meranti and Balau Group show chilling injury at 10-15°C. The species listed in the Yellow Meranti Group by Sasaki (Sasaki, 1980a) are those adapted to high altitudes (Ashton, 1983).

Table 2. Optimum seed storage temperature and comments on plant ecology. References are shown in parentheses. From (Hong & Ellis, 1996).

Species	Seed storage behaviour	Optimum temperature	Origin and ecology
Artocarpus heterophyllus	Recalcitrant	15°C (10)	Native to SE Asia and Polynesia, dominant in rain forests of tropical lowlands (13).
Camellia sinensis	Probably intermediate	1°C (1)	Native to N Burma, grows naturally at altitudes up to 2000 m (13). The trees can tolerate subzero temperatures from –5 to -20°C (14).
Carica papaya	Intermediate	10°C (4)	Native to S Mexico and Costa Rica, up to 1700 m altitudes, but the plant does not withstand frost (13).
Citrus limon	Intermediate	5°C (3)	Native to drier monsoon areas of SE Asia (13); the tree can withstand light frost (13), or even –10°C for short periods (21).
Coffea arabica	Intermediate	10°C (11)	Native to highlands of 1300-1900 m altitudes of Ethiopia, where climate is dominated by 4-5 months of dry season with extreme temperatures of 4 and 31°C (8). The tree cannot survive at 0°C (13), but can survive 2°C for 6 hours (7), and 4°C for longer periods (5, 8).
Dipterocarpus baudii	Probably recalcitrant	14°C (16)	Native to evergreen tropical lowland rain forests of SE Asia, where annual rainfall is about 2000 mm (2).
Dipterocarpus intricatus	Intermediate	2°C (18) to 6°C (17)	Native to dry dipterocarp forests of savanna zones of SE Asia, naturally grown at altitudes up to 1400 m (2).
Hevea brasiliensis	Recalcitrant	7°-10°C (6)	Native to Amazon basin, in evergreen tropical lowland rainforests, with annual rainfall of 2000-4000 mm. Despite tropical lowland origin, the plant can tolerate low temperatures; winter injury observed only when temperature is 4 – 5°C, and some clones can withstand –1°C (19).
Mangifera indica	Recalcitrant	15°C (9)	Native to rain forests of Indo-Burma, India; naturally grown from lowland to altitudes of 1300 m (13). The plant is killed by 2°C, and can tolerate extreme temperatures of 5 – 10°C and 43°C for short periods (15).
Theobroma cacao	Recalcitrant	15°C (12)	Understorey trees of tropical rain forests of S America. They are also grown at 1300 m altitude in the Venezuelan Andes (13). Low temperature limit for cocoa growing is a mean monthly minimum of 15°C, and an absolute minimum of 10°C (20).

References: (1) (Amma & Watanabe, 1983); (2) (Ashton, 1983); (3) (Barton, 1943); (4) (Bass, 1975); (5) (Bauer *et al*., 1990); (6) (Beng, 1976); (7) (Cambrony, 1992); (8) (Coste, 1992); (9) (Fu *et al*., 1990); (10) (Hanson, 1984); (11) (Hong & Ellis, 1992c); (12) (Mumford & Brett, 1982); (13) (Purseglove, 1968); (14) (Sakai & Hakoda, 1979); (15) (Singh, 1968); (16) (Tamari, 1976); (17) (Tompsett, 1987); (18) (Tompsett, 1992); (19) (Webster & Baulkwill, 1989); (20) (Wood, 1973); (21) (Yelenosky, 1978).

Table 3. Association between fruit and seed characteristics, and seed storage behaviour (O for Orthodox, Orthodox p, and Orthodox?; I for Intermediate and Intermediate?; and R for Recalcitrant and Recalcitrant? seed storage behaviour. See Part IB, Introduction).

Type of fruit	No. and characters of seeds	Families	Seed storage behaviour
Achene		Alismataceae, Amaranthaceae, Compositae, Coriaricaceae, Cyperaceae, Elaeagnaceae, Platanaceae, Plumbaginaceae, Polygonaceae, Ranunculaceae, Rosaceae, Urticaceae, Valerianaceae	O
Acorn	1-seeded nut	Fagaceae	O, R
Berry	1 to many seeds, seeds dry or arillate	Actinidiaceae, Araliaceae, Asparagaceae, Berberiaceae, Bromeliaceae, Cactaceae, Campanulaceae, Capparaceae, Caprifoliaceae, Ericaceae, Euphorbiaceae, Grossulariaceae, Liliaceae, Ranunculaceae, Solanaceae, Taxaceae, Vitaceae	O
		Caricaceae, Musaceae, Passifloraceae, Piperaceae	O, I
		Cucurbitaceae, Guttiferae, Lauraceae, Myrtaceae	O, R
	1 to 10 seeds	Ebenaceae, Meliaceae, Rutaceae	O, I, R
		Rhizophoraceae	R
Capsule	1 to many seeds, dry or arillate	Acanthaceae, Agavaceae, Aizoaceae, Alliaceae, Amaranthaceae, Begoniaceae, Bignoniaceae, Bromeliaceae, Buddlejaceae, Campanulaceae, Cannaceae, Capparaceae, Caprifoliaceae, Caryophyllaceae, Cistaceae, Clethraceae, Commelinaceae, Convolvulaceae, Crassulaceae, Dioscoreaceae, Elatinaceae, Ericaceae, Gentiaceae, Gesneriaceae, Grossulariaceae, Guttiferae, Haemodoraceae, Hamamelidaceae, Hyacinthaceae, Hydrophyllaceae, Iridaceae, Juncaceae, Liliaceae, Linaceae, Lythraceae, Malvaceae (one exception), Myrtaceae, Oleaceae, Onagraceae, Oxalidaceae, Papaveraceae, Pedaliaceae, Plantaginaceae, Polemoniaceae, Portulacaceae, Primulaceae, Tamaricaceae, Tiliaceae, Proteaceae, Ranunculaceae, Resedaceae, Rhamnaceae, Rubiaceae, Rutaceae, Salicaceae, Sapindaceae, Saxifragaceae, Scrophulariaceae, Simmondsiaceae, Solanaceae, Tiliaceae, Violaceae	O
		Bixaceae, Celastraceae, Meliaceae, Orchidaceae	O, I
		Bombacaceae, Euphorbiaceae	O, R
		Theaceae	O, I, R
	1 large seed	Hippocastanaceae	R
Caryopsis		Gramineae	O (with 3 exceptions)

Type of fruit	No. and characters of seeds	Families	Seed storage behaviour
Cone	dry seeds	Cupressaceae, Cycaceae, Pinaceae, Taxodiaceae	O
	dry or arillate seeds	Araucariaceae, Podocarpaceae	O, I, R
Drupe	1 to many small seeds	Aquifoliaceae, Araliaceae, Boraginaceae, Caprifoliaceae, Combretaceae, Cornaceae, Ericaceae, Moraceae, Myoporaceae, Myricaceae, Rhamnaceae, Rosaceae	O
	1 to 5 seeds, usually arillate	Anacardiaceae, Guttiferae, Lauraceae, Myristaceae, Sapindaceae, Sterculiaceae	O, R
		Meliaceae, Palmae, Rubiaceae	O, I, R
Follicle		Asclepidiaceae, Butomaceae, Crassulaceae, Juncaginaceae, Magnoniaceae, Proteaceae, Ranunculaceae, Rosaceae	O
		Apocynaceae, Sterculiaceae	O, R
Nut	1 to many seeds	Betulaceae, Casuarinaceae, Chenopodiaceae, Juglandaceae, Nelumbonaceae	O
	1 seed	Corylaceae, Fagaceae, Proteaceae	O, I, R
Nutlet	1 to many small seeds	Boraginaceae, Labiatae, Moraceae	O
Pod	many small seeds	Leguminosae, Moringaceae	O
	1 to 5 large seeds	Leguminosae	O, R
Pome	more than 1	Rosaceae	O
Samara		Eucommiaceae, Magnoliaceae, Oleaceae, Ulmaceae	O
		Aceraceae	O, I, R
Schizocarp		Geraniaceae, Malvaceae, Umbelliferae	O
Siliqua, silicula		Cruciferae	O (with one exception)
Utricle		Basellaceae, Illecebraceae	O

7.2. Association between taxonomic classification and seed storage behaviour

In general, species in the Chenopodiaceae, Combretaceae, Compositae, Labiatae, Solanaceae and Pinaceae are very likely to exhibit orthodox seed storage behaviour, while species in the Rhizophoraceae (in which vivipary predominates) are very likely to be recalcitrant. Species within the Leguminosae, Gramineae, Cucurbitaceae, Cruciferae and Rosaceae show orthodox seed storage behaviour, but with several notable exceptions. On the other hand, it appears that no member of the Dipterocarpaceae shows orthodox seed storage behaviour; most show recalcitrant, and a few intermediate, seed storage behaviour. Similarly, although all members of the Sapotaceae were thought to be recalcitrant, some, in fact, show recalcitrant and others intermediate seed storage behaviour. All three categories of seed storage behaviour can be found among the members of Meliaceae. See also Appendix II.

Seed storage behaviour can also differ among species within a genus, e.g. most species in the genus *Acer* are orthodox but there are some that are not. Tompsett (Tompsett, 1983a) suggested that differences in desiccation tolerance among *Araucaria* species could be geographical and taxonomic in origin; e.g. *A. angustifolia* and *A. araucana* from South America and *A. bidwillii* from Australia in the Colymbea section of *Araucaria* mostly show recalcitrant seed storage behaviour, whereas species such as *A. heterophylla*, *A. cunninghamii*, *A. columnaris* and the numerous New Caledonian species in the Eutacta section are rather more tolerant of desiccation.

7.3. Association between plant, fruit, or seed characters and seed storage behaviour

Table 3 summarizes information on fruit and seed characteristics in relation to seed storage behaviour. It is clear from that summary that certain generalizations are possible. For example, orthodox seed storage behaviour is shown by species which produce achenes, many-seeded berries, many-seeded dehiscent capsules, many dry-seeded pods (but not arillate), many dry-seeded follicles, schizocarps and utricles. Most species which produce siliques (one known exception is *Wasabia* spp.) and caryopses (three known exceptions are *Porteresia coarctata*, *Spartina* spp. and *Zizania* spp.) also produce orthodox seeds. On the other hand, all three categories of seed storage behaviour can be found among the species which produce drupes containing 1-4 seeds or many arillate seeds; pods containing 1-5 large seeds or many arillate seeds; berries containing 1-10 seeds; capsules containing 1-5 seeds, and single-seeded nuts. In particular, and in contrast to some views, not all single-seeded nuts show recalcitrant seed storage behaviour.

The arillate character, present in seeds with short life spans in open storage, is not associated with seed storage behaviour; this characteristic is present in species which produce orthodox, intermediate and recalcitrant seeds.

The deciduous character is a mechanism by which plants avoid damage from either drought or cold. This character is not associated with desiccation tolerance in the seeds, but may be associated with chilling tolerance. For example, seeds of the deciduous rubber tree (*Hevea brasiliensis*) are recalcitrant, but despite the tropical lowland origin, the seeds are best stored at 7-10°C (Beng, 1976). Seeds of deciduous Dipterocarps (e.g. *Dipterocarpus alatus*, *D. intricatus*, *D. obtusifolius*, *D. tuberculatus*) can tolerate cool temperatures, as low as 6°C, while seeds of evergreen Dipterocarps must be stored at 10-15°C or warmer to avoid damage (Tompsett, 1992).

7.4. Association between seed size and storage behaviour

Seed size alone does not determine seed storage behaviour. Nevertheless, typically recalcitrant seeds do tend to be larger than intermediate seeds, which in turn do tend to be larger than orthodox seeds. Figure 8 gives some indication of the association between thousand-seed weight (TSW, g) and seed storage behaviour among species within a genus (*Acer*), and among genera within select families. A wider sample might change the overall picture. The heaviest TSW recorded for orthodox seeds are 6300 g in *Hardwickia pinnata* Roxb. (Leguminosae) and 5000-8000 g (at 10% moisture content) in cashew (*Anacardium occidentale* L.) (Anacardiaceae). If cashew is harvested at the end of the seed-filling phase, the fresh nut weight will be 13 g/nut (ca. 45% moisture content). Therefore species which produce seeds with TSW >13 000 g are unlikely to show orthodox seed storage behaviour. On the other hand, seeds with TSW between 30 and 13 000 g may show orthodox, intermediate or recalcitrant seed storage behaviour, and so seed size *per se* provides no indication of seed storage characteristics within this range. Similarly although species with smaller seeds (TSW <25 g) are likely to show orthodox seed storage behaviour, there are sufficient exceptions (e.g. intermediate seed storage behaviour within Orchidaceae and *Wasabia japonica* within Cruciferae) to indicate that this generalization is based on probability and is not prescriptive.

7.5. Association between seed moisture content at maturity (harvest maturity in crops) or shedding (wild species) and seed storage behaviour

Figure 9 shows information on the moisture content of seeds at maturity in crops (typically harvest maturity) or at shedding in wild species (termed MCS, seed moisture content at shedding) for selected species showing orthodox, intermediate or recalcitrant seed storage behaviour. While some discrimination is apparent within Figure 9, there is also considerable overlap. For species with recalcitrant seed storage behaviour these moisture contents are distributed between 36 and 90%, for intermediate between 23 and 55%, and for orthodox between <20 and 50%. Thus, it appears that seeds shed at moisture contents above 60% (w.b.) are likely to show recalcitrant seed storage behaviour, and that those shed or harvested at moisture contents of around 20% or below are very likely to show orthodox seed storage behaviour. However, while species with MCS <35% may not show recalcitrant seed storage behaviour, if MCS is between about 25 and 55% then no generalization is possible. It should, however, be clear that as more data become available this picture may change.

7.6. The use of several criteria combined to indicate likely seed storage behaviour

In sections 7.1-7.5 we have shown that most generalizations on probable seed storage behaviour based on a single criterion are subject to rather too many exceptions to be helpful. Nevertheless, it may be possible to develop a multiple-criteria predictive framework to suggest seed storage behaviour. In Figure 10 we have combined information on seed weight, seed moisture content at shedding and seed storage behaviour. In this presentation all species which combine a TSW of 2500 g and below with MCS of 23% and below (below and to the left of the dotted line) show orthodox seed storage behaviour, while those at the combinations of weights and moisture contents at shedding greater than those shown by the broken line show recalcitrant seed storage behaviour. However, evidence of all three types of seed storage behaviour can be detected between the two lines shown in Figure 10.

Clearly, while the development of a multiple-criteria decision framework for seed storage behaviour is worth pursuing, it will be necessary to involve more than two criteria in such schemes.

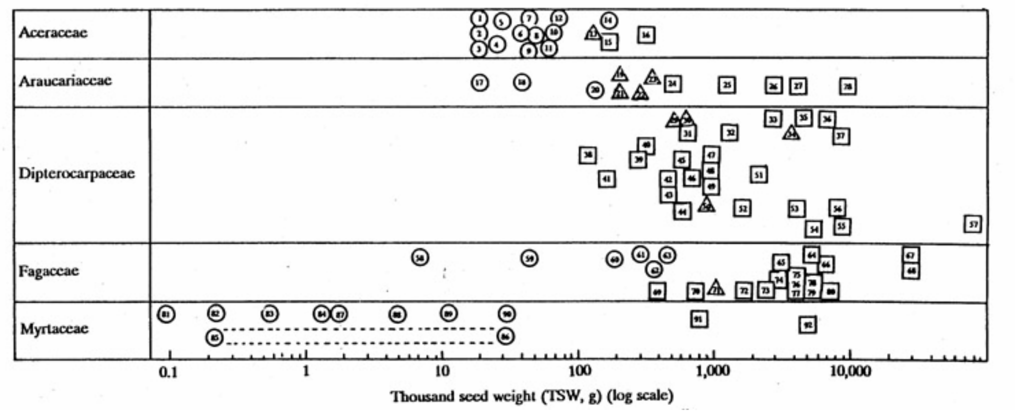

Fig. 8. Distribution of thousand-seed weight (TSW, g) for 92 species within 27 genera of 5 families. Circles indicate orthodox (including orthodox p and orthodox?; see Part IB, Introduction), triangles intermediate (including intermediate?), and squares recalcitrant (including recalcitrant?) seed storage behaviour. TSW values are from Part II. **Aceraceae**: 1, *Acer rubrum*; 2, *A. spicatum*; 3, *A. sieboldianum*; 4, *A. rufinerve*; 5, *A. ginnala*; 6, *A. pensylvanicum*; 7, *A. japonicum*; 8, *A. negundo*; 9, *A. tataricum*; 10, *A saccharum*; 11, *A. palmatum*; 12, *A. campestre*; 13, *A. macrophyllum*; 14, *A. platanoides*; 15, *A. pseudoplatanus*; 16, *A. saccharinum*. **Araucariaceae**: 17, *Agathis australis*; 18, *Agathis robusta*; 19, *Agathis macrophylla*; 20, *Araucaria cunninghamii*; 21, *A. scopulorum*; 22, *A. rulei*; 23, *A. columnaris*; 24, *A. hunsteinii*; 25, *A. heterophylla*; 26, *A. araucana*; 27, *A. angustifolia*; 28, *A. bidwilli*. **Dipterocarpaceae**: 29, *Dipterocarpus intricatus*; 30, *D. tuberculatus*; 31, *D. turbinatus*; 32, *D. crinitus*; 33, *D. baudii*; 34, *D. alatus*; 35, *D. zeylanicus*; 36, *D. obtusifolius*; 37, *D. pilosus*; 38, *Hopea helferi*; 39, *H. odorata*; 40, *H. wightiana*; 41, *Shorea acuminata*; 42, *S. parviflora*; 43, *S. leprosula*; 44, *S. dasyphylla*; 45, *S. bracteola*; 46, *S. pauciflora*; 47, *S. ovalis*; 48, *S. macroptera*; 49, *S. assamica*; 50, *S. platyclados*; 51, *S. roxburghii*; 52, *Anisoptera glabra*; 53, *Balanocarpus heimii*; 54, *Dryobalanops aromatica*; 55, *Dryobalanops oblongifolia*; 56, *Parashorea densiflora*; 57, *Vatica* sp. **Fagaceae**: 58, *Nothofagus obliqua*; 59, *N. procera*; 60, *Fagus sylvatica*; 61, *Fagus grandifolia*; 62, *Castanopsis sempervirens*; 63, *Castanopsis chrysophylla*; 64, *Lithocarpus densiflorus*; 65, *Castanea dentata*; 66, *C. mollissina*; 67, *C. crenata*; 68, *C. sativa*; 69, *Quercus vaccinifolia*; 70, *Q. falcata*; 71, *Q. emoryi*; 72, *Q. velutina*; 73, *Q. serrata*; 74, *Q. robur*; 75, *Q. rubra*; 76, *Q. borealis*; 77, *Q. alba*; 78, *Q. acutissima*; 79, *Q. suber*; 80, *Q. semecarpifolia*. **Myrtaceae**: 81, *Metrosiderox polymorpha*; 82, *Callistemon lanceolatus*; 83, *Melaleuca leucadendron*; 84, *Leptospermum scoparium*; 85, *Eucalyptus tereticornis*; 86, *Eucalyptus saligna*; 87, *Tristania conferta*; 88; *Syncarpia laurifolia*; 89, *Psidium guajava*; 90, *Myrtus communis*; 91, *Eugenia jambolana*; 92, *E. grandis*. The TSW of *Eucalyptus* spp. are shown by the two species with extreme TSW values. From (Hong & Ellis, 1996).

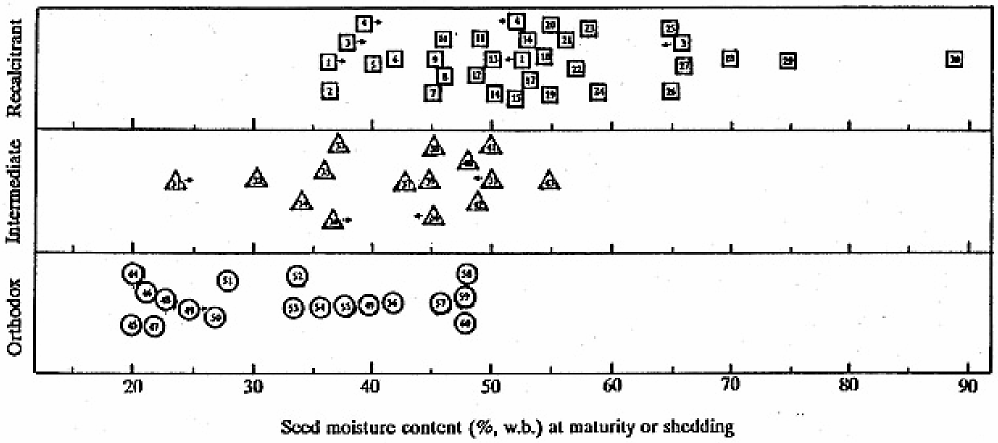

Fig. 9. Seed moisture content at maturity or shedding (MCS) for 60 species and seed storage behaviour. Data on MCS are from Part II. Circles represent orthodox (including orthodox p and orthodox?, see Part IB, Introduction), triangles intermediate (including intermediate?), and squares recalcitrant (including recalcitrant?) seed storage behaviour. 1, *Hevea brasiliensis*; 2, *Nephelium lappaceum*; 3, *Symphonia globulifera*; 4, *Durio zibethinus*; 5, *Hopea hainanensis*; 6, *Shorea acuminata*; 7, *Theobroma cacao*; 8, *Dimocarpus longan*; 9, *Shorea roxburghii*; 10, *Dryobalanops aromatica*; 11, *Aesculus hippocastaneum*; 12, *Quercus robur*; 13, *Shorea robusta*; 14, *Eugenia jambos*; 15, *Lansium domesticum*; 16, *Araucaria hunsteinii*; 17, *Artocarpus heterophyllus*; 18, *Dipterocarpus baudii*; 19, *Hancornia speciosa*; 20, *Myristica fragrans*; 21, *Balanocarpus heimii*; 22, *Coffea liberica*; 23, *Acer pseudoplatanus*; 24, *Calamus scipionum*; 25, *Persea americana*; 26, *Garcinia mangostana*; 27, *Avicennia marina*; 28, *Artocarpus champeden*; 29, *Telfairia occidentalis*; 30, *Sechium edule*; 31, *Elaeis guineensis*; 32, *Zizania palustris*; 33, *Shorea platyclados*; 34, *Azadirachta indica*; 35, *Araucaria columnaris*; 36, *Citrus limon*; 37, *Dacrycarpus dacrydioides*; 38, *Veitchia merillii*; 39, *Citrus reticulata*; 40, *Coffea arabica*; 41, *Coffea canephora*; 42, *Oreodoxa regia*; 43, *Carica papaya*; 44, *Oryza sativa*; 45, *Lens culinaris*; 46, *Glycine max*; 47, *Carya illinoensis*; 48, *Triticum aestivum*; 49, *Fagus sylvatica*; 50, *Annona muricata*; 51, *Acer platanoides*; 52, *Annona cherimolia*; 53, *Vitis vinifera*; 54, *Araucaria cunninghamii*; 55, *Cucumis melo*; 56, *Prunus avium*; 57, *Cucurbita moschata*; 58, *Punica granatum*; 59, *Lycopersicon esculentum*; 60, *Capsicum annum*. From (Hong & Ellis, 1996).

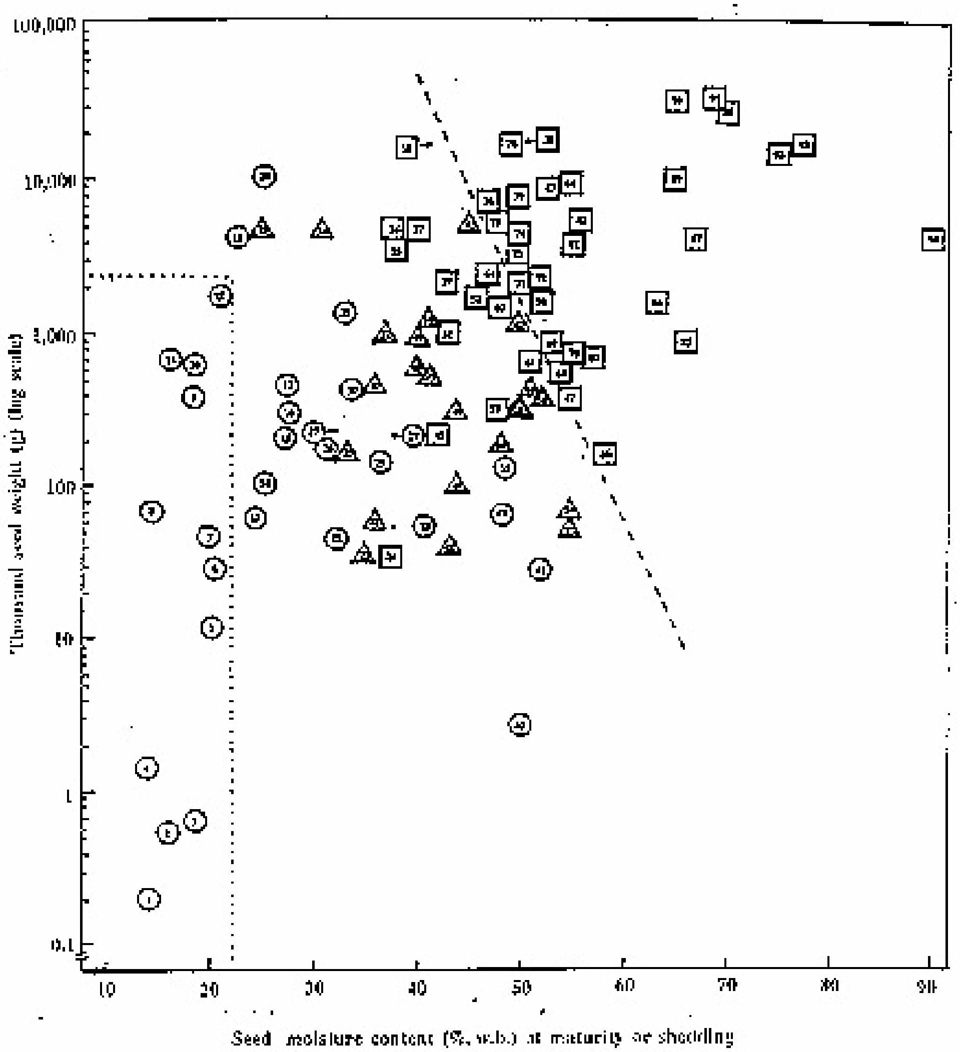
100,000
10,000
1,000
100
10
1
0.1
Thousand seed weight (g) (log scale)
10
20
30
40
50
60
70
80
90
Seed moisture content (%, w.b.) at maturity or shedding

Fig. 10. Seed storage behaviour of 94 contrasting species (number within symbol) in relation to seed moisture content at harvest/natural shedding (MCS) and thousand seed weight (TSW, log scale). Circles represent orthodox (including orthodox p and orthodox?, see Part IB, Introduction), triangles intermediate (including intermediate?), and squares recalcitrant (including recalcitrant?) seed storage behaviour. Data on MCS and TSW are from Part II.
1, *Saccharum officinarum*; 2, *Trifolium repens*; 3, *Lactuca sativa*; 4, *Brassica juncea*; 5, *Psidium guajava*; 6, *Oryza sativa*; 7, *Hordeum vulgare*; 8, *Albemoschus esculentus*; 9, *Glycine max*; 10, *Phaseolus vulgaris*; 11, *Ricinus communis*; 12, *Vicia faba*; 13, *Fraxinus excelsior*; 14, *Michelia champaca*; 15, *Acer platanoides*; 16, *Zea mays*; 17, *Annona muricata*; 18, *Carya illinoensis*; 19, *Elaeis guineensis*; 20, *Anacardium occidentale*; 21, *Vitis vinifera*; 22, *Piper nigrum*; 23, *Zizania palustris*; 24, *Porteresia coarctata*; 25, *Acer macrophyllum*; 26, *Terminalia brownii*; 27, *Fagus sylvatica*; 28, *Arum maculatum*; 29, *Araucaria cunninghamii*; 30, *Annona cherimolia*; 31, *Araucaria columnaris*; 32, *Shorea platyclados*; 33, *Phoenix dactylifera*; 34, *Dipterocarpus alatus*; 35, *Nephelium lappaceum*; 36, *Hevea brasiliensis*; 37, *Calophyllum maria*; 38, *Durio zibethinus*; 39, *Theobroma cacao*; 40, *Lycopersicon esculentum*; 41, *Punica granatum*; 42, *Podocarpus dacrydioides*; 43, *Malus domestica*; 44, *Citrus reticulata*; 45, *Shorea acuminata*; 46, *Citrus aurantium*; 47, *Azadirachta indica*; 48, *Manilkara achras*; 49, *Chrysophyllum cainito*; 50, *Quercus emoryi*; 51, *Shorea macroptera*; 52, *Dimocarpus longan*; 53, *Carica papaya*; 54, *Averrhoa carambola*; 55, *Cucurbita maxima*; 56, *Citrus limon*; 57, *Baccaurea motleyana*; 58, *Coffea arabica*; 59, *Citrus sinensis*; 60, *Diospyros kaki*; 61, *Shorea pauciflora*; 62, *Roystonea regia*; 63, *Landolphia kirkii*; 64, *Shorea roxburghii*; 65, *Veitchia merrillii*; 66, *Acer pseudoplatanus*; 67, *Acer saccharinum*; 68, *Araucaria hunsteinii*; 69, *Dysoxylum cauliflorum*; 70, *Nectandra ambigens*; 71, *Couepia polyandra*; 72, *Guilfoylia monostylis*; 73, *Eugenia jambos*; 74, *Araucaria araucana*; 75, *Dryobalanops aromatica*; 76, *Araucaria angustifolia*; 77, *Dipterocarpus obtusifolius*; 78, *Aesculus hippocastanum*; 79, *Diospyros confertiflora*; 80, *Coffea liberica*; 81, *Podocarpus henkelii*; 82, *Balanocarpus heimii*; 83, *Artocarpus heterophyllus*; 84, *Myristica fragrans*; 85, *Garcinia mangostana*; 86, *Dipterocarpus crinitus*; 87, *Quercus cerris*; 88, *Castanea sativa*; 89, *Persea americana*; 90, *Mangifera indica*; 91, *Castanospermum australe*; 92, *Telfairia occidentale*; 93, *Areca catechu*; 94, *Sechium edule*. The dotted and broken lines are discussed in the text. From (Hong & Ellis, 1996).

Part IB. Information on Seed Storage Behaviour

Introduction

Part II of this handbook summarizes information on survival (or otherwise) in seed storage for over 7000 species from 251 families. In each case we have attempted to classify seed storage behaviour into one of the three groups discussed at length in Part IA.

The definitions of orthodox in particular, intermediate and recalcitrant seed storage behaviour are comparatively precise. Only in a limited number of species are sufficiently comprehensive data available to satisfy these definitions, however. Hence, in order to provide as comprehensive a listing of species as possible we have often had to base our decision-making on less than comprehensive data sets. For this purpose, species have been classified into one of eight categories titled: **O**rthodox; **O**rthodox **p**; **Or**thodox**?**; **I**ntermediate; **I**ntermediate**?**; **R**ecalcitrant; **R**ecalcitrant**?**; and **U**ncertain.

Orthodox

The category **O**rthodox is used where we are either certain or almost certain that the species shows orthodox seed storage behaviour. The criteria applied in Part II of the Compendium are:

? Evidence of desiccation tolerance to <7% mc and survival (i.e. good maintenance of viability) in storage at subzero temperatures.
? Defined as orthodox by the authors shown, e.g. (Gordon & Rowe, 1982) and we have no evidence to the contrary, and/or currently listed as being stored in seed genebanks (classification here assumes that accessions are being tested regularly after entry into long-term stores and that listing by the genebank reflects accession survival in storage).
? No loss in viability (whole seeds) when exposed to liquid nitrogen at least overnight, e.g. (Pence, 1991a).
? Evidence of seed survival for >10 years.

Othodox p

The category **O**rthodox **p** (i.e. **O**rthodox **p**robable) has been used here where viability has been maintained for ?3 years but <10 years in open storage at ambient temperatures. This is because it is unlikely that either intermediate or recalcitrant seeds can survive beyond 2 years in open storage at ambient temperatures, and in most cases the seeds die within one year under such conditions. Hence in the **O**rthodox **p** category we suggest a high probability that the species shows orthodox seed storage behaviour and we would recommend attempted storage under IPGRI preferred conditions.

Orthodox?

The category **O**rthodox**?** implies that the probability that the species shows orthodox seed storage behaviour is >0.5, but that further investigation is likely to be necessary before attempting storage at the IPGRI preferred conditions for long-term seed storage. The criteria applied in Part IB of the Compendium are:

? Defined as orthodox by the authors shown, but some contradictory evidence is available.
? Longevity in open storage at ambient temperatures is ?1 but <3 years.
? Tolerant of desiccation to 15-18% moisture content, but no data available concerning desiccation tolerance to lower moisture contents.
? Air-dry storage has been recommended by the authors shown.
? Seeds reported to tolerate desiccation or where sun-drying has been recommended by the authors shown.
? Analogous (e.g. seed size and ecology) with closely related species which show orthodox seed storage behaviour.

We recommend that until further results are available the seeds of species shown as **O**rthodox**?** should be stored at 10-12% mc and 5-15°C (depending upon species).

Intermediate

The criteria applied in Part II of the Compendium for classification as **I**ntermediate seed storage behaviour are that seeds tolerate desiccation to about 10-12% mc, but further desiccation reduces viability, and/or there is more rapid reduction in viability during the storage of dry seeds at cooler (cf. warmer) temperatures.

Intermediate?

The criteria applied in Part II of the Compendium for **I**ntermediate**?** are:

? 'Excessive' drying reported to damage seed viability (e.g. *Corylus*).
? Analogous (e.g. seed size, ecology) to closely related species with intermediate seed storage behaviour. For example, in *Musa* four species show intermediate seed storage behaviour, so the suspicion must be that the remaining species have a better than even probability of showing intermediate seed storage behaviour.

Species shown as **I**ntermediate**?** are not believed to be recalcitrant; the doubt concerns whether they show intermediate or orthodox seed storage behaviour. Where classified in this category we suggest that intermediate seed storage behaviour is more likely than orthodox seed storage behaviour. Further investigations are required, and until such results are available it is recommended that the seeds be stored at about 10-12% moisture content with 5-15°C (depending on species).

Recalcitrant

The criteria applied for classification as **R**ecalcitrant seed storage behaviour in Part II of the Compendium are:

? Lowest safe moisture content >20%.
? Defined as such by authors shown and we have no evidence to the contrary.

Recalcitrant?

The criteria applied for **R**ecalcitrant**?** (i.e. provisionally classified as recalcitrant) in Part II of the Compendium are:

? 'short-lived' (in general).
? Difficult to maintain viability.
? Only 'moist storage' recommendations in the literature.
? Analogous (e.g. seed size, ecology) to closely related species which show recalcitrant seed storage behaviour, e.g. *Artocarpus* spp. other than *A. heterophyllus* where desiccation tolerance is lacking.

Uncertain

Finally, the category **U**ncertain has been applied for species where the data precludes classification into one of the above categories. In some of these cases the classification of seed storage behaviour is likely to be "obvious", despite the above criteria not having been met.

Species are listed by family. This listing by familty and taxa should help to some extent when dealing with species in which seed storage behaviour is not known. For example, all species listed within Chenopodiaceae, Compositae and Pinaceae show a tendency to orthodox seed storage behaviour.

The taxonomic classification into families and genera adopted here is that given in Brummitt (Brummitt, 1992). Estimates of the number of species within a genus are from Mabberley (Mabberley, 1987). Information on geographical distribution, natural habitat and ecology is mainly from Brummitt (Brummitt, 1992) and Mabberley (Mabberley, 1987), but occasionally from Young and Young (Young & Young, 1992) or as indicated. Information on fruit and seed characters is from

Bailey (Bailey, 1961), Purseglove (Purseglove, 1968), (Purseglove, 1972) and Mabberley (Mabberley, 1987). Common names are from Bailey (Bailey, 1961), Purseglove (Purseglove, 1968), (Purseglove, 1972) and Young and Young (Young & Young, 1992).

In some families (see Preface) the species names have been checked for synonymy and correct taxonomic authority. Displaced species names previously used by authors of seed references are placed in brackets as are other synonyms. Taxonomic or name difficulties or uncertainties are marked with an asterisk before the species name. In the other families, species synonymy has not been checked and readers should be aware of this. Similarly, in most cases taxonomic authorities have only been included if provided by the authors of the seed references.

For each species listed, information is presented in three sections. The first two quote information widely from Mabberley (Mabberley, 1987). The first includes characters of the plant (deciduous, succulent, etc.), the fruit (type of fruit, whether or not dehiscent, number of seeds per fruit, etc.), the seed (dry or arillate, thousand-seed weight (TSW), moisture content at maturity/shedding (MCS), etc.). The second comprises information on geographical distribution and adaptation. This information may be useful in estimating seed storage behaviour where it has not yet been established (see Part IA, Section 7). Where it was felt appropriate, the above information has been summarized at the generic level. The third summarizes published information on seed storage and provides a classification of seed storage behaviour.

We classify species in one of the eight categories mentioned above. However, many authors did not use the terms orthodox, intermediate and recalcitrant seed storage behaviour in their publications and in other cases our classification may differ from that of the original authors. For example, Tompsett (Tompsett, 1987), (Tompsett, 1990), (Tompsett, 1992), (Tompsett, 1994) classified *Dipterocarpus alatus* as ‘orthodox’, but we classify it here as ‘intermediate’. Similarly, Bonner (Bonner, 1990) classified *Citrus limon* and *Salix glauca* as ‘suborthodox’, but according to our system of classification the former is ‘intermediate’ and the latter is ‘orthodox’. In such cases, and in those cases where the information available on seed storage behaviour is in some way contradictory we provide additional comment.

Information on thousand-seed weight (TSW) is collated from Schopmeyer (Schopmeyer, 1974a), FAO (FAO, 1975) and Ellis (Ellis, 1984b), or as shown. These estimates are not always determined in the same manner (e.g. estimates will be at different moisture contents), and sometimes fruit rather than seed weight has been given (particularly in forest tree species). Note also that the term seed or whole seed herein often refers to the unit of propagation (propagule) rather than the true seed.

Moisture content (mc) throughout this document is always quoted as the percentage of the fresh weight (wet weight basis, w.b.) according to the rules of the International Seed Testing Association (ISTA, 1993a), (ISTA, 1993b). Where moisture content was expressed as a percentage on the dry basis (M_D) in the original publication, we have converted values to percentage wet weight basis (M_W) using the formula

$$M_W = (100 \times M_{D)} \ / \ (100 + M_D)$$

Seeds recorded as having been maintained successfully in long-term storage at RBG Kew, WP were all dried, packaged, stored at subzero temperatures and then tested for germination. All have been verified by an acknowledged taxonomic expert.

Up to 1977, collections at RBG Kew, WP were dried using ambient conditions/silica gel. Subsequently, collections (by far the majority in the following list) were dried for >1 month at 15% r.h. and 15°C (or most recently, at about 13% r.h. and 20°C). The pre-1977 collections were redried under these conditions and therefore will have had moisture contents that varied slightly during storage. This should be borne in mind when referring to the viability data. With the exception of a few species represented only by stored collections dried solely using the less controlled regime (indicated in list), all species have been dried under the more controlled conditions recommended by IPGRI (Cromarty *et al.*, 1982), stored at subzero temperatures and then tested for germination. The number of seeds used in the germination tests varied in relation to the total collection size. Except where specifically indicated, all germination is ?75% and empty or damaged seeds have been taken into account. Actual changes in germination with storage time are shown. Increases in germination are due to loss of dormancy during storage or sampling error. The age of the oldest collection in store represents the number of years between collection and the last successful germination test; retests are carried out about every 10 years. Where no data are presented, the period was less than one year. Bearing in mind variations in post-harvest history and initial quality, these figures should help to illustrate the absolute minimum longevities that might be expected in a conventional long-term seedbank.

There are two appendixes to this volume. Appendix I lists the known seed storage viability constants and Appendix II summarizes the distribution of type of seed storage behaviour in each of the families.

The information in the following pages will be available on-line in a database maintained by IPGRI. The current data presented should act as a base line from which a much improved picture of seed storage behaviour in the plant kingdom can be built. Accordingly, IPGRI welcomes corrections, omissions and indeed new information in order that this database can be maintained and developed. We recommend that the protocol developed for determining seed storage behaviour (Hong & Ellis, 1996) be followed in order to ensure that the probability of incorrect classification of seed storage behaviour is minimized as this database is maintained and developed.

Appendix I. Viability Constants

								Years of storage (1) at -20°C & dried to:	
Family	**Species**	**K_E**	**C_W**	**C_H**	**C_Q**	**References[1]**	**Notes**	**5% mc (fwb)**	**15%rh, 15°C (2)**
Aceraceae	*Acer platanoides*	7.22	4.23	0.0329	0.000478	(Dickie *et al.*, 1991)	Storage expt. at only 1 temp.	147	
Alliaceae	*Allium cepa*	6.975	3.47	0.04	0.000428	(Ellis & Roberts, 1981)		413	465
Alliaceae	*Allium cepa*	9.083	5.81	0.0329	0.000478	(Ellis et al., 1990d)	Storage expt. at only 1 temp.	843	1031
Araucariaceae	*Araucaria columnaris*	5.66	2.68	0.033	0.000478	(Tompsett, 1984a), (Tompsett, 1992)		49	
Araucariaceae	*Araucaria cunninghamii*	7.49	3.73	0.033	0.000478	(Tompsett, 1992)	Derived from limited data	615	
Caryophyllaceae	*Gypsophila elegans*	9.6	5.36	0.04	0.0004	RBG Kew, unpublished	Derived from limited data	8526	
Chenopodiaceae	*Beta vulgaris*	8.943	4.723	0.0329	0.000478	(Ellis et al., 1990d)	Storage expt. at only 1 temp.	3514	
Chenopodiaceae	*Chenopodium quinoa*	8.58	5.02	0.0329	0.000478	(Ellis et al., 1988)	Storage expt. at only 1 temp.	945	
Combretaceae	*Terminalia brassii*	5.016	2.161	0.0329	0.000478	(Tompsett, 1986b), (Dickie et al., 1990)		26	208
Compositae	*Guizotia abyssinica*	7.578	4.78	0.0329	0.000478	(Ellis et al., 1989)	Storage expt. at only 1 temp.	138	
Compositae	*Guizotia abyssinica*	7.494	4.257	0.0372	0.00048	(Zewdie & Ellis, 1991d)		322	
Compositae	*Helianthus annuus*	6.74	4.16	0.0329	0.000478	(Ellis et al., 1988)	Storage expt. at only 1 temp.	55	101
Compositae	*Lactuca sativa*	6.895	4.2	0.0329	0.000478	(Kraak & Vos, 1987), (Dickie et al., 1990		73	158
Compositae	*Lactuca sativa*	7.938	5.25	0.0329	0.00047	(Ellis et al., 1989)	Storage expt. at	149	391

								Years of storage (1) at -20°C & dried to:	
Family	**Species**	**K_E**	**C_W**	**C_H**	**C_Q**	**References[1]**	**Notes**	**5% mc (fwb)**	**15%rh, 15°C (2)**
					8		only 1 temp.		
Cruciferae	*Brassica juncea*	7.768	4.56	0.0329	0.000478	(Ellis et al., 1989)	Storage expt. at only 1 temp.	305	1493
Cruciferae	*Brassica napus*	7.718	4.54	0.0329	0.000478	(Ellis et al., 1989)	Storage expt. at only 1 temp.	281	
Cucurbitaceae	*Cucumis melo*	7.299	3.707	0.0367	0.000473	(Kuo, 1991)		490	
Cucurbitaceae	*Cucurbita pepo*	6.913	3.604	0.04	0.0004	RBG Kew, unpublished	Derived from limited data	296	
Dipterocarpaceae	*Dipterocarpus alatus*	5.92	2.69	0.033	0.000478	(Tompsett, 1992)	Derived from limited data	88	
Dipterocarpaceae	*Dipterocarpus intricatus*	6.18	2.77	0.033	0.000478	(Tompsett, 1992)	Derived from limited data	141	
Euphorbiaceae	*Manihot esculenta*		5.8			(Ellis *et al.*, 1981)			
Gramineae	*Eleusine coracana*	9.508	5.08	0.0329	0.000478	(Ellis et al., 1989)	Storage expt. at only 1 temp.	7266	
Gramineae	*Eragrostis tef*	10.098	6.01	0.0329	0.000478	(Ellis et al., 1989)	Storage expt. at only 1 temp.	6327	
Gramineae	*Eragrostis tef* cv. Muri	9.727	5.185	0.0329	0.00054	(Zewdie & Ellis, 1991d)		9596	
Gramineae	*Eragrostis tef* cvs.	9.927	5.185	0.0329	0.00054	(Zewdie & Ellis, 1991d)		15208	
Gramineae	*Hordeum vulgare*	9.144	5.342	0.0329	0.000478	(Ellis & Roberts, 1980b), (Dickie et al., 1990)		2061	688
Gramineae	*Oryza sativa*	8.668	5.03	0.0329	0.000478	(Ellis et al., 1989)	Storage expt. at only 1 temp.	1138	402
Gramineae	*Oryza sativa* ssp. *indica*	8.81	4.904	0.0329	0.000478	(Ellis et al., 1992)	Storage expt. at only 1 temp.	1933	706

								Years of storage (1) at -20°C & dried to:	
Family	**Species**	K_E	C_W	C_H	C_Q	**References**[1]	**Notes**	**5% mc (fwb)**	**15%rh, 15°C (2)**
Gramineae	*Oryza sativa* ssp. *japonica*	8.416	4.904	0.0329	0.000478	(Ellis et al., 1992)	Storage expt. at only 1 temp.	780	285
Gramineae	*Oryza sativa* ssp. *javanica*	8.736	4.904	0.0329	0.000478	(Ellis et al., 1992)	Storage expt. at only 1 temp.	1630	596
Gramineae	*Pennisetum glaucum*	8.728	4.86	0.0329	0.000478	(Ellis et al., 1989) as *P. americanum*)	Storage expt. at only 1 temp.	1718	691
Gramineae	*Phleum pratense*	9.571	5.262	0.04	0.0004	RBG Kew, unpublished	Derived from limited data	9338	
Gramineae	*Phleum pratense* cv. *Erecta*	8.678	4.75	0.0329	0.000478	(Ellis et al., 1989)	Storage expt. at only 1 temp.	1828	
Gramineae	*Phleum pratense* cv. *S325*	8.138	4.75	0.0329	0.000478	(Ellis et al., 1989)	Storage expt. at only 1 temp.	527	
Gramineae	*Setaria italica*	8.678	4.95	0.0329	0.000478	(Ellis et al., 1989)	Storage expt. at only 1 temp.	1325	
Gramineae	*Sorghum bicolor*	10.588	6.305	0.041	0.000349	(Kuo *et al.*, 1990)		19890	6106
Gramineae	*Triticum aestivum*	9.42	5.859	0.0329	0.000478	(Ellis et al., 1990d)	Storage expt. at only 1 temp.	1693	508
Gramineae	*Zea mays*	8.579	4.91	0.0329	0.000478	SSLR, unpublished	Storage expt. at only 1 temp.	1125	460
Hamamelidaceae	*Liquidambar styraciflua*	6.55309	3.033052	0.0081	0.00151	(Bonner, 1994)	Data based on 5 years storage	27	
Hamamelidaceae	*Liquidambar styraciflua*	6.384753	2.70571	0.0306	0.000967	(Bonner, 1994)	Data based on 10 years storage	143	
Leguminosae	*Arachis hypogaea*	6.718	4.089	0.0329	0.000478	(Ellis et al., 1990d)	Storage expt. at only 1 temp.	58	236
Leguminosae	*Cicer arietinum*	8.901	4.847	0.0329	0.000478	(Ellis et al., 1982), (Dickie et al., 1990)		2613	1115

Family	Species	K_E	C_W	C_H	C_Q	References[1]	Notes	Years of storage (1) at -20°C & dried to: 5% mc (fwb)	15%rh, 15°C (2)
Leguminosae	*Cicer arietinum*	8.502	4.602	0.0295	0.000491	(Ellis, 1988)		1307	
Leguminosae	*Glycine max*	7.525	4.086	0.0329	0.000478	(Ellis et al., 1982), (Dickie et al., 1990)		374	321
Leguminosae	*Glycine max*	7.292	3.996	0.0295	0.000491	(Ellis, 1988)		214	184
Leguminosae	*Lupinus polyphyllus*	6.217	2.761	0.04	0.0004	(Dickie & Bowyer, 1985)		231	
Leguminosae	*Phaseolus vulgaris*	9.09	4.761	0.0329	0.000478	(Ellis et al., 1990d)	Storage expt. at only 1 temp.	4637	
Leguminosae	*Pisum sativum*	9.858	5.39	0.0329	0.000478	(Ellis et al., 1989)	Storage expt. at only 1 temp.	9876	3180
Leguminosae	*Psophocarpus tetragonolobus*		3.9			(Ellis *et al.*, 1985c)			
Leguminosae	*Trifolium subterraneum*	7.21	3.51	0.04	0.0004	RBG Kew, unpublished	Derived from limited data	682	
Leguminosae	*Vigna radiata*	10.858	6.27	0.0329	0.000478	(Ellis et al., 1989)	Storage expt. at only 1 temp.	23960	
Leguminosae	*Vigna unguiculata*	9.401	5.118	0.0329	0.000478	(Ellis et al., 1982), (Dickie et al., 1990)		5342	1687
Leguminosae	*Vigna unguiculata*	9.102	4.967	0.0295	0.000491	(Ellis, 1988)		2891	1042
Linaceae	*Linum usitatissimum*	7.76	4.86	0.0329	0.000478	(Ellis et al., 1988)	Storage expt. at only 1 temp.	185	509
Meliaceae	*Entandophragma angolense*	4.6	2.21	0.033	0.000478	(Tompsett, 1992)	Derived from limited data	9	
Meliaceae	*Khaya senegalensis*	4.76	2.15	0.033	0.000478	(Tompsett, 1992)	Derived from limited data	15	
Meliaceae	*Swietinia humilis*	5.393	2.391	0.0329	0.00047	(P.B. Tompsett, unpubl.),		42	314

Family	Species	K_E	C_W	C_H	C_Q	References[1]	Notes	Years of storage (1) at -20°C & dried to:	
								5% mc (fwb)	15%rh, 15°C (2)
					8	(Dickie et al., 1990)			
Papaveraceae	*Papaver nudicaule*	6.838	4.101	0.027	0.000313	(Belletti *et al.*, 1991)		67	
Pedaliaceae	*Sesamum indicum*	7.19	4.02	0.04	0.000428	(Ellis *et al.*, 1986)	Storage expt. at only 1 temp.	279	1332
Pinaceae	*Pinus elliottii*	5.587688	1.449494	0.0326	0.00101	(Bonner, 1994)	Data based on 5 years storage	182	
Pinaceae	*Pinus elliottii*	5.246319	0.983174	0.0508	0.000571	(Bonner, 1994)	Data based on 10 years storage	608	
Pinaceae	*Pinus occidentalis*	5.047441	1.677614	0.0206	0.00126	(Bonner, 1994)	Data based on 5 years storage	17	
Pinaceae	*Pinus occidentalis*	5.101286	1.674234	0.0354	0.000838	(Bonner, 1994)	Data based on 10 years storage	55	
Pinaceae	*Pinus taeda*	3.618404	-0.256684	0.000644	0.00122	(Bonner, 1994) (4)	Data based on 5 years storage	6	
Pinaceae	*Pinus taeda*	3.278271	-0.729973	0.0348	0.000328	(Bonner, 1994) (4)	Data based on 10 years storage	62	
Ranunculaceae	*Delphinium ambiguum*	7.67	3.12	0.04	0.0004	RBG Kew, unpublished	Derived from limited data	3685	
Ranunculaceae	*Ranunculus sceleratus*	6.98	5.01	0.0329	0.000428	R.J. Probert, RBG Kew, unpublished	Storage expt. at only 1 temp.	24	41(3)
Rosaceae	*Malus domestica*	7.316	4.119	0.04	0.000428	(Dickie, 1988)	C_W and C_Q from *Hordeum*	318	
Scrophulariaceae	*Digitalis purpurea*	7.49	5.61	0.0329	0.000478	F.R. Hay, RBG Kew, unpublished	Storage expt. at only 1 temp.	30	258(3)
Ulmaceae	*Ulmus carpinifolia*	5.83	3.035	0.0329	0.000478	(Tompsett, 1986b), (Dickie et al., 1990)		41	32

[1] Parentheses = constants derived from data presented in reference.

(1) Viability 97.7 falling to 84.1% (1 probit).

(2) Equilibrium mc/rh equation from (Dickie et al., 1990) and (Cromarty *et al.*, 1982).

(3) Based on data by R.J. Probert, unpublished.

Appendix II. List of plant families in this Compendium and the number of species in the different categories of seed storage behaviour

			Total no. of species in										
Family			**Mabberley (Mabberley, 1987)**	**this Compendium**	**Percentage collated here[1]**	**O**	**Op**	**O?**	**I**	**I?**	**R**	**R?**	**U**
Acanthaceae	D		4300	13	0.30	6	7						
Aceraceae	D		113	33	29.20	17		10		1	2		3
Actinidiaceae	D		355	6	1.69	3		3					
Agavaceae	M	Total & % incl.assoc. families	410	30	7.32	19		2					
Aizoaceae	D		2400	10	0.42	3	4	3					
Alismataceae	M		95	7	7.37	2		5					
Alliaceae	M	See Liliaceae		17		17							
Aloaceae	M		400	3	0.75	2		1					
Alstroemeriaceae	M	See Liliaceae		5		4		1					
Amaranthaceae	D		800	35	4.38	31	1	3					
Amaryllidaceae	M	See Liliaceae		4		1	1	1			1		
Anacardiaceae	D		850	53	6.24	9	10	20			4	6	4
Annonaceae	D		2050	14	0.68	7		3				2	2
Anthericaceae	M	See Liliaceae		5		4		1					
Apocynaceae	D		2100	27	1.29	8	7	7			2		3
Aquifoliaceae	D		420	8	1.90		1	7					
Araceae	M		2950	12	0.41	4		6			1		1
Araliaceae	D		800	14	1.75	2	2	10					
Araucariaceae	G		31	17	54.84	3		1	4	2	5		2
Aristolochiaceae	D		410	1	0.24	1							
Asclepiadaceae	D		2850	14	0.49	12	1	1					
Asparagaceae	M		50	5	10.00	1	3	1					
Asphodelaceae	M	See Liliaceae		6		4	2						
Avicenniaceae	D		14	1	7.14						1		
Balanitaceae	D		25	1	4.00	1							
Balsaminaceae	D		850	5	0.59	2	1	2					

			Total no. of species in										
Family			**Mabberley (Mabberley, 1987)**	**this Compendium**	**Percentage collated here[1]**	**O**	**Op**	**O?**	**I**	**I?**	**R**	**R?**	**U**
Basellaceae	D		15	2	13.33		1	1					
Begoniaceae	D		900	4	0.44	2	2						
Berberidaceae	D		570	18	3.16	1	3	14					
Betulaceae	D	Total & % incl. assoc. families	150	34	22.67	13	1	13					
Bignoniaceae	D		725	33	4.55	9	11	11		1	1		
Bixaceae	D	Total & % incl. assoc. families	16	3	18.75				1				
Bombacaceae	D		250	12	4.80	2	6	2			2		
Boraginaceae	D		2500	38	1.52	15	15	8					
Bromeliaceae	M		2100	23	1.10	3	17	3					
Buddlejaceae	D	See Loganiaceae		5		2		3					
Burseraceae	D		540	6	1.11			5					1
Butomaceae	M		1	1	100.00		1						
Buxaceae	D		60	1	1.67								1
Cactaceae	D		1650	6	0.36	5	1						
Callitrichaceae	D		17	1	5.88			1					
Calycanthaceae	D		9	4	44.44			4					
Campanulaceae	D		1950	36	1.85	32	3	1					
Canellaceae	D		16	1	6.25					1			
Cannabaceae	D		3	3	100.00	1	1	1					
Cannaceae	M		25	4	16.00	3	1						
Canotiaceae	D		3	1	33.33	1							
Capparaceae	D		675	15	2.22	11	2	1			1		
Caprifoliaceae	D		400	34	8.50	17	11	6					
Caricaceae	D		31	7	22.58				1	6			
Caryocaraceae	D		24	1	4.17								1
Caryophyllaceae	D		2070	158	7.63	132	17	9					
Casuarinaceae	D		70	16	22.86	5	1	10					
Cecropiaceae	D		200	1	0.50			1					
Celastraceae	D		1300	14	1.08	3		8		2		1	
Ceratophyllaceae	D		2	1	50.00			1					

			Total no. of species in										
Family			**Mabberley (Mabberley, 1987)**	**this Compendium**	**Percentage collated here[1]**	**O**	**Op**	**O?**	**I**	**I?**	**R**	**R?**	**U**
Cercidiphyllaceae	D		1	1	100.00	1							
Chenopodiaceae	D		1300	107	8.23	91	8	8					
Chrysobalanaceae	D		460	2	0.43						2		
Cistaceae	D		175	28	16.00	23	4	1					
Clethraceae	D		64	4	1.56	1		3					
Cobaeaceae	D		10	1	20.00			1					
Cochlospermaceae	D	See Bixaceae		2		1		1					
Colchicaceae	M	See Liliaceae		1		1							
Combretaceae	D		500	31	6.20	20	4	4	1				2
Commelinaceae	M		620	3	0.48	3							
Compositae	D		21000	431	2.05	305	70	54					2
Connaraceae	D		380	2	0.53	2							
Convallariaceae	M	See Liliaceae		2		2							
Convolvulaceae	D		1650	31	1.88	25	5	1					
Coriariaceae	D		5	2	40.00	1		1					
Cornaceae	D		90	15	16.67	3	11						1
Corylaceae	D	See Betulaceae		7		2		1		1			3
Corynocarpaceae	D		4	1	25.00				1				
Crassulaceae	D		1500	28	1.87	21	3	4					
Cruciferae	D		3000	520	17.33	509	8	2	1				
Cucurbitaceae	D		760	40	5.26	30	6	2			2		
Cupressaceae	G		113	44	38.94	28	4	12					
Cycadaceae	G		20	4	20.00			3					1
Cyperaceae	M		3600	45	1.25	27	2	16					
Cyrillaceae	D		14	1	7.14			1					
Daphniphyllaceae	D		10	1	10.00			1					
Datiscaceae	D		4	1	25.00							1	
Dioscoreaceae	M		630	18	2.86	6	1	11					
Dipsacaceae	D		250	13	5.20	10		3					
Dipterocarpaceae	D		530	88	16.60				4	1	44	38	1

Family			Total no. of species in										
			Mabberley (Mabberley, 1987)	this Compendium	Percentage collated here[1]	O	Op	O?	I	I?	R	R?	U
Dracaenaceae	M	See Agavaceae		6		3	1	2					
Ebenaceae	D		485	19	3.92	1	2	3		2	2	6	3
Elaeaginaceae	D		45	8	17.78		3	5					
Elaeocarpaceae	D		520	4	0.77						1	3	
Elatinaceae	D		32	1	3.13	1							
Epacridaceae	D		400	5	1.25	1		4					
Ephedraceae	G		40	6	15.00	5		1					
Ericaceae	D		3350	60	1.79	49	2	9					
Eriocaulaceae	M		1200	1	0.08			1					
Erythroxylaceae	D		260	2	0.77			1				1	
Eucommiaceae	D		1	1	100.00	1							
Euphorbiaceae	D		7950	44	0.55	19	6	12			1	2	4
Fagaceae	D		1050	78	7.43	3	2	2		1	18	51	1
Flacourtiaceae	D		875	6	0.69		1	3					2
Fouquieriaceae	D		11	1	9.09	1							
Gentianaceae	D		1200	31	2.58	29	2						
Geraniaceae	D		730	16	2.19	9	3	4					
Gesneriaceae	D		2400	6	0.25	4	2						
Ginkgoaceae	G		1	1	100.00			1					
Globulariaceae	D		250	1	0.40	1							
Gnetaceae	G		28	1	3.57	1							
Goodeniaceae	D		430	2	0.47	2							
Gramineae	M		9000	504	5.60	427	15	55	3		2	2	
Griseliniaceae	D		6	1	16.67						1		
Grossulariaceae	D		150	22	14.67	9	3	10					
Guttiferae	D		1350	38	2.81	13	3	6			7	9	
Haemodoraceae	M		85	6	7.06	2		4					
Haloragaceae	D		100	2	2.00			2					
Hamamelidaceae	D		90	11	12.22	4	1	6					
Heliconiaceae	M		100	0	0.00								

Family			Total no. of species in										
			Mabberley (Mabberley, 1987)	this Compendium	Percentage collated here[1]	O	Op	O?	I	I?	R	R?	U
Hernandiaceae	D		68	1	1.47			1					
Hippocastanaceae	D		15	9	60.00						2	7	
Hostaceae	M	See Liliaceae		1		1							
Hyacinthaceae	M	See Liliaceae		10		10							
Hydrangeaceae	D		170	4	2.35	1	1	2					
Hydrocharitaceae	M		90	2	2.22				1			1	
Hydrophyllaceae	D		275	5	1.82	3	1	1					
Hypoxidaceae	M	See Liliaceae		1				1					
Icacinaceae	D		320	2	0.63	1						1	
Illecebraceae	D		100	5	5.00	3	1	1					
Iridaceae	M		1800	22	1.22	17		5					
Irvingiaceae	D	See Simaroubaceae		1		1							
Juglandaceae	D		59	16	27.12	1	5	8					2
Juncaceae	M		325	24	7.38	17		7					
Juncaginaceae	M		18	1	5.56	1							
Labiatae	D		5600	134	2.39	103	23	8					
Lardizabalaceae	D		21	2	9.52			2					
Lauraceae	D		2200	35	1.59	1		2			12	14	6
Lecythidaceae	D		280	9	3.21	1		2		2	3		1
Leguminosae	D		16400	1088	6.63	866	85	123			11	2	1
Lentibulariaceae	D		245	2	0.82			2					
Liliaceae	M	Total & % incl. assoc. families	4550	64	1.41	8							
Limnanthaceae	D		8	2	25.00	2							
Linaceae	D		300	7	2.33	5	2						
Loasaceae	D		260	4	1.54	3	1						
Loganiaceae	D	Total & % incl. assoc. families	600	9	1.50	1	1	2					
Lomandraceae	M	See Xanthrorrhaceae		1				1					
Loranthaceae	D		940	1	0.11			1					
Lythraceae	D		580	16	2.76	5	4	6					1
Magnoliaceae	D		200	17	8.50	2	4	4				3	4

Family			Total no. of species in										
			Mabberley (Mabberley, 1987)	this Compendium	Percentage collated here[1]	O	Op	O?	I	I?	R	R?	U
Malesherbiaceae	D		27	1	3.70	1							
Malpighiaceae	D		1100	1	0.09							1	
Malvaceae	D		1550	84	5.42	74	2	6	1		1		
Melanthiaceae	M	See Liliaceae		3		3							
Melastomataceae	D		4750	2	0.04	1		1					
Meliaceae	D		575	63	10.96	9	5	8	3	3	17	13	5
Meliosmaceae	D			1								1	
Menispermaceae	D		520	2	0.38	1		1					
Menyanthaceae	D		40	2	5.00	1		1					
Molluginaceae	D		100	2	2.00	2							
Monimiaceae	D		450	2	0.44		1				1		
Moraceae	D		1200	43	3.58	5	4	13			14	7	
Moringaceae	D		14	2	14.29		2						
Musaceae	M		42	6	14.29			1	3	2			
Myoporaceae	D		220	6	2.73	3	3						
Myricaceae	D		50	7	14.00	2	1	4					
Myristicaceae	D		440	8	1.82	1		1			6		
Myrsinaceae	D		1250	2	0.16	2							
Myrtaceae	D		3850	141	3.66	69	9	41			6	15	1
Nelumbonaceae	D		2	2	100.00	2							
Nesogenaceae	D		7	1	14.29	1							
Nyctaginaceae	D		350	2	0.57		1	1					
Nymphaeaceae	D		60	4	6.67	1						2	1
Olacaceae	D		200	1	0.50	1							
Oleaceae	D		900	37	4.11	12	11	14					
Onagraceae	D		650	107	16.46	101	1	5					
Orchidaceae	M		17500	81	0.46	30	8	15	7	12			9
Oxalidaceae	D		575	3	0.52			1	1	1			
Paeoniaceae	D		34	1	2.94		1						
Palmae	M		2650	121	4.57	5	4	17	7	6	7	39	36

Family			Total no. of species in		Percentage collated here[1]	O	Op	O?	I	I?	R	R?	U
			Mabberley (Mabberley, 1987)	this Compendium									
Pandaceae	D		18	2	11.11	1		1					
Papaveraceae	D		210	49	23.33	43	5	1					
Parnassiaceae	D			1									1
Passifloraceae	D		530	8	1.51				1	7			
Pedaliaceae	D		95	6	6.32	5		1					
Phormiaceae	M	See Agavaceae		3		1		1				1	
Phytolaccaceae	D		65	1	1.54	1							
Pinaceae	G		194	107	55.15	82	10	11					4
Piperaceae	D		1940	6	0.31		3	2	1				
Pittosporaceae	D		240	8	3.33			4				3	1
Plantaginaceae	D		255	15	5.88	12	3						
Platanaceae	D		6	3	50.00	3							
Plumbaginaceae	D		440	9	2.05	5	3	1					
Podocarpaceae	G		155	10	6.45	1		0	2		5	2	
Podostemaceae	D		275	5				4					1
Polemoniaceae	D		275	9	3.27	6	1	2					
Polygalaceae	D		950	4	0.42	3		1					
Polygonaceae	D		1150	45	3.91	30	7	5			1		2
Pontederiaceae	M		31	1	3.23			1					
Portulacaceae	D		400	8	2.00	7	1						
Potamogetonaceae	M		90	5	5.56			4					1
Primulaceae	D		800	33	4.13	25	5	3					
Proteaceae	D		1350	69	5.11	9	1	53				1	5
Ranunculaceae	D		1750	88	5.03	72	3	13					
Resedaceae	D		75	6	8.00	4	1	1					
Rhamnaceae	D		875	42	4.80	11	13	18					
Rhipogonaceae	M	See Liliaceae		1							1		
Rhizophoraceae	D		130	9	6.92					1	6	2	
Rosaceae	D		3100	187	6.03	66	40	74			1	2	4
Rubiaceae	D		10400	47	0.45	24	3	12	3		1	2	2

			Total no. of species in										
Family			**Mabberley (Mabberley, 1987)**	**this Compendium**	**Percentage collated here[1]**	**O**	**Op**	**O?**	**I**	**I?**	**R**	**R?**	**U**
Rutaceae	D		1700	55	3.24	12	3	9	13	4	1	6	7
Salicaceae	D		435	52	11.95	45		5	2				
Salvadoraceae	D		11	2	18.18			1				1	
Santalaceae	D		500	1	0.20		1						
Sapindaceae	D		1325	34	2.57	9	1	8			8	7	1
Sapotaceae	D		1000	27	2.70	1			2	4	5	13	2
Saxifragaceae	D		475	11	2.32	4	2	5					
Scrophulariaceae	D		4450	113	2.54	92	17	4					
Simaroubaceae	D	Total & % incl.assoc. families	170	6	3.53			4					1
Simmondsiaceae	D		1	1	100.00	1							
Smilacaceae	M		225	3	1.33		3						
Solanaceae	D		2600	147	5.65	138	4	5					
Staphyleaceae	D		27	1	3.70	1							
Sterculiaceae	D		1500	31	2.07	13	2	8		1	2	4	1
Stylobasiaceae	D	See Surianaceae		2		2							
Strelitziaceae	M		7	1	14.29				1				
Stylidiaceae	D		170	1	0.59	1							
Styracaceae	D		165	5	3.03	2		3					
Surianaceae	D	Total & % incl. assoc. families	5	3	60.00						1		
Tamaricaceae	D		78	2	2.56			1				1	
Taxaceae	G		20	7	35.00		5	2					
Taxodiaceae	G		14	10	71.43	8		2					
Tecophilaeaceae	M	See Liliaceae		1		1							
Theaceae	D		520	9	1.73	1		1		2	2	3	
Theophrastaceae	D		90	1	1.11	1							
Thymelaeaceae	D		720	8	1.11	3		1			3	1	
Tiliaceae	D		725	22	3.03	15	2	3					2
Trapaceae	D		1	1	100.00							1	
Tropaeolaceae	D		88	1	1.14	1							
Typhaceae	M		10	6	60.00	1		5					

			Total no. of species in										
Family			**Mabberley (Mabberley, 1987)**	**this Compendium**	**Percentage collated here[1]**	**O**	**Op**	**O?**	**I**	**I?**	**R**	**R?**	**U**
Ulmaceae	D		140	25	17.86	8	3	11				1	2
Umbelliferae	D		3100	76	2.45	57	10	8					1
Urticaceae	D		1050	5	0.48	1	3	1					
Valerianaceae	D		400	5	1.25	2	2	1					
Verbenaceae	D		1900	28	1.47	13	1	9				3	2
Violaceae	D		830	7	0.84	2		5					
Viscaceae	D		450	1	0.22							1	
Vitaceae	D		800	9	1.13	1	1	7					
Vochysiaceae	D		210	1	0.48			1					
Xanthorroeaceae	M	Total & % incl. assoc. families	60	4	6.67			3					
Zamiaceae	G		100	3	3.00			3					
Zannichelliaceae	M		8	1	12.50		1						
Zingiberaceae	M		1300	3	0.23	1		1	1				
Zosteraceae	M		17	2	11.76							2	
Zygophyllaceae	D		250	8	3.20	8							
Total			235350	6866	2.92	4353	647	1091	65	63	217	285	145
Summarized total of O / I / R / U						6091			128		502		145
Percentage of O / I / R / U						88.7			1.9		7.3		2.1
Summary gymnosperms						128	19	36	6	2	10	2	7
Summary dicots						3594	568	883	36	41	195	238	91
Summary monocots						631	60	172	23	20	12	45	47

[1] Percentage of total species.

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Part II. Compendium

Note to the reader:

The information on seed storage behaviour for the more than 7000 taxa is now available through the online searchable database 'IPGRI Species Compendium' on IPGRI's web site at www.ipgri.cgiar.org/themes/exsitu/IPGRIspeciescompendium