Seed Storage Behaviour – what do we know now, that we did not know 50 years ago?

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Global Crop Diversity Trust GROW webinar, 16 May 2024 plants MDPI

Review

Seed Longevity—The Evolution of Knowledge and a Conceptual Framework

Jayanthi Nadarajan [1,*], Christina Walters [2], Hugh W. Pritchard [3,4], Daniel Ballesteros [5,*] and Louise Colville [3]

Citation: Nadarajan, J.; Walters, C.; Pritchard, H.W.; Ballesteros, D.; Colville, L. Seed Longevity—The Evolution of Knowledge and a Conceptual Framework. *Plants* 2023, *12*, 471. https://doi.org/10.3390/ plants12030471

Talk Scope

- Seed storage – effect of moisture content
- Seed storage classification
- Relationship between seed moisture content, RH and temperature
- Cytoplasmic solidification - molecular motion and seed longevity
- Can we predict seed storage behaviour?
- Ageing of orthodox seeds during storage
- Seed storage recommendations – orthodox, oily, recalcitrant seeds
- Take home messages

The beginning of seed storage science

In **1832**, Augustin Pyramus de Candolle of France included a chapter on seed preservation in his book "Physiologie Végétale." (Plant Physiology)

He pointed out that the vitality of seeds would be prolonged if stored under conditions to protect them from heat, moisture, and oxygen

In 1908 Ewart created a list of short-, medium- and long-lived seeds stored under ambient environments.

50 years ago, Roberts and Ellis published an article on Predicting the storage life of seeds. *Seed Sci. Tech.* **1973**, *1*, 499–514.

Seed storage science and technology have advanced ever since...

Seed Storage Science

It is the most efficient approach to ensure the long-term availability of plant genetic resources.

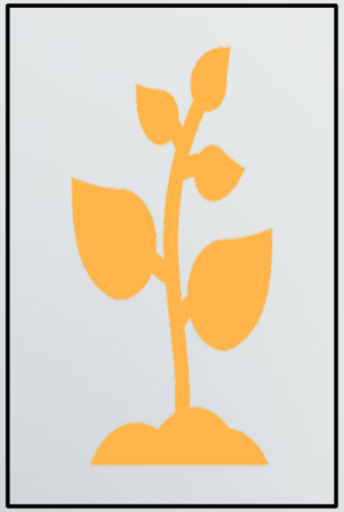
The last 50 years have seen the basic question asked how long can seeds live?

The reliable prediction of the duration for which seeds remain viable (i.e., lifespan or longevity) has been a concern for more than 100 years.

Understandings of different seed storage classifications

Understandings of factors contributing to seed longevity has led to major advancements in gene banking.

Seed storage for industry/breeders/farmers



Focus on economically important crop species

Preserve planting stocks from one season until the next

Farmers and breeders found the advantage of carrying over seeds for 2 or more years – improved soil quality

Different seed species and varieties; mostly vegetable, flower, and forage seeds—move freely in world commerce

Provide supplies of desired genetic stocks for use in years following periods of low production

Seed storage for genebanking

Protecting food plant biodiversity

Readily available source of material for research, re-introduction

Counter for the loss of diversity in human diets and in ecosystems

Insurance policy against species extinction

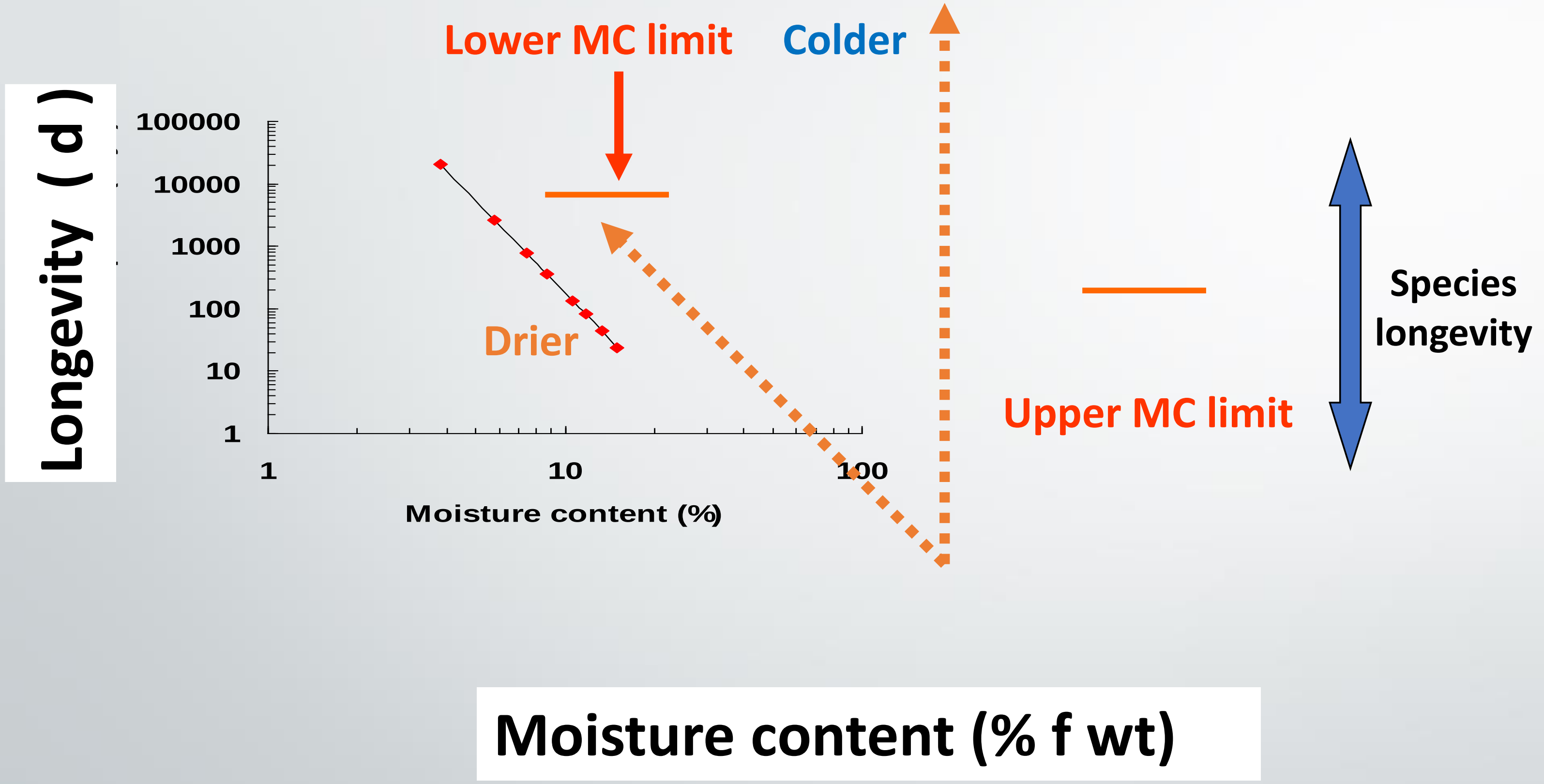
To conserve and promote biodiversity for food and nutrition

There are more than 1750 seed banks in the world

Storing a combined total of about 7 million accessions of food and forage crop diversity (FAO)

Dedicated wild species seed banks

Scientific basis of seed storage – seed moisture content



- Seed moisture is the most important factor in maintaining viability during seed storage
- Harrington's rule of thumb
- Low metabolic rates delayed seed ageing in dry state
- Ultra-low drying to 2% - imbibitional damage!

Caution: not all seeds respond to desiccation equally!!

Seed storage behaviour

- Classification of seed storage behaviour is largely dependent on tolerance to desiccation
- Seeds that do not survive desiccation are frequently referred to as ‘recalcitrant’ on account of difficulties in storing them
- A larger proportion of species produces desiccation tolerant seeds, termed ‘orthodox,’ which tend to be more amenable to dry-cold storage
- The orthodox versus recalcitrant delineation provides an immediate perspective on the investment of infrastructure for effective conservation of the two types of seeds in genebanks

Orthodox seeds

Desiccation tolerance is a continuous phenotype

Orthodox with limited desiccation ability’, ‘sub-orthodox’, intermediate, Class II and ‘minimally recalcitrant’

Recalcitrant seeds

Basic seed storage classification

“Orthodox” (desiccation-tolerant)

- seeds tolerate desiccation to low (c. 5 %) moisture contents
- seed longevity increases with decreasing moisture content and lower temperature

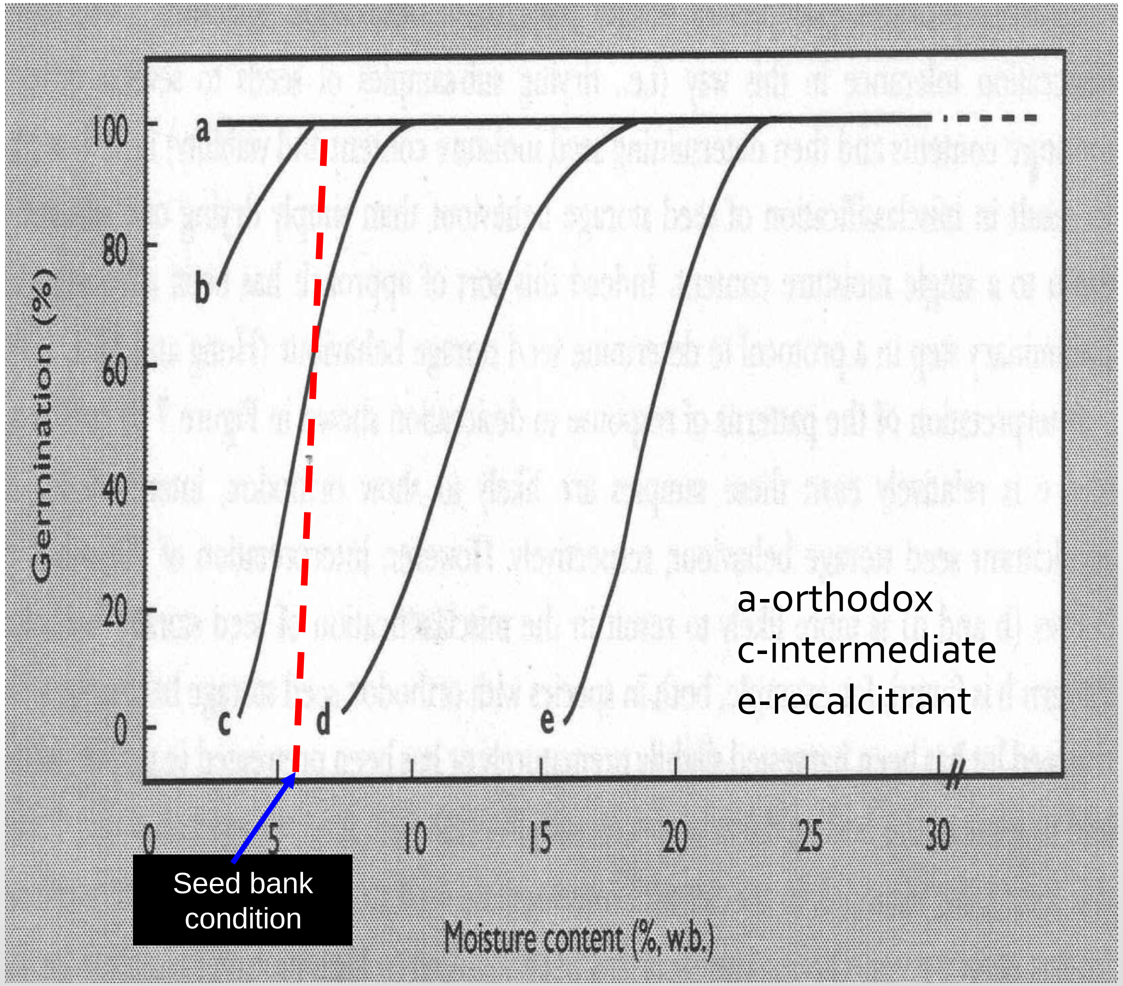
“Recalcitrant” (desiccation-sensitive)

- seeds killed by desiccation to comparatively high (20 – 25 %) moisture contents
- storage at ambient is only possible for short periods (months)

“Intermediate” seeds

- tolerant to desiccation to a considerable extent
- dry seeds are more sensitive to storage at 10 °C temperature or below.

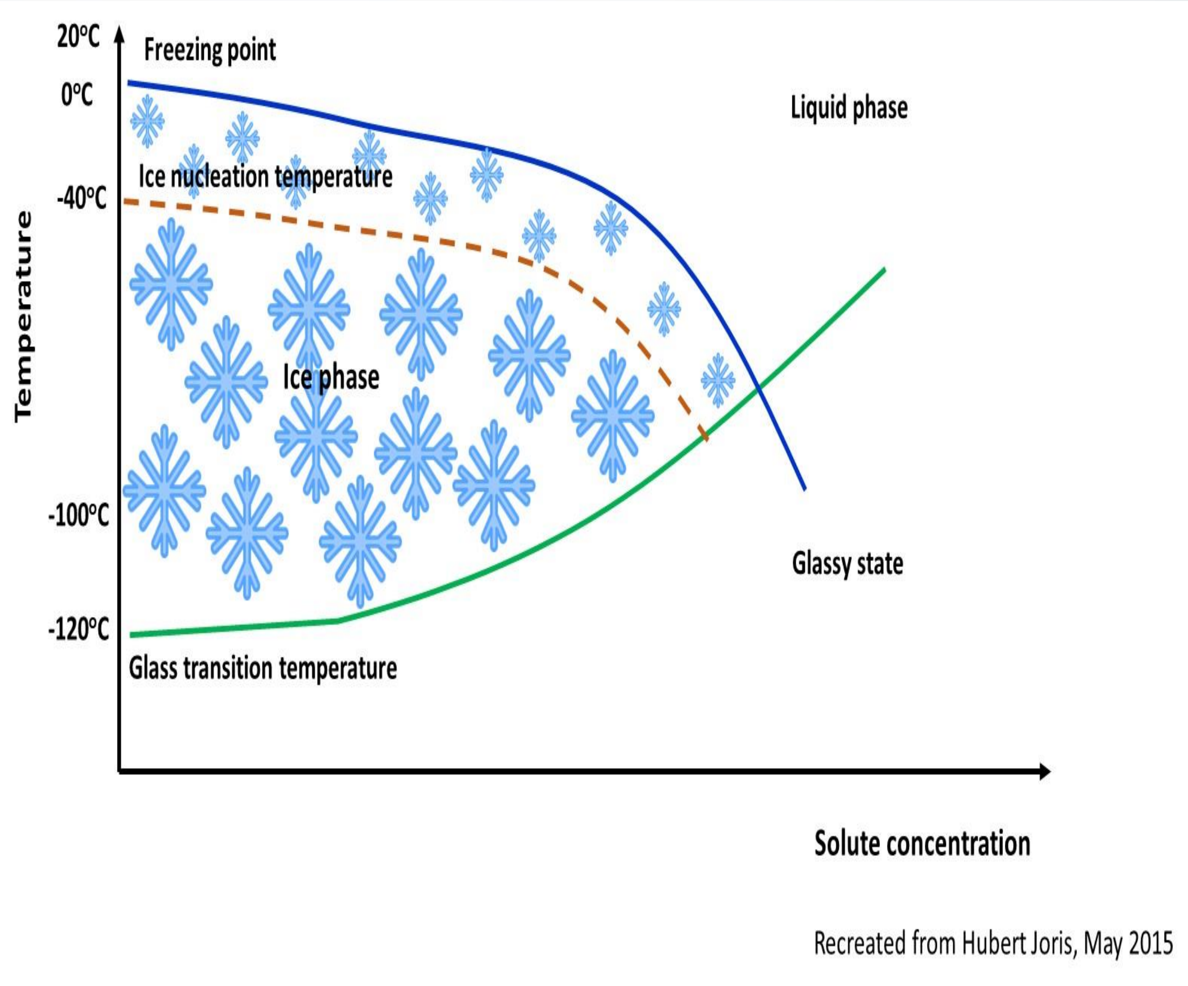
Critical MC for different seed categories



(Hong & Ellis, 1996)

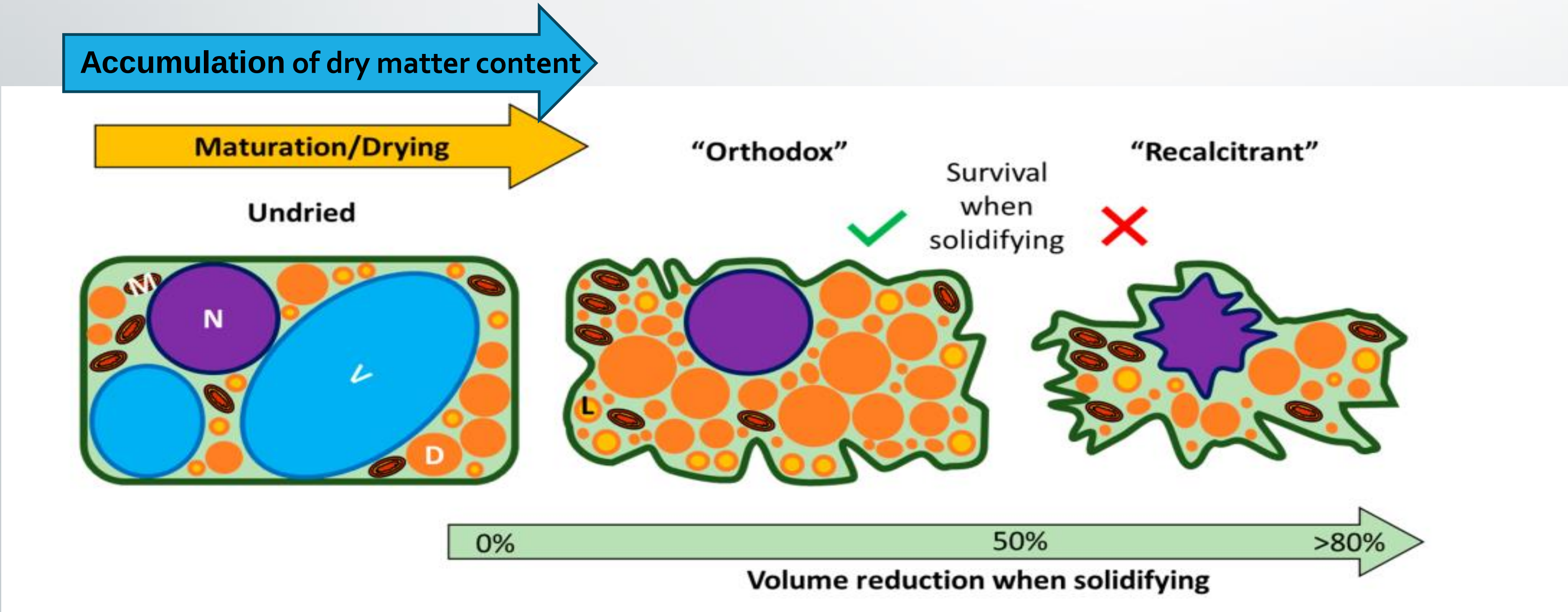
Cytoplasmic solidification and glass formation

- Glass formation, also called vitrification, describes how fluid cytoplasm solidifies when liquid water is removed or when ice formation is prevented.
- During desiccation, the hydrated cytoplasm, concentrates and becomes increasingly viscous as the remaining dry components squeeze together.
- The mixture begins to hold its own shape when dried to RH between 50% and 25% (above 0 °C), resisting further compaction; that is, it solidifies, becoming a glass.
- The initial understanding was that glasses form in the cytoplasm of orthodox seeds but not in recalcitrant seeds
- Hence, the presence of glasses was hypothesised to confer protection from desiccation for orthodox seeds.



Cytoplasmic solidification – orthodox vs recalcitrant seeds

- Transition from fluid to solid occurs in both desiccation-tolerant and sensitive cells alike.
- Rather, it may be the extent of cell shrinkage that occurs before a glass forms that distinguishes recalcitrant and orthodox categories.
- Cells stocked with dry matter reserves (orthodox seeds) are denser and shrink less, given the same desiccation force, than cells containing a lot of water (recalcitrant seeds).

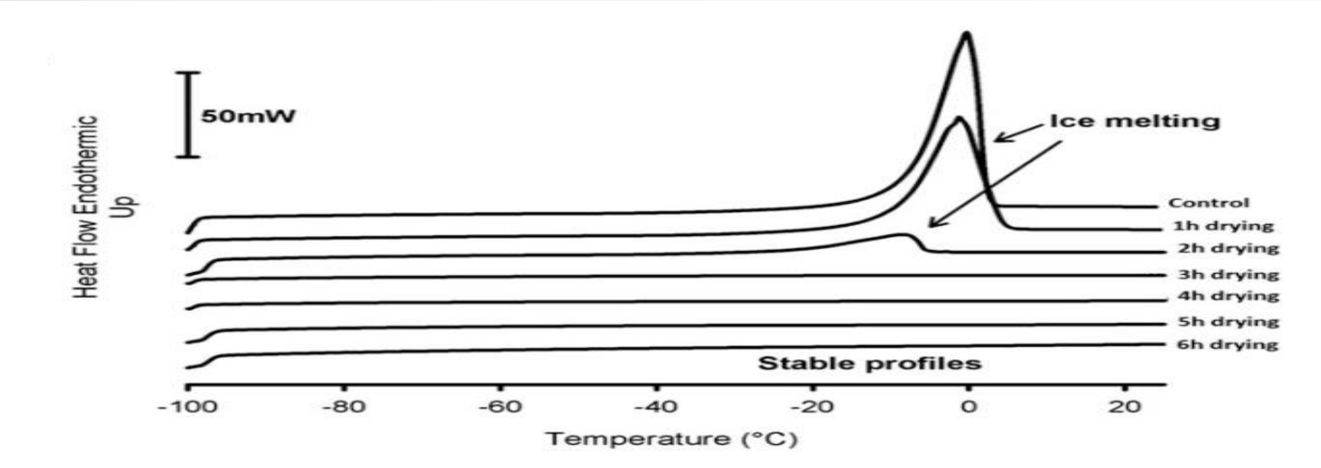


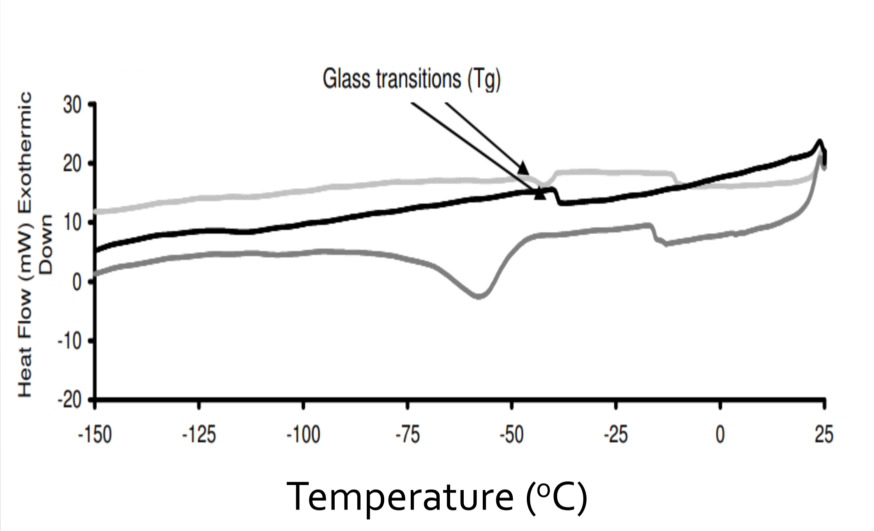
Nadarajan et al. 2023 (https://doi.org/10.3390/plants12030471)

Determination of glassy state using DSC thermal analysis

- Understanding the physical properties of water in seed tissues being stored at sub-zero temperatures is pivotal.
- Water-solute molecular properties provide information about ice formation potential, glass transition and vitrified state of the samples.
- DSC thermal analysis provides the feasibility to quantify freezable, non-freezable water and if the cells have reached vitrification.

Differential Scanning Calorimetry





Nadarajan et al. CryoLetters **29(2),**95-110 (2008)

How stable is your glass?

- Glass stability in crucial
- Seeds stored well below T_g (glass transition temperatures)
- DSC has been the method of choice because of its availability, familiarity and its ease of operation and interpretation.
- However, at low sample water contents, DSC signals become small and diffuse and the assignment of T_g becomes difficult.
- DMA is the most sensitive to local motion, it provides the most credible information on changes in sample viscosity that occur during glass transition.

Dynamic mechanical analyser

Source:Microsoft PowerPoint - SPE DMA 2019 (4spe.org)

Methods for Determination of Glass Transitions in Seeds

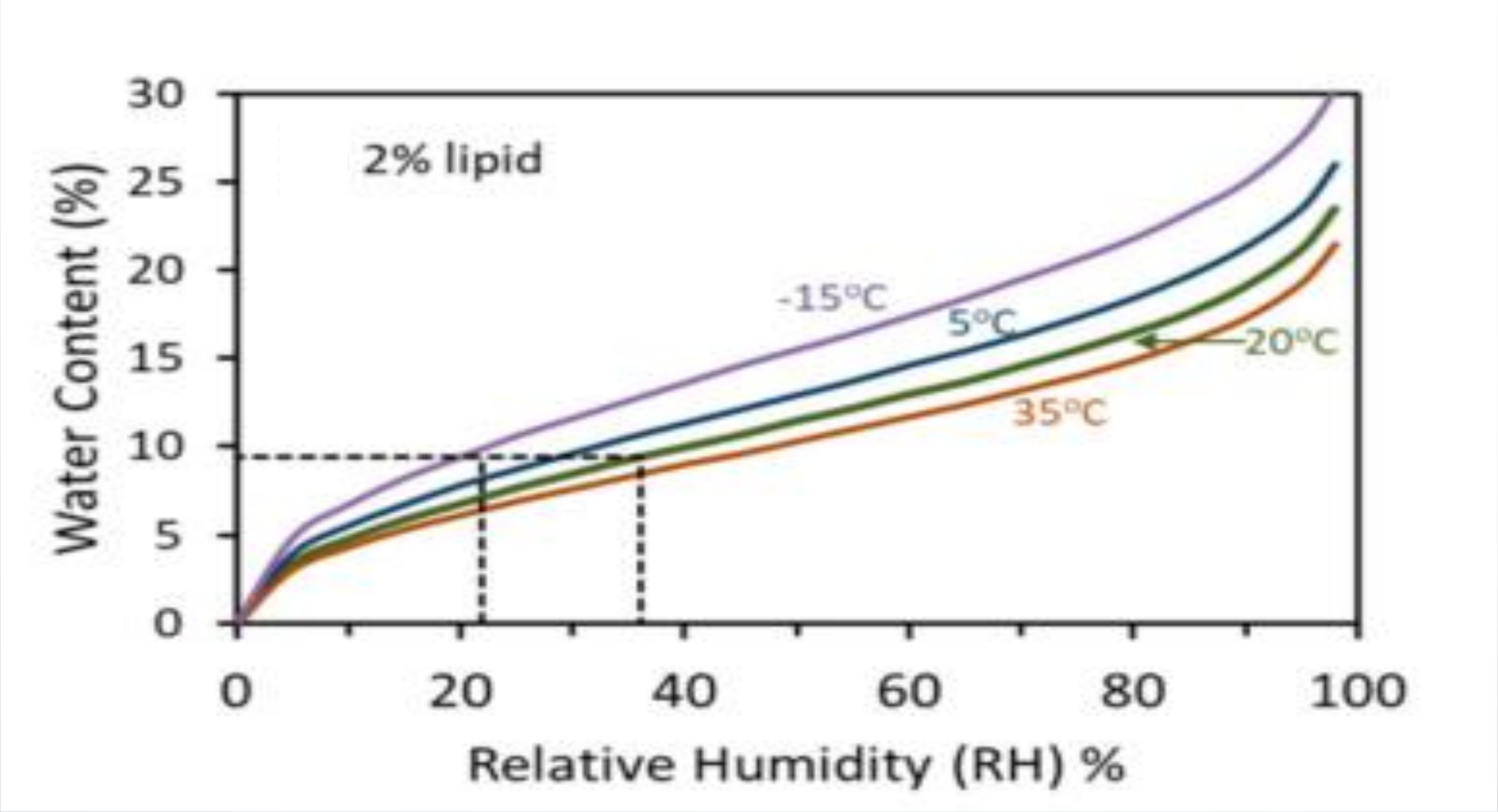
Annals of Botany, Volume 74, Issue 5, November 1994, Pages 525–530, https://doi.org/10.1006/anbo.1994.1150

2011 Nov;68(4):607-19. doi: 10.1111/j.1365-313X.2011.04711.x. Epub 2011 Sep 9.

Detailed characterization of mechanical properties and molecular mobility within dry seed glasses: relevance to the physiology of dry biological systems

Daniel Ballesteros[1], Christina Walters

Seed moisture content, RH and Temperature



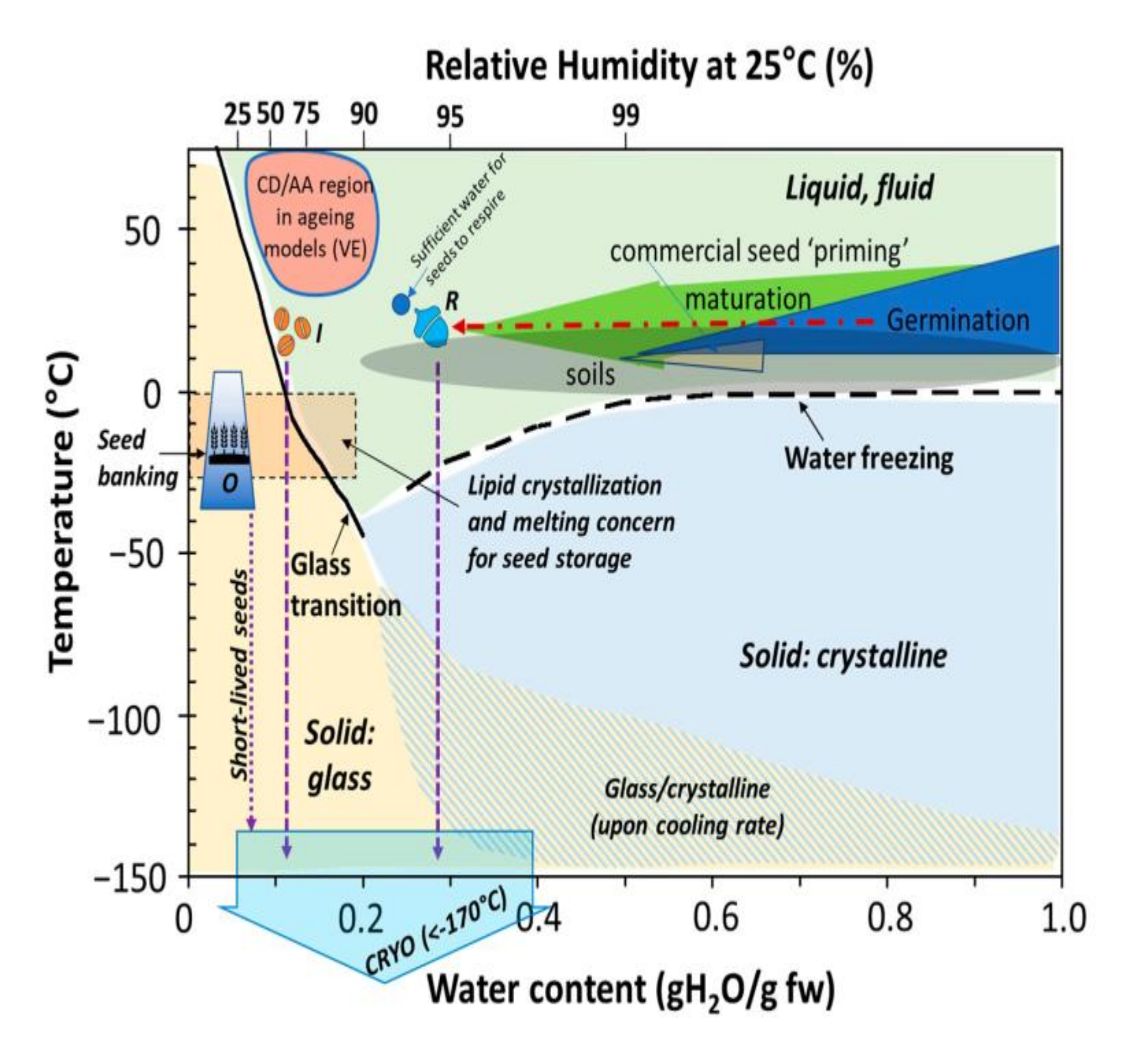
- Seed storage is affected by moisture content, temperature and relative humidity.
- These factors are inter-related
- Representative **Water sorption isotherms** for seeds with 2% lipid

Dashed lines show the drying conditions needed to meet FAO (2014) standards. That is, storing a seed containing 2% lipid at 20% RH and -15 °C requires adjusting the water content to 9.4%.

Advanced seed storage classification

- Seeds that exhibit orthodox behaviour can be stored using refrigerators (medium-term) or freezers (long term).
- Some orthodox seeds can be short-lives and require cryopreservation to prolong shelf life (purple arrow in “short-lived” seeds).
- Most seeds exhibiting intermediate and all recalcitrant seeds require cryogenic storage (purple arrow for “recalcitrant” and “intermediate” seeds).

Phase diagram of seed physical states and storage challenges for the different seed storage behaviours



Nadarajan et al. 2023 (https://doi.org/10.3390/plants12030471)

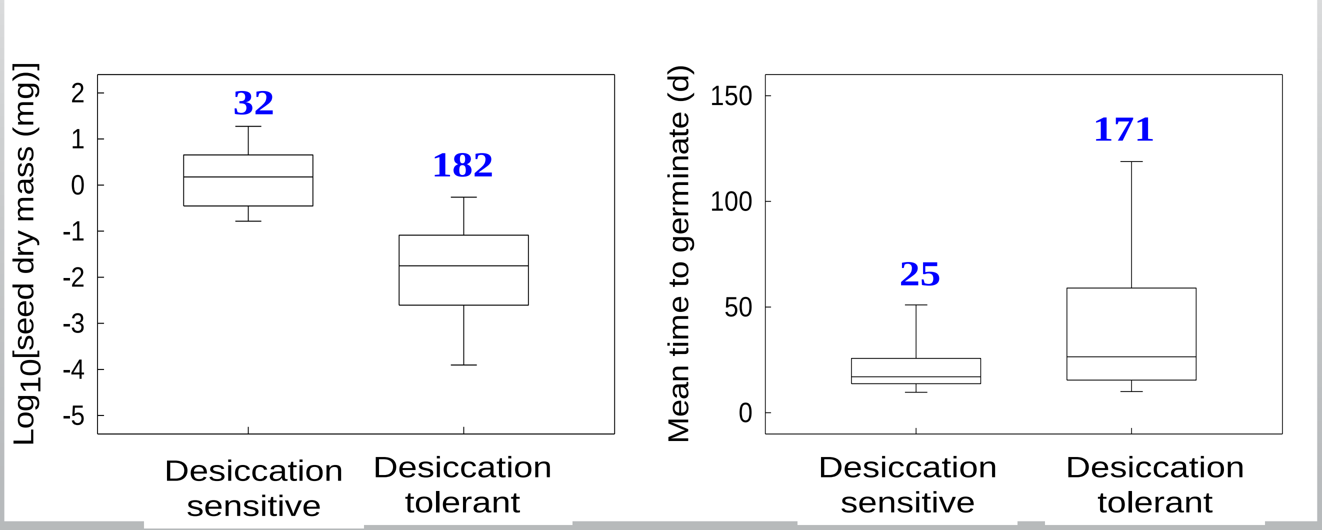
How to predict seed storage behaviour?

- Seed physiology
- Seed morphology
- Desiccation sensitivity assessment
- Ecological / habitat

Seed Information Database: Royal Botanic Gardens, Kew; (https://data.kew.org.sid/) managed by the Society for Ecological Restoration (SER).

Seed physiology (germination / dormancy)

- Orthodox seeds have a clear end phase of seed development and maturation before germination
- Orthodox seeds usually have dormancy
- There is no clear end phase of seed development before start of germination for desiccation-sensitive seeds
- Desiccation-sensitive seeds germinate rapidly – i.e. no dormancy
- Desiccation-sensitive seeds are usually bigger



Daws et al. Ann Bot. 2006 97(4): 667–674.

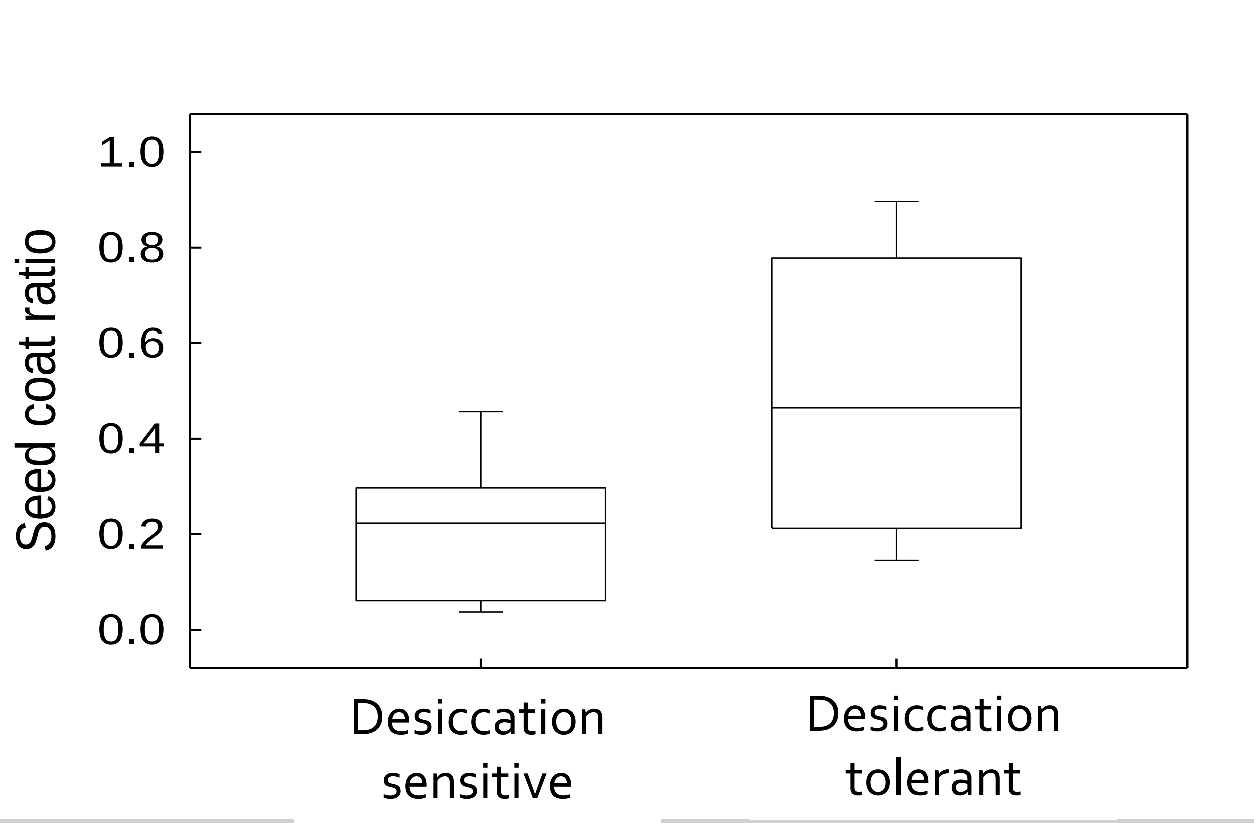
Watch out for: Inter- and intra- population maturation heterogeneity

- Maturation uniformity at collection is important for preparation of the seeds for storage
- Seed maturation period may vary with and within populations
- Different maturity stages can be found along one branch at seed collection
- Seeds may show difference responses to desiccation

Seedling vigour compromised by early seed harvest

Nadarajan et al. 2020. New Zealand Journal of Botany

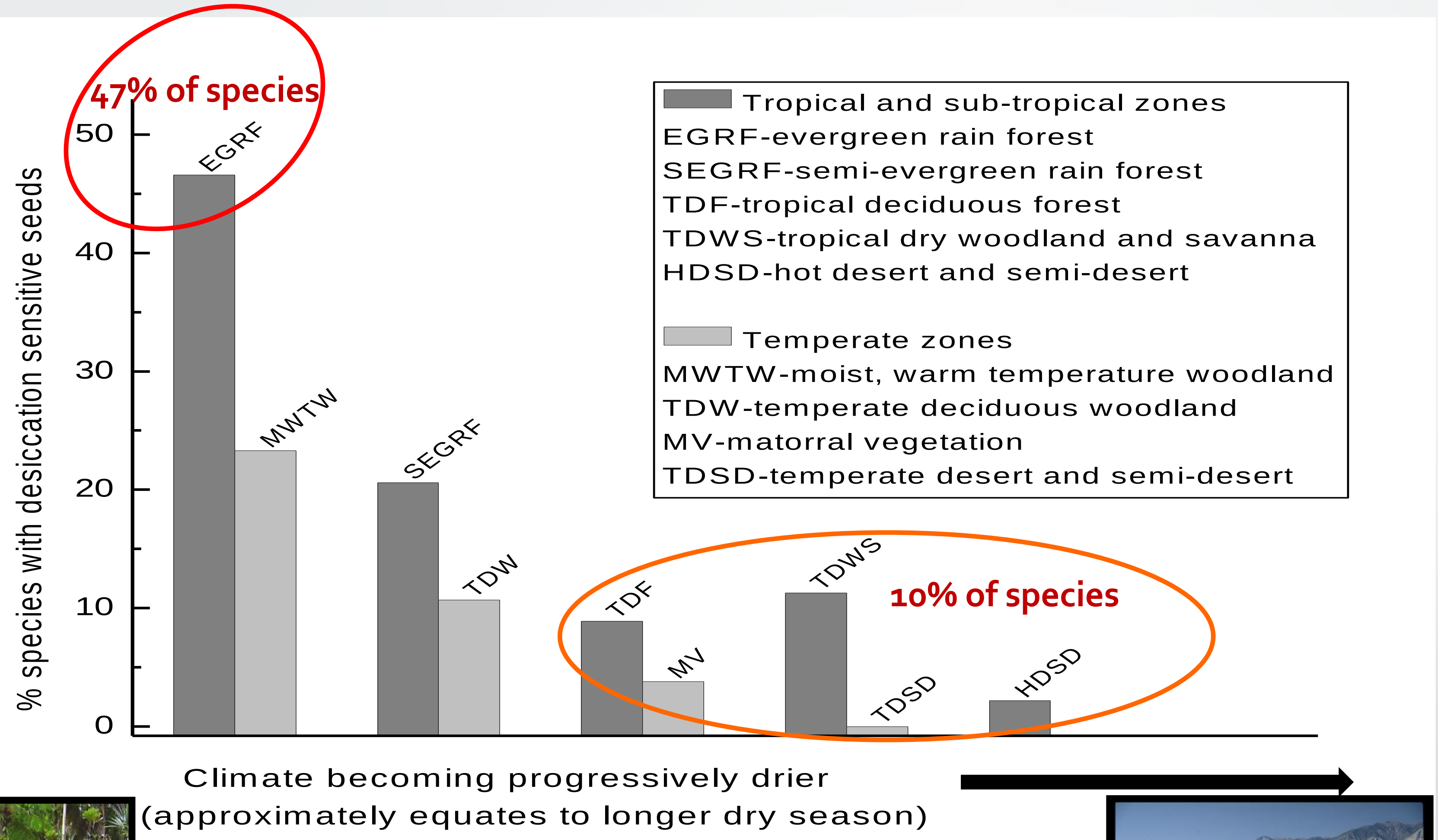
Seed morphology (seed coat to endosperm ratio)



- Desiccation-sensitive seeds have fleshy endosperm and thinner 'coats'

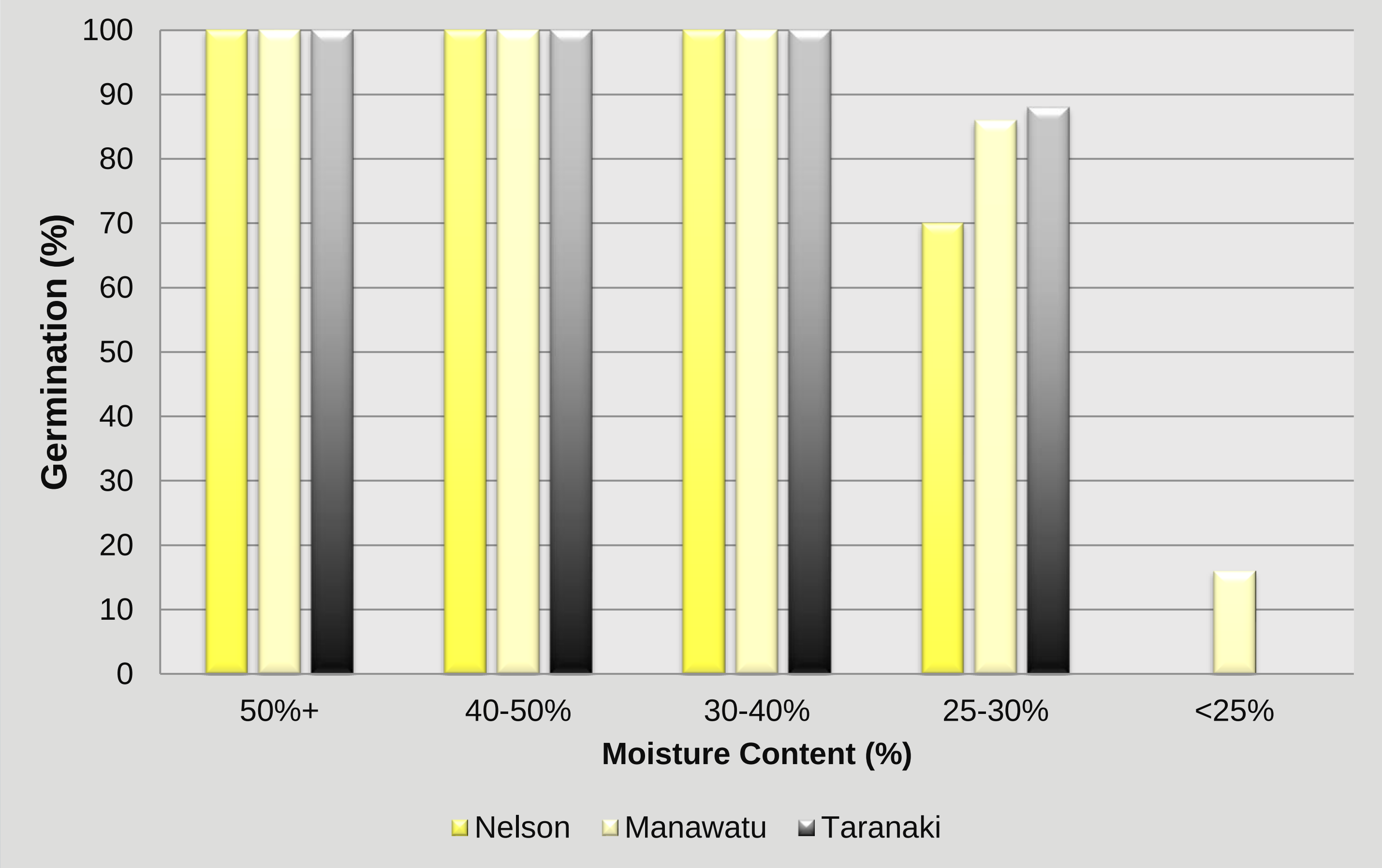
Daws et al. Ann Bot. 2006 97(4): 667–674.

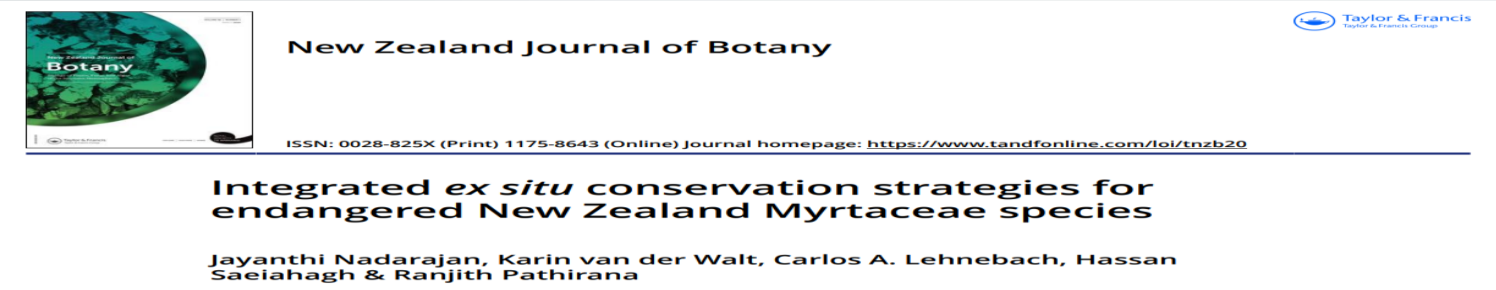
Desiccation sensitivity and ecological habitat



(Source: Tweddle et al. (2003). Ecological aspects of seed desiccation sensitivity. Journal of Ecology 91, 294-304)

Seed desiccation sensitivity – population heterogeneity



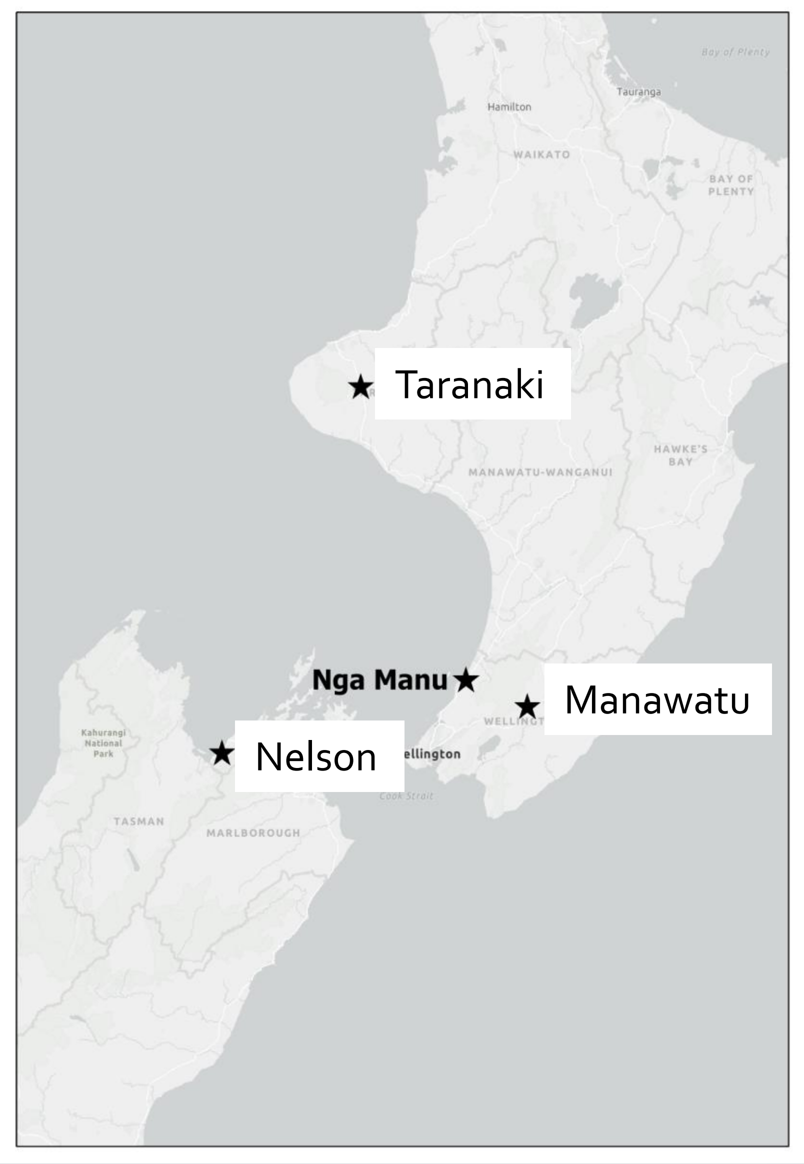

New Zealand Journal of Botany

Taylor & Francis

ISSN: 0028-825X (Print) 1175-8643 (Online) Journal homepage: https://www.tandfonline.com/loi/tnzb20

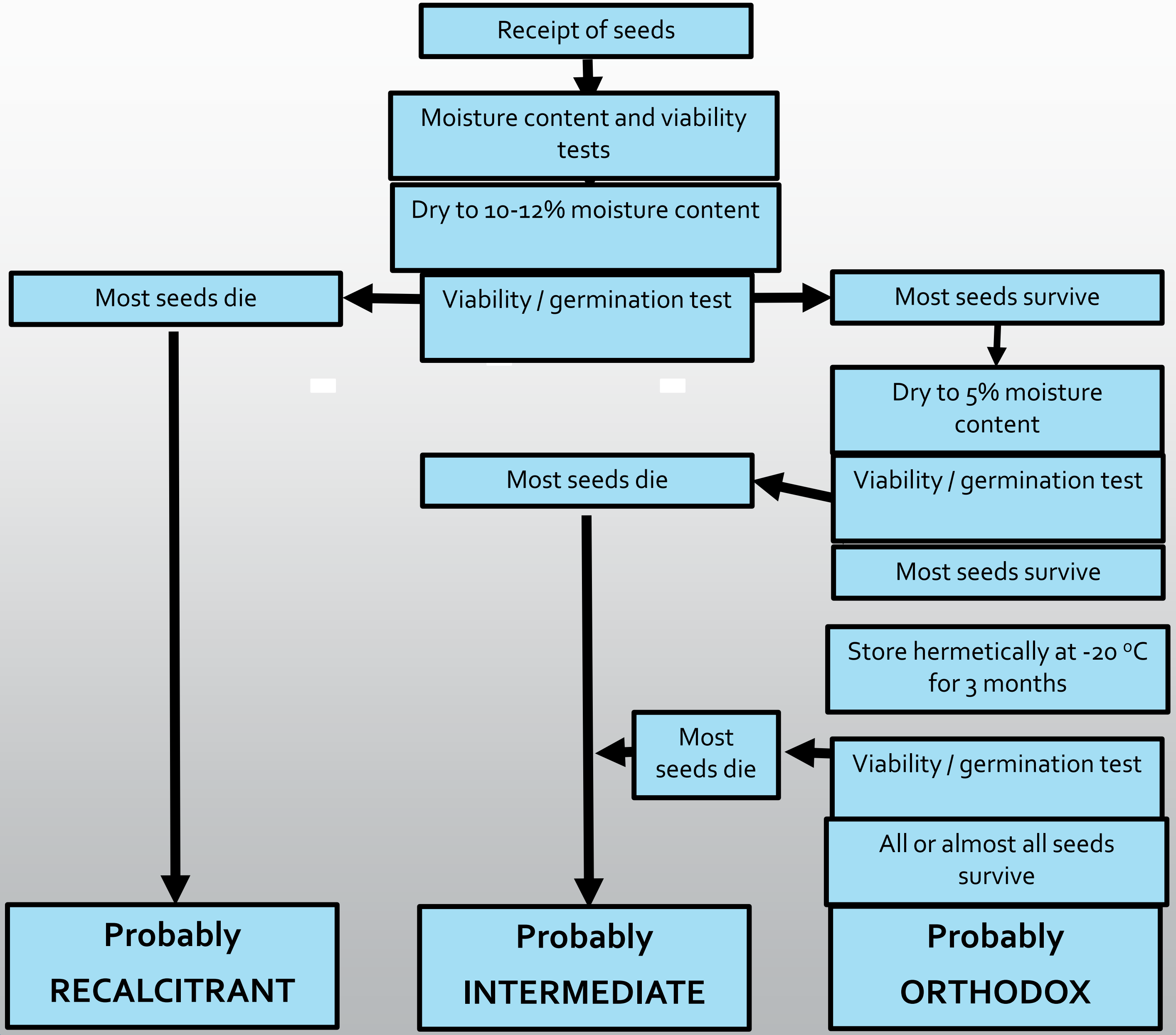
Integrated *ex situ* conservation strategies for endangered New Zealand Myrtaceae species

Jayanthi Nadarajan, Karin van der Walt, Carlos A. Lehnebach, Hassan Saeiahagh & Ranjith Pathirana



Syzygium maire populations studied

Desiccation sensitivity assessment

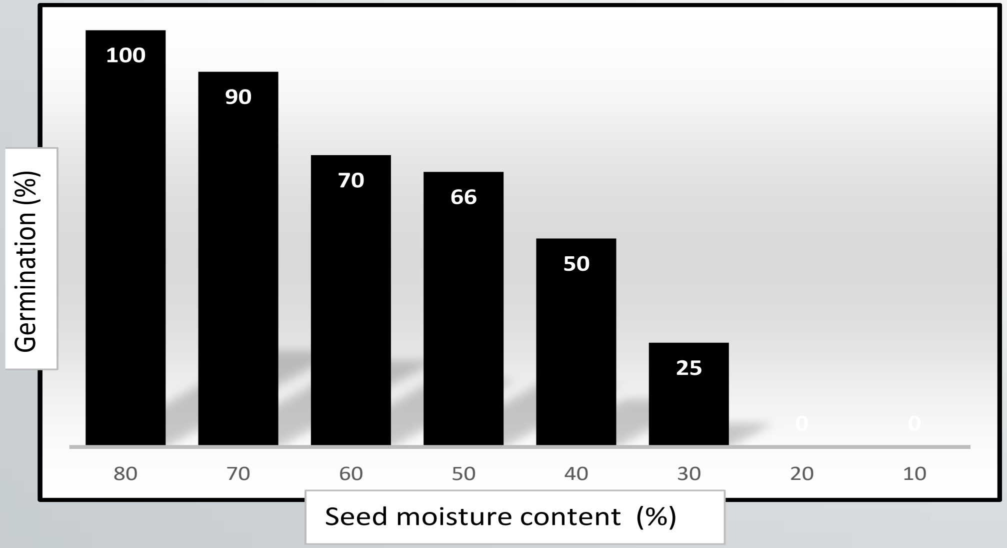


Syzygium maire seed storage behavior?

Clues

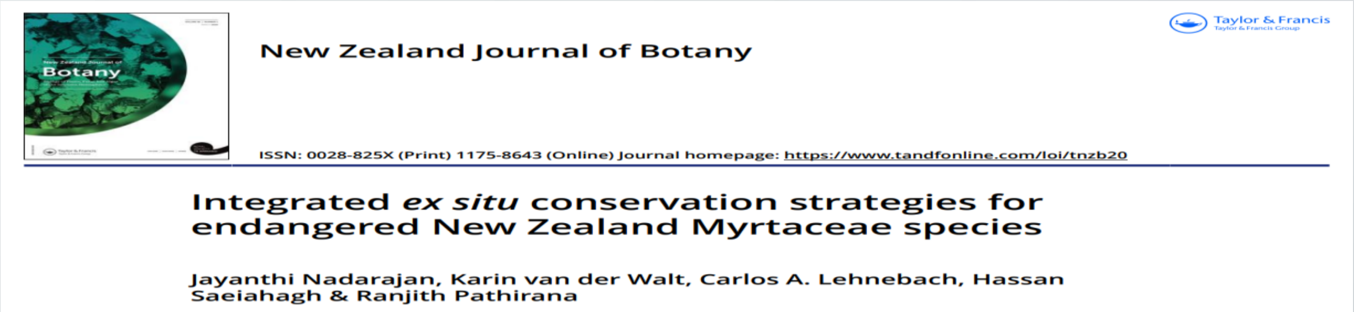
- Humid habitats
- Fleshy seeds
- Thin seed coat

Prediction → **Recalcitrant seed**



Germination of *S. maire* seeds at collection (80% moisture content) and following desiccation to various moisture contents (n = 100).

Findings: Seeds are recalcitrant and do not tolerate desiccation to moisture contents (MC) below 20%.



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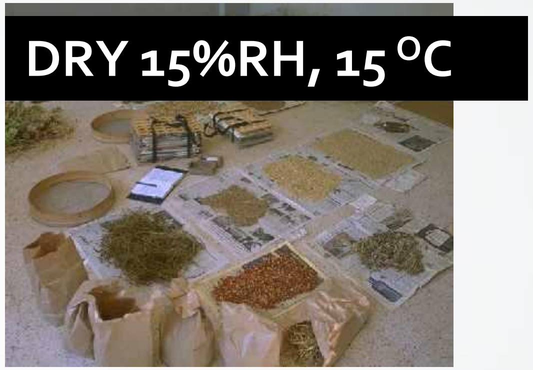
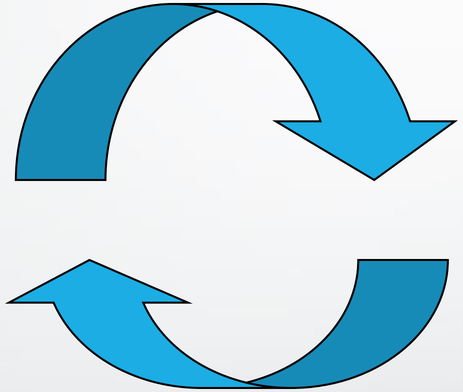
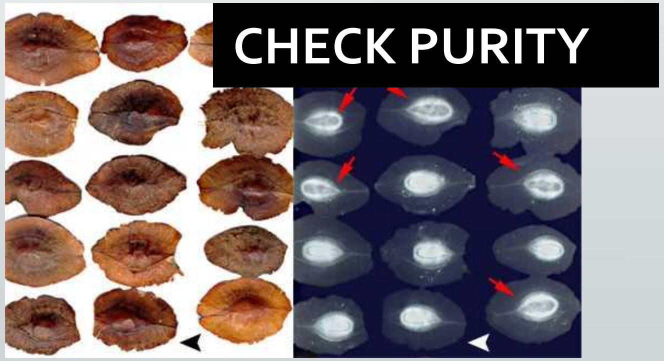
Storage recommendations for seeds with different storage behaviour

Orthodox seeds - conventional seed banking



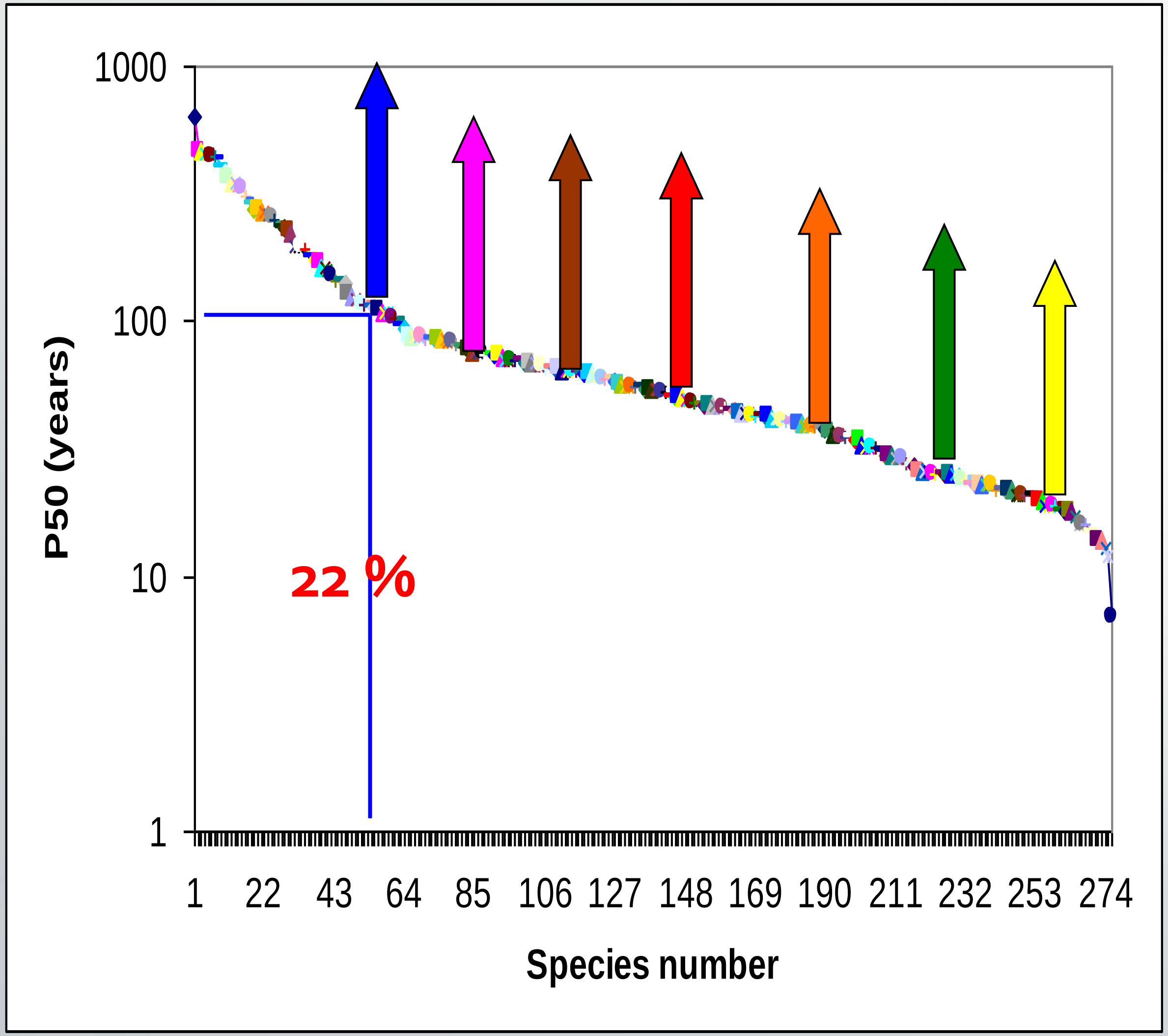




Genebank standards at -18 ^{o}C / 15% relative humidity (FAO/IPGRI 1994; FAO 2013)

Image source: RBGKew

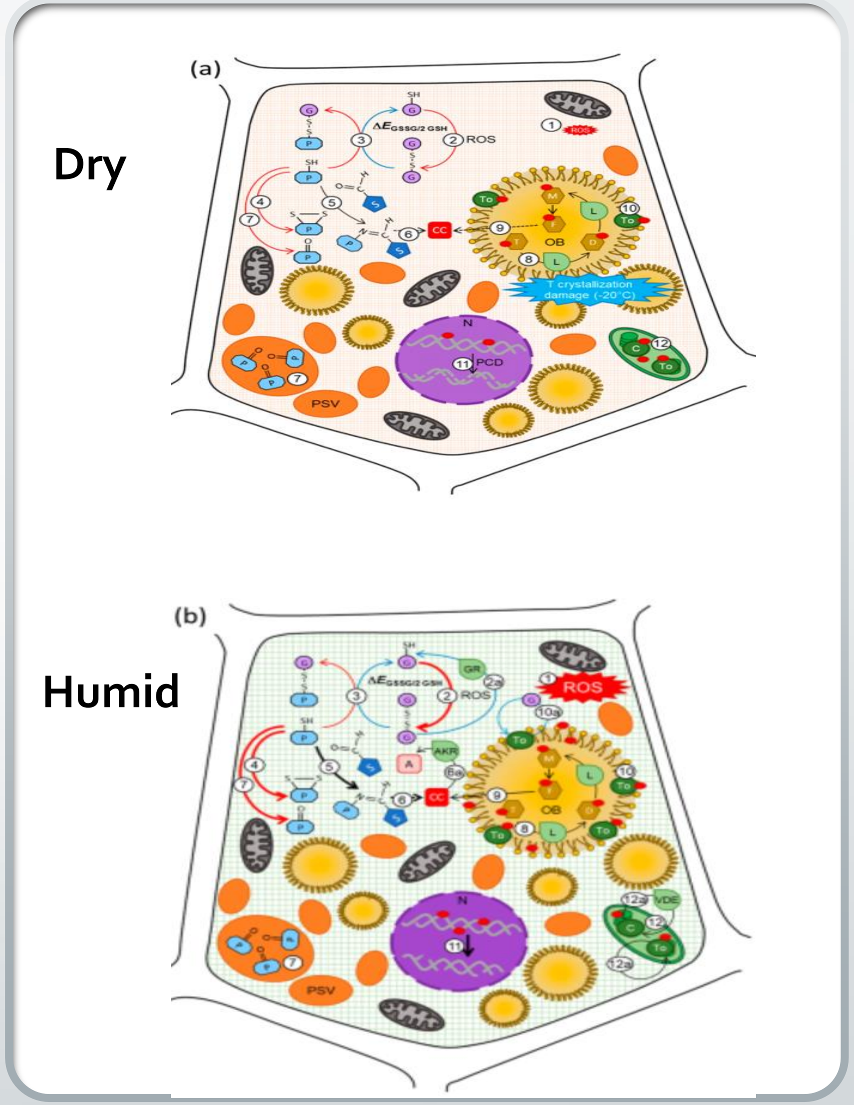
Data emerging for viability decline in seed bank



- Half-life for 276 species stored for 38 years at 5° C then at -18°C (c. 25) years was >100 years only for 61 (22%) of the species (Li & Pritchard, TIPS 2009; modified from Walters et al 2005)
- 26 % of collections from 46 families show significant drop in viability during 20 years storage under seed bank conditions (Probert *et al*., 2009 *Annals of Botany*)
- We know that cell shrinkage beyond a certain percentage is lethal.
- Once the cytoplasm solidifies, cell shrinkage continues to occur but over an extremely protracted timeframe, something that may be related to the ageing seen in dry orthodox seeds

Seed ageing at dry state vs 'accelerated ageing'

- Much of the research on the mechanisms of seed ageing has been conducted on seeds stored at elevated moisture and temperature conditions, known as 'accelerated ageing' or 'controlled deterioration'.
- However, caution is needed when interpreting the data and relating that to the actual seed longevity in dry storage as molecular mechanisms in dry cold storage are very different from that of the artificial ageing environment.
- It is now widely recognised that accelerated ageing and controlled deterioration conditions do not mimic the process of ageing under long term, dry-cold storage.

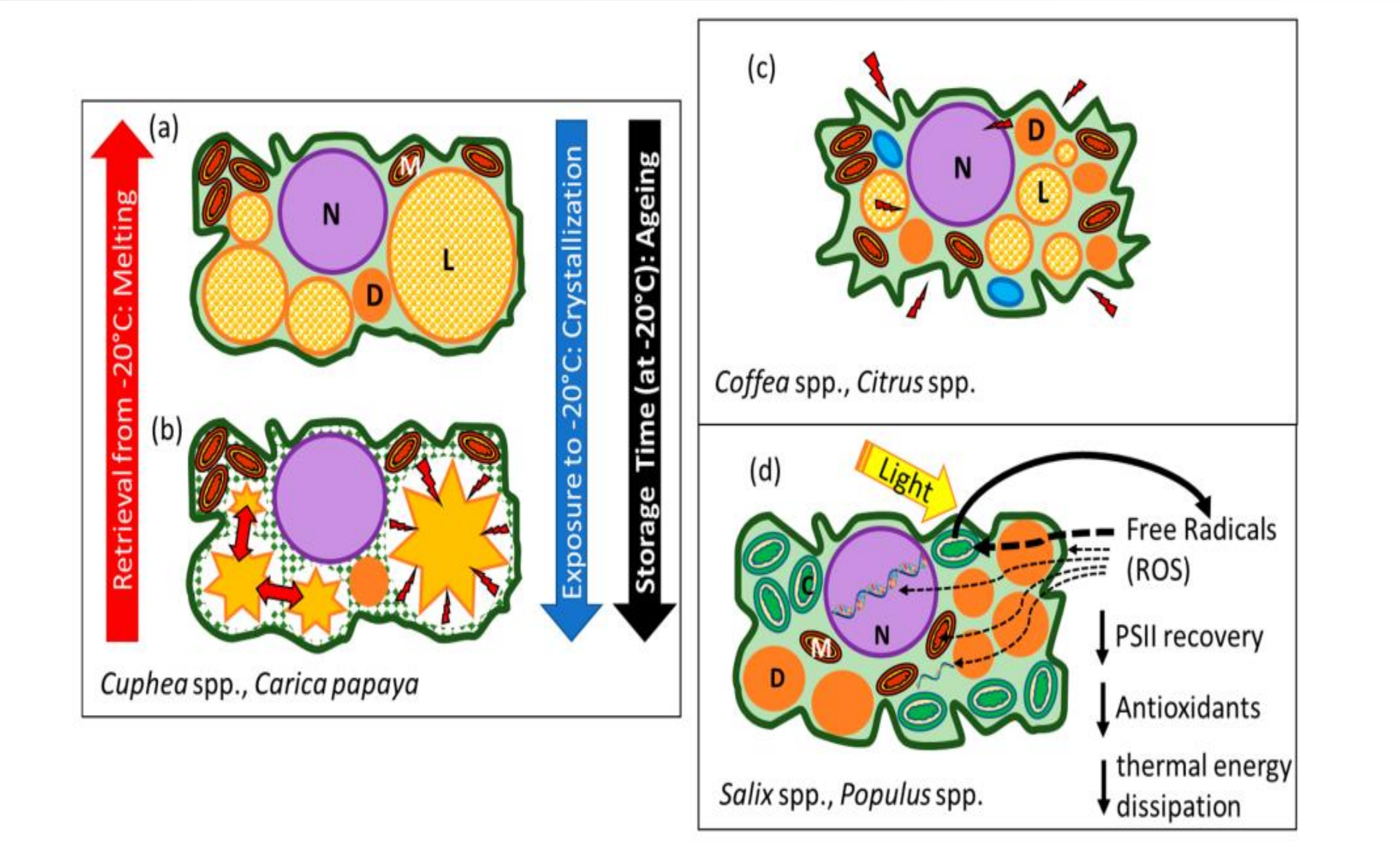


Factors that may influence oily seed storage

- Seed lipid content
- Fatty acid profile
- Lipid thermal behaviour
- Lipid body size

Cytoplasmic solidification in oily seeds

Schematic diagram of the hypothetical dry architecture of ‘intermediate’ seed storage behaviour

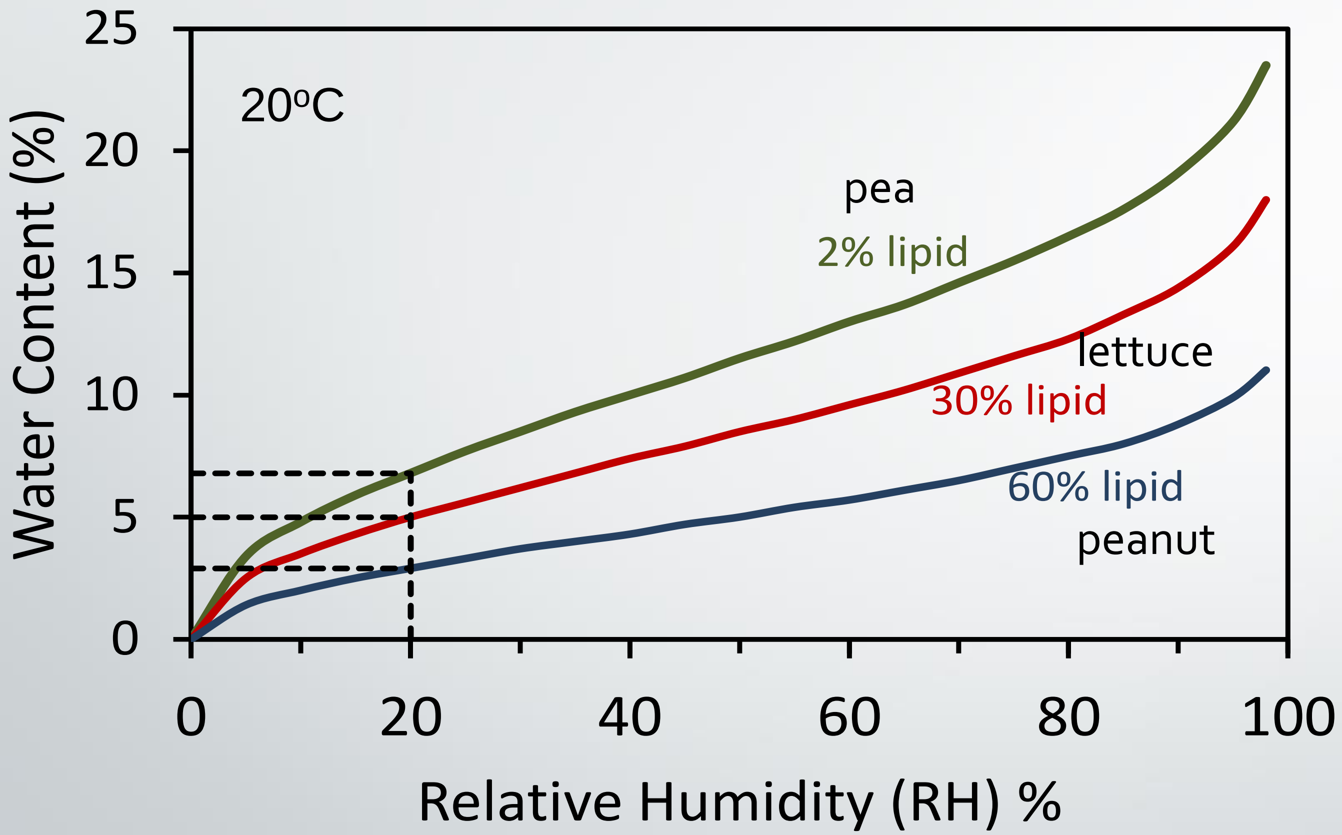


Red arrows and lighting symbols represent areas of physicochemical stress due to drying or lipid crystallisation

- Cells that survived drying may be damaged in the freezer when storage lipids crystallise and leave large gaps in the glassy matrix and increase the potential for oxidative damage or structural collapse.
- Cells that survive sufficient drying to approach cytoplasmic solidification but die with further drying.

Nadarajan et al. 2023 (https://doi.org/10.3390/plants12030471)

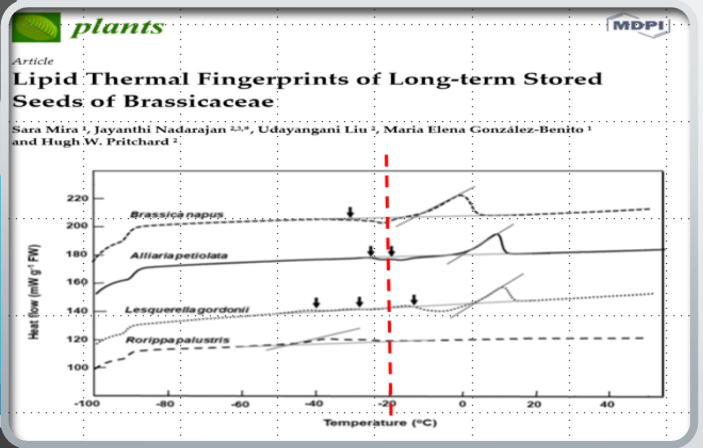
Water sorption isotherms for seeds with different lipid contents



- The relationship between water content and RH in seeds calculated from the Seed Information Database module (Royal Botanic Gardens Kew, 2022) for seeds at 20ºC and different lipid contents.
- The dashed lines represent water contents associated with 20% RH for the correspondence seeds (water contents: **6.8%** for pea, **5.0%** for lettuce and **2.9%** for peanut respectively).
- Hence seeds with different lipid contents will equilibrate to different water contents at the same RH.

Nadarajan et al. 2023 (https://doi.org/10.3390/plants12030471)

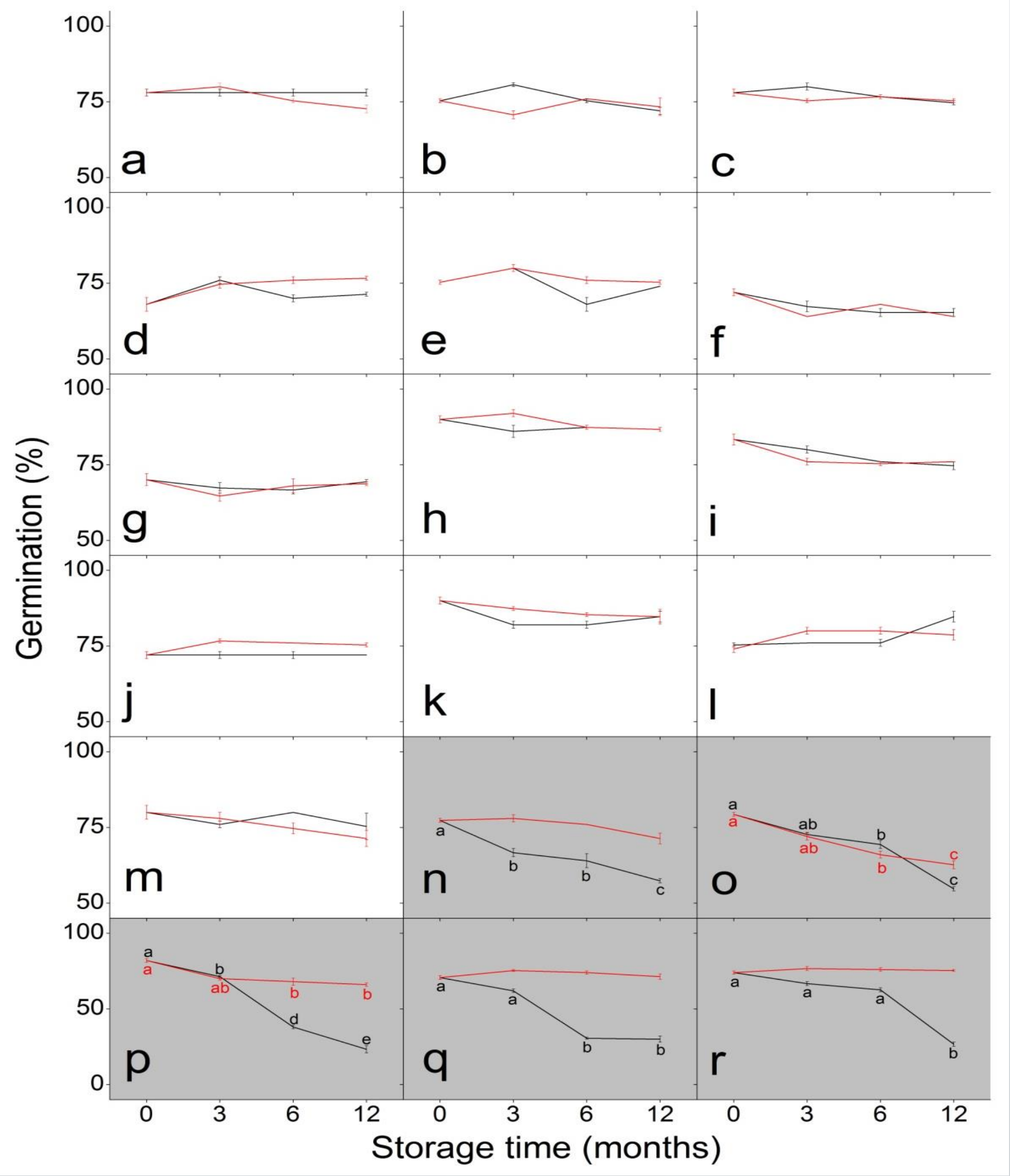
Comparative lipid thermal fingerprinting of long-term stored Brassicaceae oily seeds after 40 years storage



Mira S, Nadarajan J, Liu U, González-Benito ME, Pritchard HW. Lipid Thermal Fingerprints of Long-term Stored Seeds of Brassicaceae. Plants (Basel). 2019 Oct 14;8(10):414. doi: 10.3390/plants8100414. PMID: 31615156; PMCID: PMC6843794.

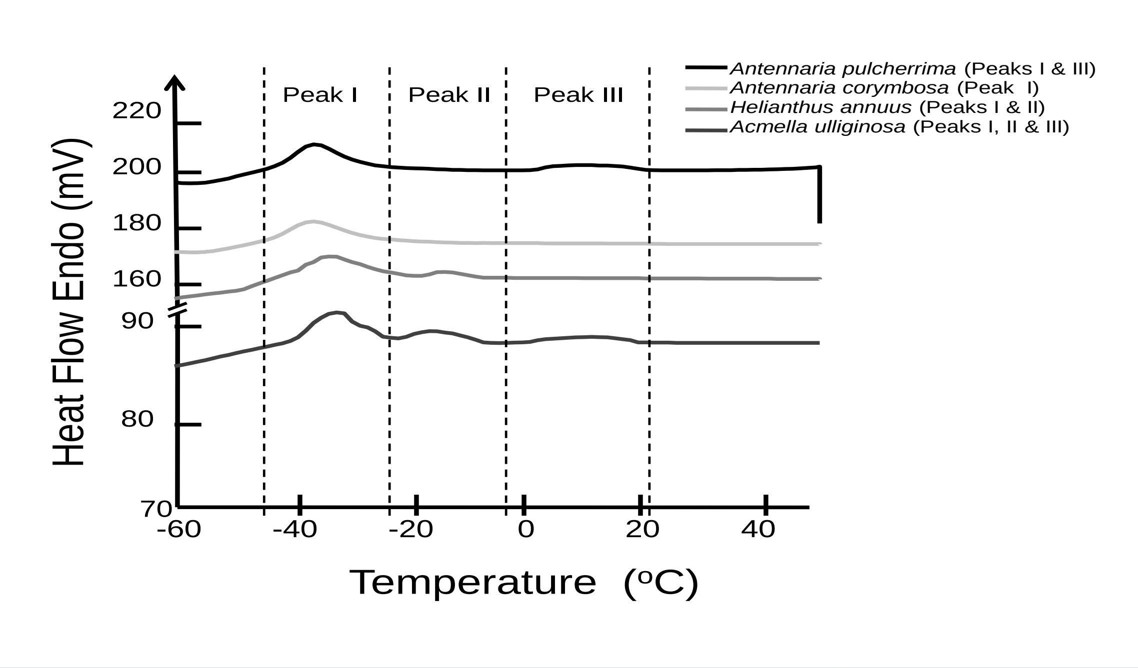
- Long-lived seeds showed they contained lipids with much lower melting end temperatures (c. 0 to −30°C) and multiple lipid phases did not occur at the storage temperature.
- In contrast, relatively poor storing oily seeds at −20°C tended to have lipids with crystallization and melting transitions spread over a wide temperature range that spanned the storage temperature, plus a melting end temperature of around 15°C.
- We concluded that seeds tolerate long-term cold, dry storage best when the seed lipids have thermal stability, i.e. when they are at low risk of phase change.
- Poor storage could be associated with the presence of a metastable lipid phase at the temperature at which they are being stored.
- Multiple features of the seed lipid thermal fingerprint could be used as biophysical markers to predict potential poor performance of oily seeds during long-term, decadal storage.

Asteraceae (sunflower family) seed storage

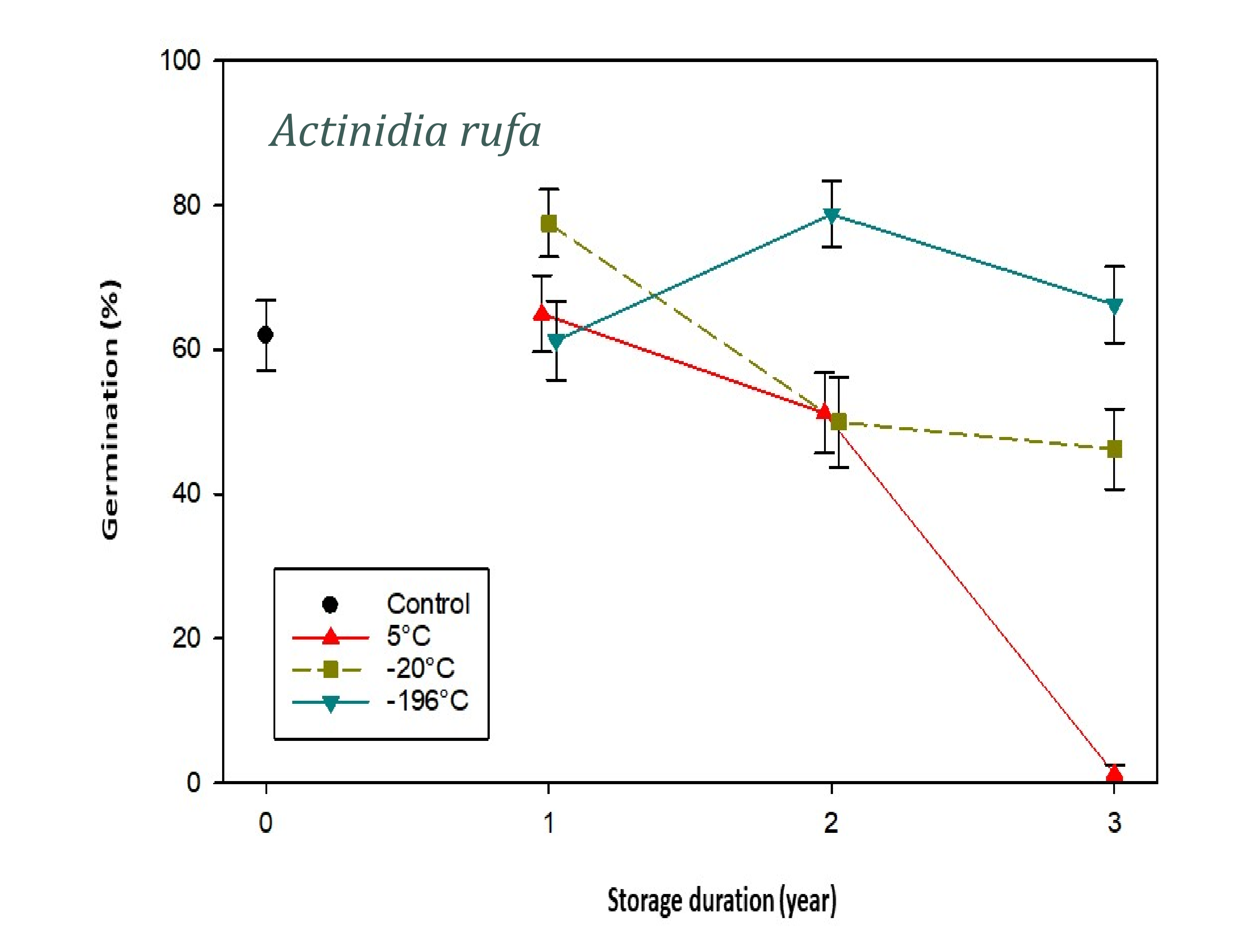


— −20 ºC
— −196 ºC

- 18 species compared for storage at −20ºC & −196ºC.
- Two groups were identified i) short lived ii) long-lived species at −20ºC
- Short lived species not necessarily have high oil content but do have high lipid melt temperature
- We are studying if fatty acid chain length and oil body size have influence on short-lived species



Kiwifruit (*Actinidia* sp) seed storage

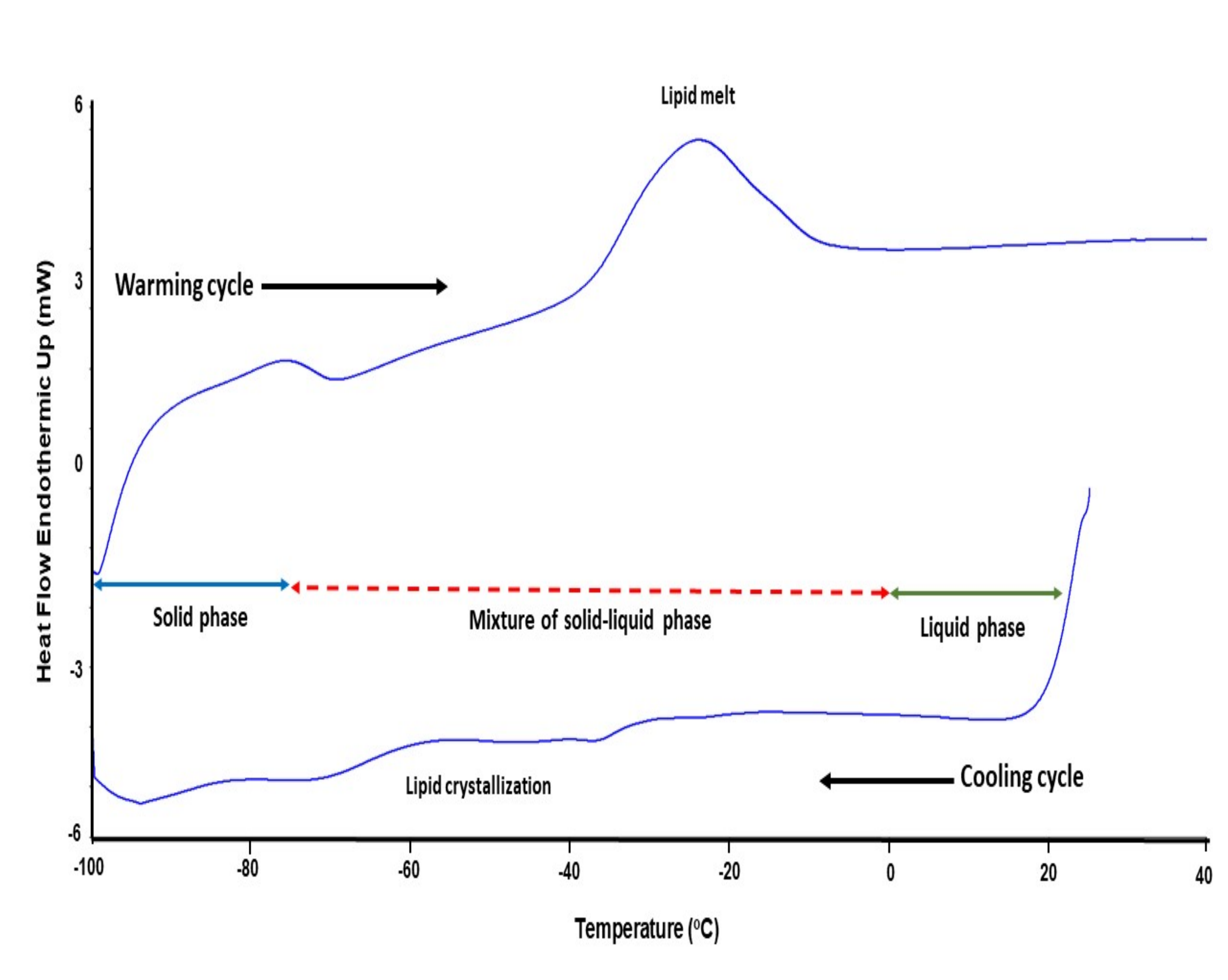


- Kiwifruit seeds - desiccation tolerant and should be bankable at −20°C.
- However, our previous study on seed storage of seven species at different temperatures for three years showed declines in seed germination at 5°C and −20°C.

Nadarajan et al 2024. Manuscript in press in Acta Horticulturae

Kiwifruit seed lipid thermal fingerprinting

- kiwifruit seeds have high oil content (c. 30%).
- DSC thermal analysis revealed that their lipids are in transitional phase (mixture of liquid and solid phase) at −20^{o}C.
- Seed lipid thermal fingerprints for rapidly identifying potentially short-lived oily seeds under dry-cold storage environments – can be used as a biophysical marker.



Differential scanning calorimetry (DSC) cooling and warming thermograms for *Actinidia rufa* seeds

Nadarajan et al 2024. Manuscript in press in Acta Horticulturae

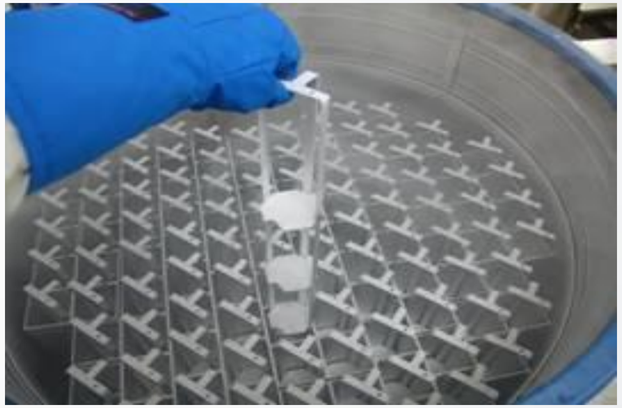
Recommendation for storage of orthodox ‘short-lived’ and intermediate (oily seeds) seeds

For short to medium term storage at 5ºC and -20ºC respectively

For long term cryopreservation is recommended

Critical factors in seed cryopreservation

1. Seed maturity



2. Seed moisture content

- Most critical factor
- Optimum moisture content must be attained
- High or low create problems

3. Cooling / rewarming rates

- A significant factor in survival

4. Physical damage to seed:

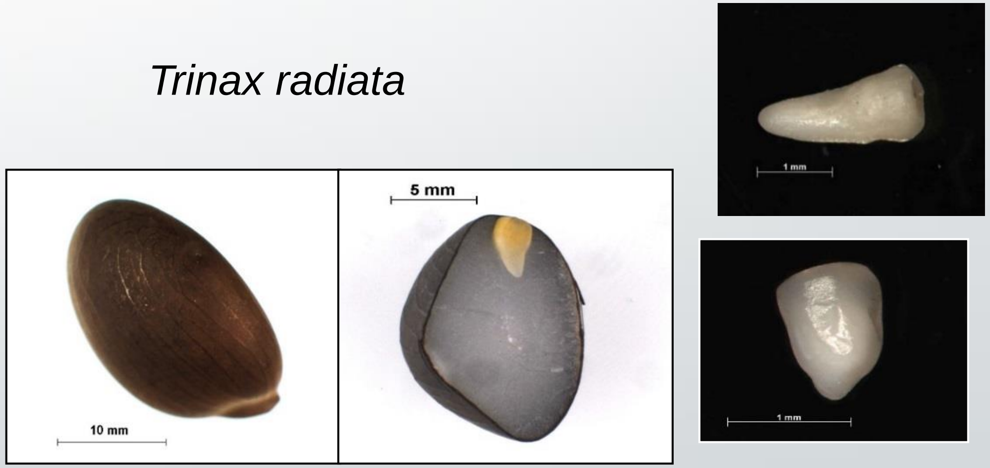
- If the seed matrices are capable of expanding and contracting with such cooling/rewarming stress.
- Depends on the size and surface area of the seeds.

Embryo and axis cryopreservation

- Whole seed cryopreservation can only be applied to seeds of orthodox and intermediate (oily) seeds.
- For desiccation sensitive seeds, excised zygotic embryos have been used.
- Challenges are particularly significance for cryopreservation of recalcitrant seed species that produce large seeds
- These have to be handled as excised embryonic axes which poses additional challenge.
- **Post-cryo recovery:** generally, involve *in vitro* manipulations (tissue culture, embryo rescue, somatic embryogenesis, shoot micropropagation) and need to be established prior to storage

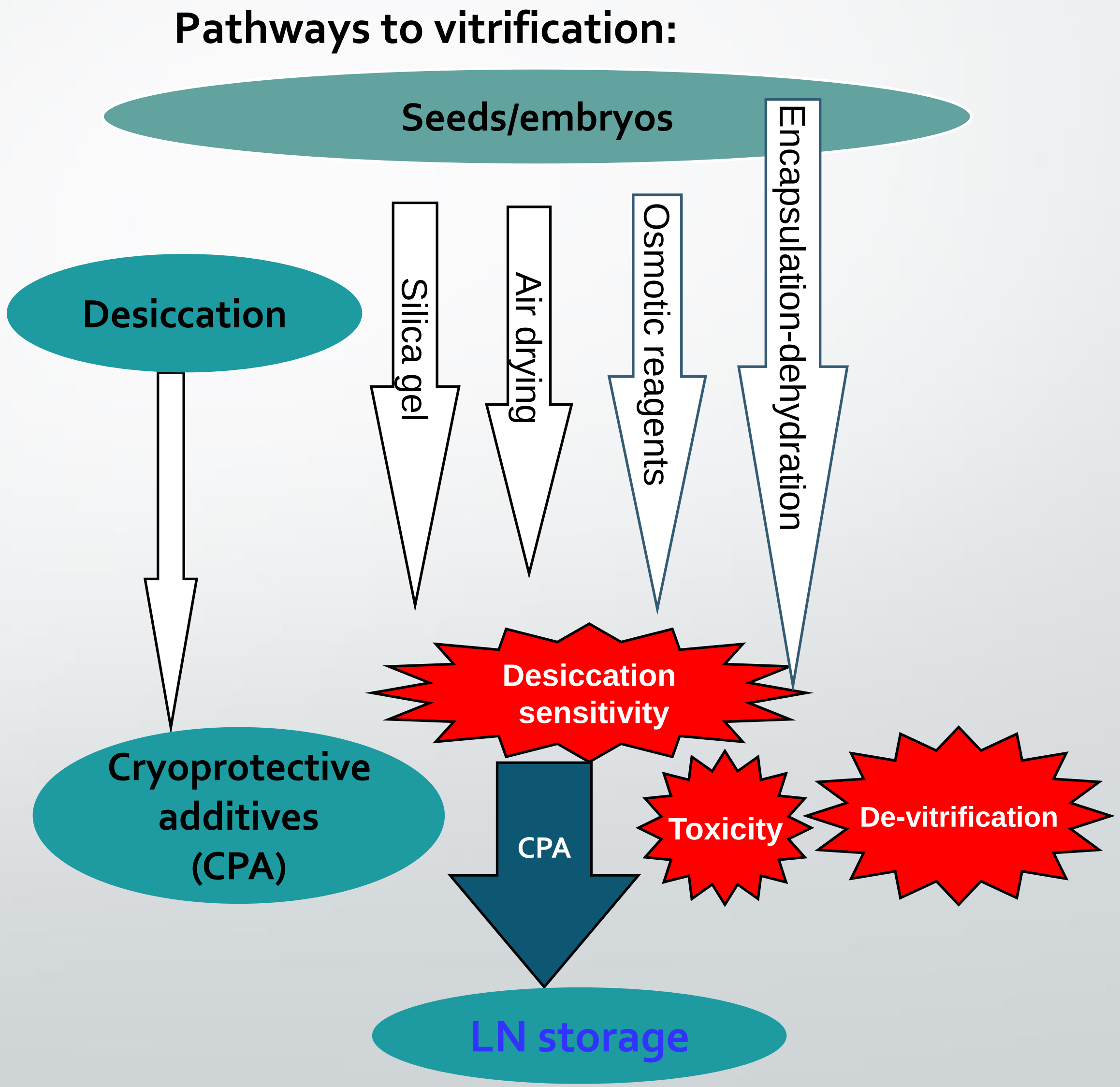
Cycas revoluta

Trinax radiata



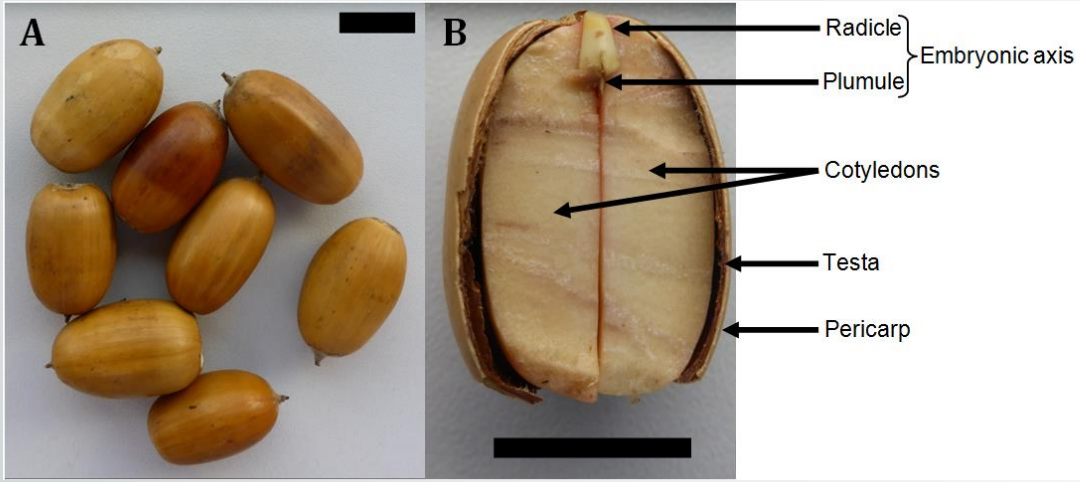
Different cryopreservation techniques

1. Air drying followed by rapid freezing
2. Encapsulation-dehydration
3. Vitrification — using cryoprotectants
4. Encapsulation-vitrification
5. Droplet freezing
6. Vacuum infiltration vitrification
7. Cryo-plates
8. Cryo-mesh



Embryo tissue heterogeneity

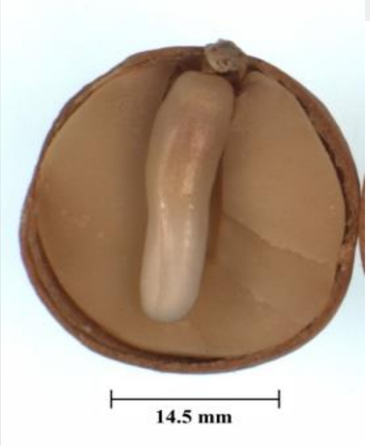
- Embryo size and shape
- Chemical composition (lipid fluidity, visco-elasticity, hydrophobicity)
- Heterogeneity of embryo tissue
- Physiological status
  - Desiccation sensitivity
  - Physiological maturity
  - Redox status



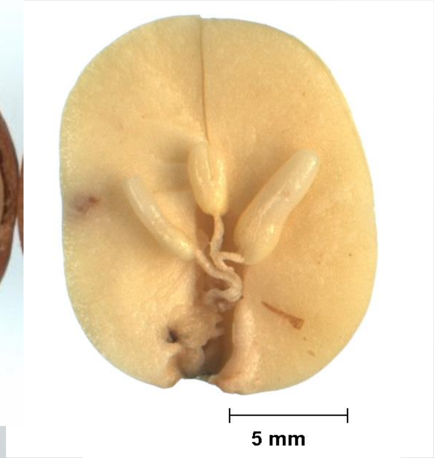
Quercus robur

2 cm

Aesculus hippocastanum (horse chestnut)

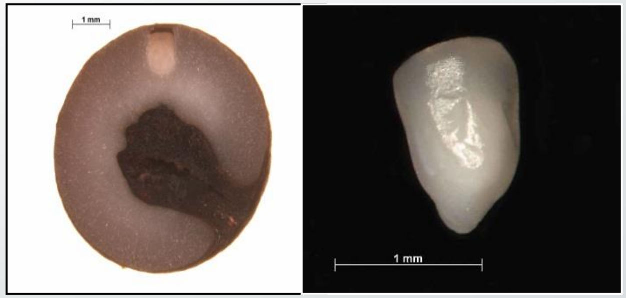


Dioon edule – single embryo



Dioon edule – polyembryonic

Carica papaya

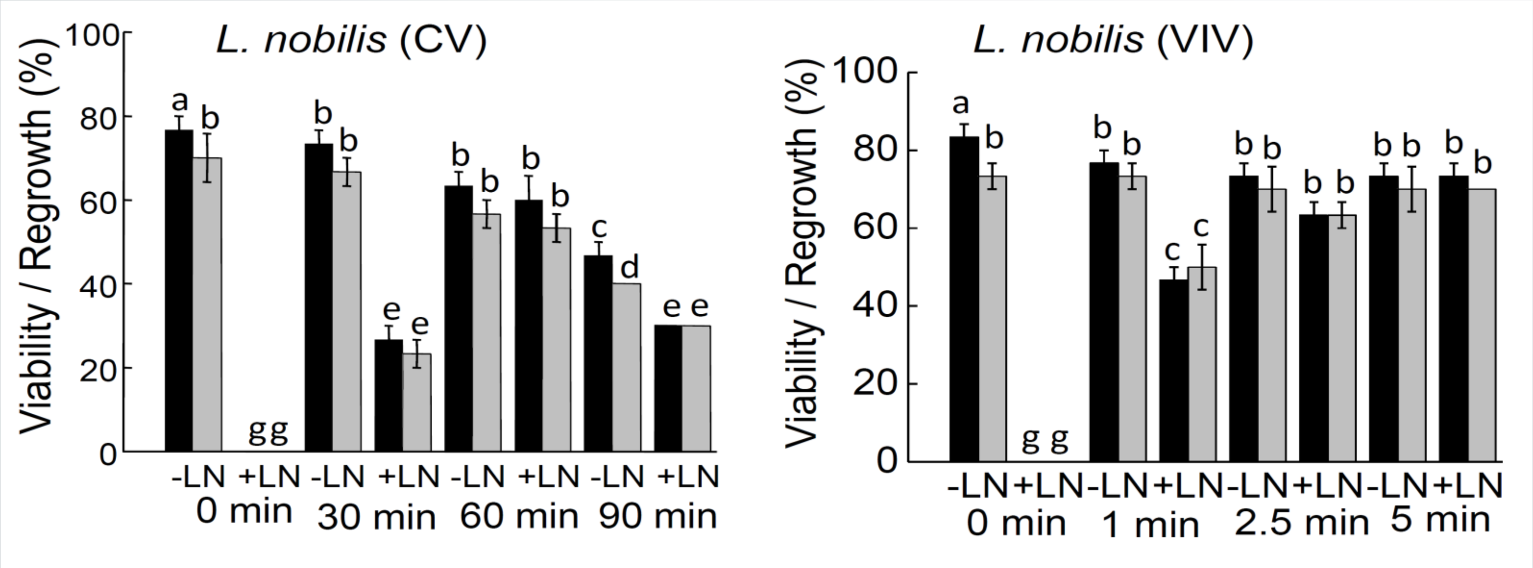


Thrinax radiata

Arenga westerhoutii

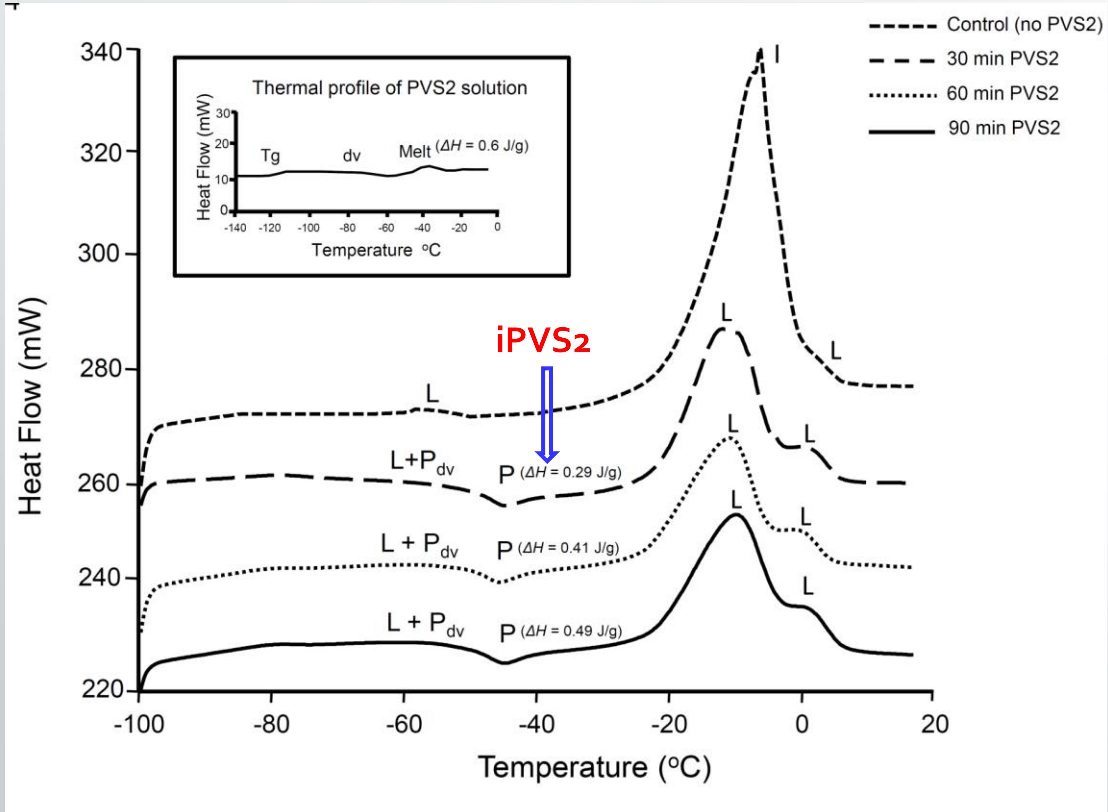
Comparative studies on conventional and vacuum infiltration vitrification (VIV) for *Laurus nobilis* embryos

- Heterogeneity in morphology, physiology and cellular chemistry of plant tissues can compromise successful cryoprotection and cryopreservation.
- We have developed an innovative method of vacuum infiltration vitrification (VIV) at 381 mm (15 in) Hg (50 kPa) that ensures the rapid and uniform permeation of Plant Vitrification Solution 2 (PVS2) cryoprotectant into plant embryos and their successful cryopreservation
- VIV-cryopreservation offered a 10-fold reduction in PVS2 exposure times, higher embryo viability and regrowth and greater effectiveness at two pre-treatment temperatures ($0^{o}C$ and $25^{o}C$).
- VIV cryopreservation may form the basis of a generic, high throughput technology for cryo genebanks.

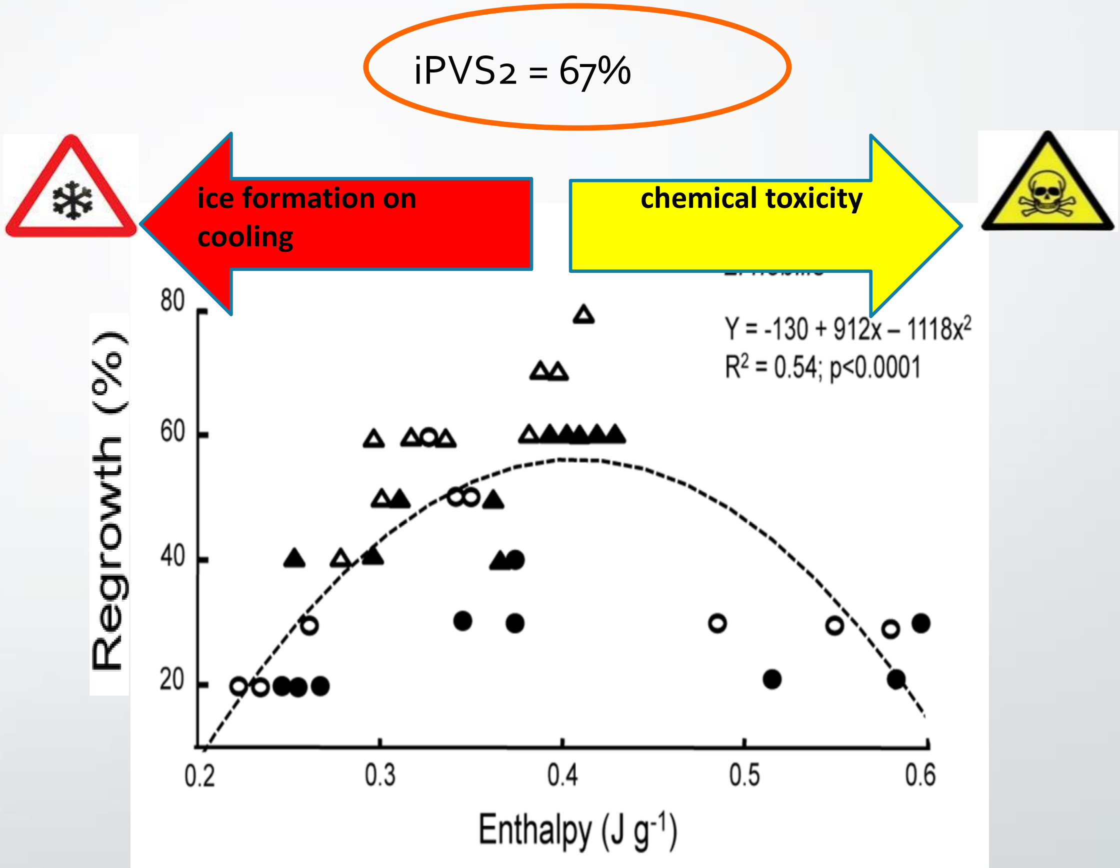


(Nadarajan J & Pritchard HW (2014). PLOS|ONE DOI: 10.1371/journal.pone.0096169)

Quantification of internal PVS2 (iPVS2) using DSC



DSC thermograms for *Carica papaya* embryos treated with PVS2 for 30, 60 and 90 min



Regrowth following cryo in relation to iPVS2

Nadarajan J & Pritchard HW (2014). Biophysical characteristics of successful oilseed embryo cryoprotection and cryopreservation using vacuum infiltration vitrification, an innovation in plant cell preservation. PLOS|ONE DOI: 10.1371/journal.pone.0096169

Advancements in cryobiotechnology and cryo-engineering

- Biophysical studies to ensure glass stability can be achieved and sustained in cryo-banked materials
- Thermal analysis using DSC is applied to help to optimise vitrification-based cryoprotection protocols
- Modulated DSCs and Dynamic mechanical analysers have been used to identify glass transitions more accurately
- Programmable freezers are used for stepwise freezing
- Cryo-microscopy to visualise localised ice crystallisation
- Personalised cryoprotectant treatments
- Rapid freezing in slush nitrogen temperature at -207^{o}C instead of in liquid nitrogen temperature at -196^{o}C

Programmable freezer

Differential scanning calorimetry

Dynamic mechanical analyser (DMA)

Take home messages

What we have learnt

- Seed ageing is influenced by external and internal factors and that could be measured through physiological, cytological and genetic changes.
- Increasing understanding of factors induce cytoplasmic solidification and affect glassy properties. Cytoplasmic solidification slows down, but does not stop, the chemical reactions involved in ageing.
- Chromosome damage and gene mutations increase with storage time and are inversely correlated with post-storage germination.
- Increases in oxygen tension, temperature and humidity were already known to accelerate ageing, but it was the gradual accumulation of toxic metabolites that was considered the main cause of ageing.
- Continued degradation of proteins, lipids and nucleic acids damage cell constituents and reduce the seed’s metabolic capacity, eventually impairing the ability to germinate.

More shell needs to be removed before we can see the whole seeds
– more discoveries yet to be made –

Emerging research areas in seed storage

Biochemical changes in seeds during storage

Oxidative stress in seeds during storage

RNA integrity in seeds during cold-dry storage

Seed dormancy and storage

Seed microbiome and storage

Cryobiotechnology and biophysics

Conclusions

Seed storage biology is a complex science covering seed physiology, biophysics, biochemistry and multi-omic technologies.

Simultaneous knowledge advancement in these areas is necessary to improve seed storage efficacy for crops and wild species biodiversity conservation.

Translation of Science into Practice

Technology Transfer Platforms

Hands on Workshops

Trainings Videos

Technical guidelines

Webinars

Discussion Forums

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THANK YOU

Thank you!

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