Ecological significance of physical dormancy

Ganesh K. Jaganathan

jganeshcbe@gmail.com

American Journal of Botany

Article

MECHANICS OF DORMANCY IN SEEDS†

Wm. Crocker

† Invitation paper read before the Botanical Society of America and affiliated societies at Columbus, December 29, 1915.

New Phytologist

Review

Tansley review

Seed dormancy and the control of germination

William E. Finch-Savage[1] and Gerhard Leubner-Metzger[2]

Seed Science Research

cambridge.org/ssr

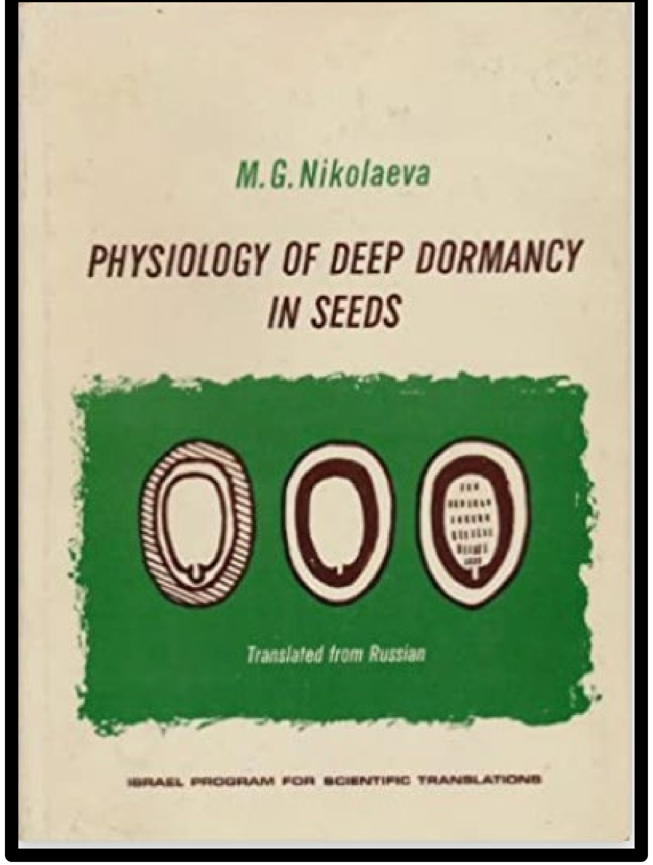
Review Paper

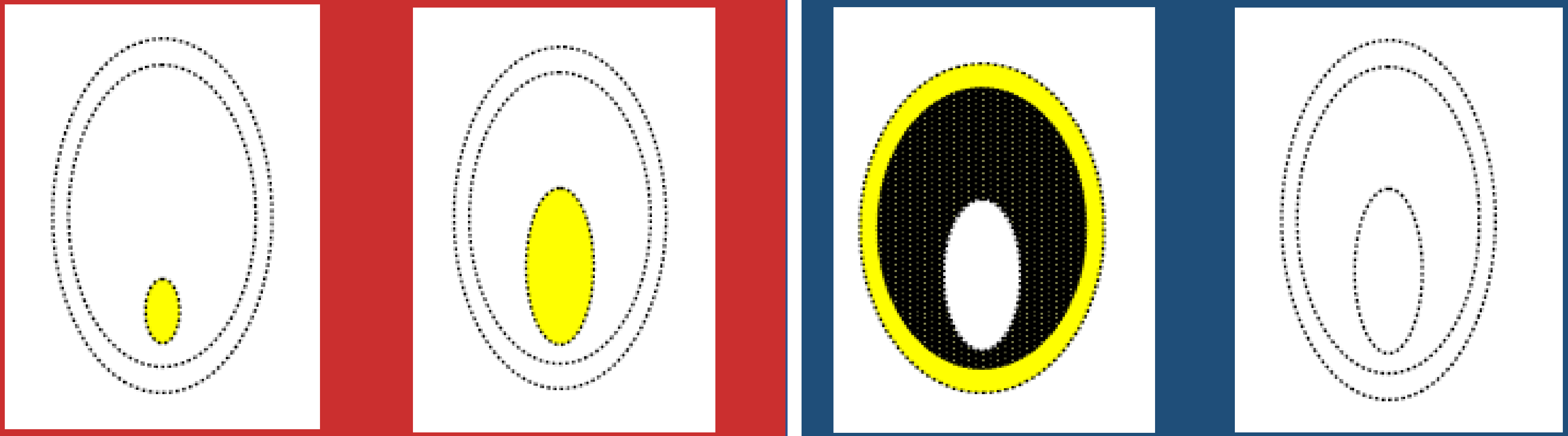
Cite this article: Baskin JM, Baskin CC (2021). The great diversity in kinds of seed dormancy: a revision of the Nikolaeva–Baskin classification system for primary seed dormancy. *Seed Science Research* 1–29.

The great diversity in kinds of seed dormancy: a revision of the Nikolaeva–Baskin classification system for primary seed dormancy

Jerry M. Baskin[1] and Carol C. Baskin[1,2]*

[1]Department of Biology, University of Kentucky, Lexington, KY 40506-0225, USA and [2]Department of Plant and Soil Sciences, University of Kentucky, Lexington, KY 40506-0312, USA





Morphological

Physiological

Morpho-physiological

Physical

Combinational
(Physical plus physiological)

Coexist with other traits

-Desiccation sensitive (Recalcitrant)

-epicotyl dormancy

Do not coexist with other traits

MD= morphological dormancy; PD=physiological dormancy; MPD= morphophysiological dormancy; PY= physical dormancy; PY+PD or PYPD= combinational dormancy

PY occurs due to the impermeable nature of the seed/fruit coat.

Thus, structures such as endosperm, cotyledon, embryo would not influence PY.

But, these structures influence PD in PY+PD.

Table 1. Seed dormancy classes in different *Quercus* subgenera and sections.

Scheme	Subgenus (Section)	Root Dormancy	Shoot Dormancy	Dormancy Class
Q. acutissima Carruth. [11]	*Cerris* (*Cerris*)	PD		PD
Q. cerris L. [12]	*Cerris* (*Cerris*)	ND	DD	DD
Q. suber L. [12,13]	*Cerris* (*Cerris*)	ND	PD	epicotyl PD
Q. variabilis Blume [12]	*Cerris* (*Cerris*)	ND	DD	DD
Q. annulata Sm. [12]	*Cerris* (*Cyclobalanopsis*)	ND	DD	DD
Q. austrocochinchinenesis Hickel and A.Camus [14]	*Cerris* (*Cyclobalanopsis*)	ND	DD	DD
Q. camusiae Trel. ex Hickel & A.Camus [12]	*Cerris* (*Cyclobalanopsis*)	PD/PY *	DD	PD/PY *
Q. chungii F.P.Metcalf [15]	*Cerris* (*Cyclobalanopsis*)	ND	DD	DD
Q. fleuryi Hickel and Camus [12]	*Cerris* (*Cyclobalanopsis*)	PD/PY *	DD	PD/PY *
Q. glauca Thunb. [12]	*Cerris* (*Cyclobalanopsis*)	PD/PY *	DD	PD/PY *
Q. glaucoides M.Martens and Galeotti [16]	*Cerris* (*Cyclobalanopsis*)	PD		PD
Q. multinervis Cheng & Hong [12]	*Cerris* (*Cyclobalanopsis*)	PD/PY *	DD	PD/PY *
Q. schottkyana Rehd. and Wils. [12]	*Cerris* (*Cyclobalanopsis*)	PD/PY *	DD	PD/PY *
Q. aquifolioides Rehd. and Wils. [17]	*Cerris* (*Ilex*)	ND	ND	ND
Q. floribunda Wall. [18–20]	*Cerris* (*Ilex*)	ND	ND	ND

Physical dormancy in recalcitrant seeds?

Sun et al. (2021) Forests

Annals of Forest Science (2021) 78:10
https://doi.org/10.1007/s13595-021-01032-9

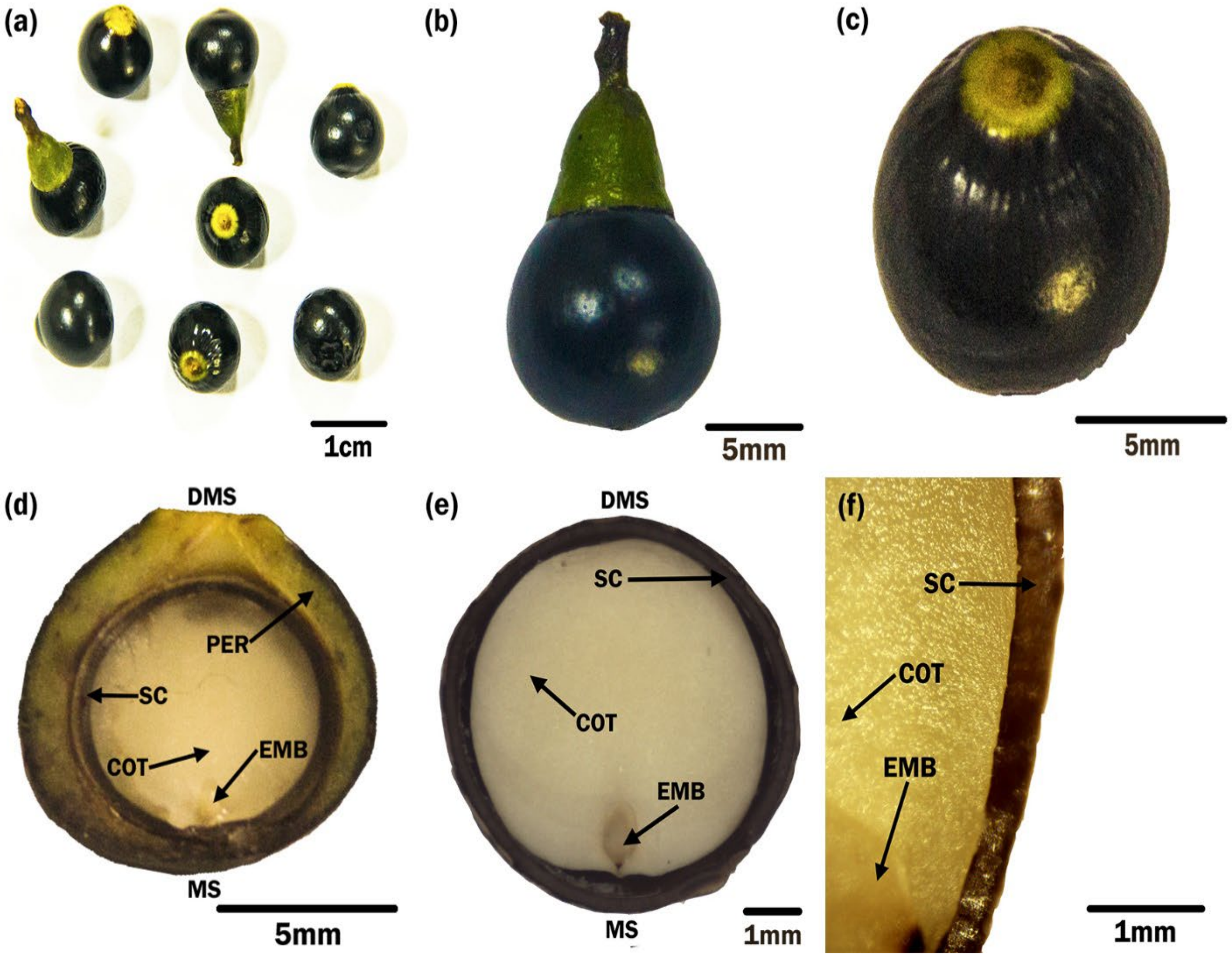
REVIEW PAPER

Check for updates

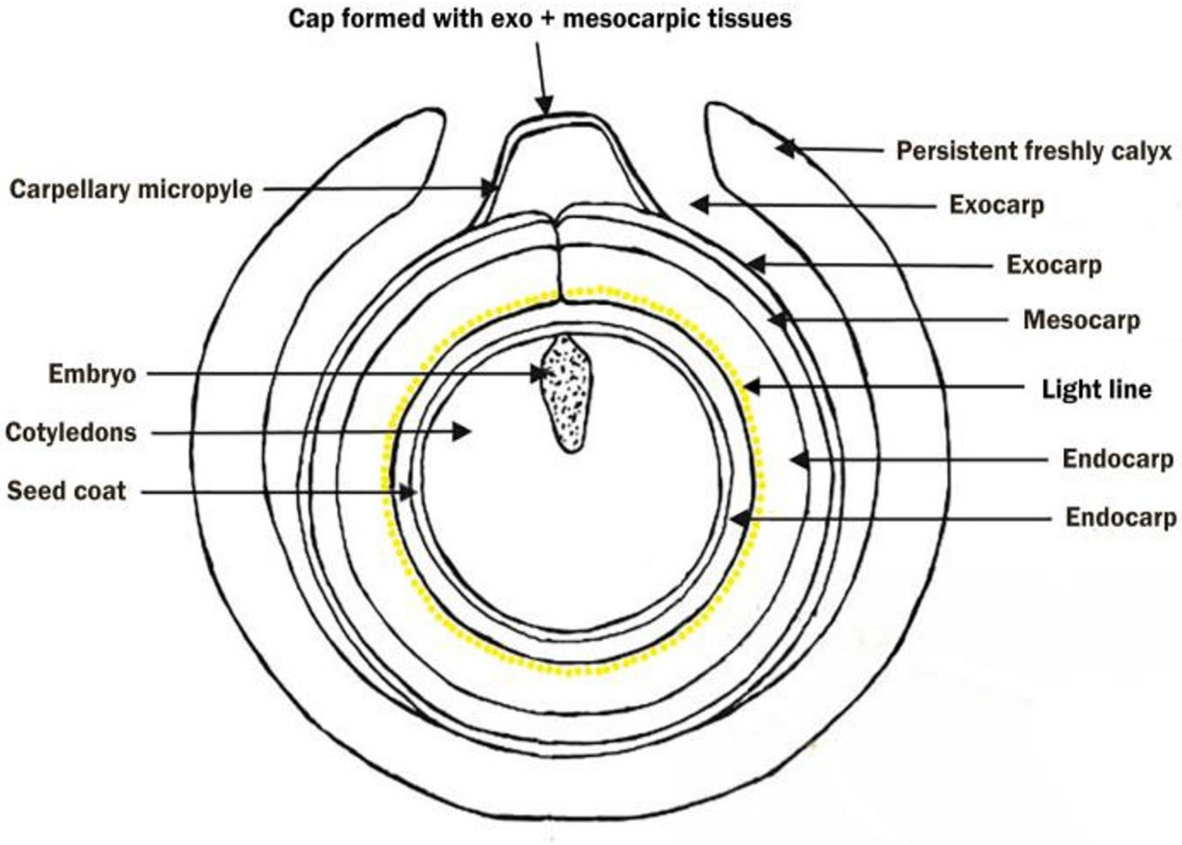
Ecological insights into the coexistence of dormancy and desiccation-sensitivity in Arecaceae species

Ganesh K. Jaganathan[1]

Physical barrier ≠ Physical dormancy

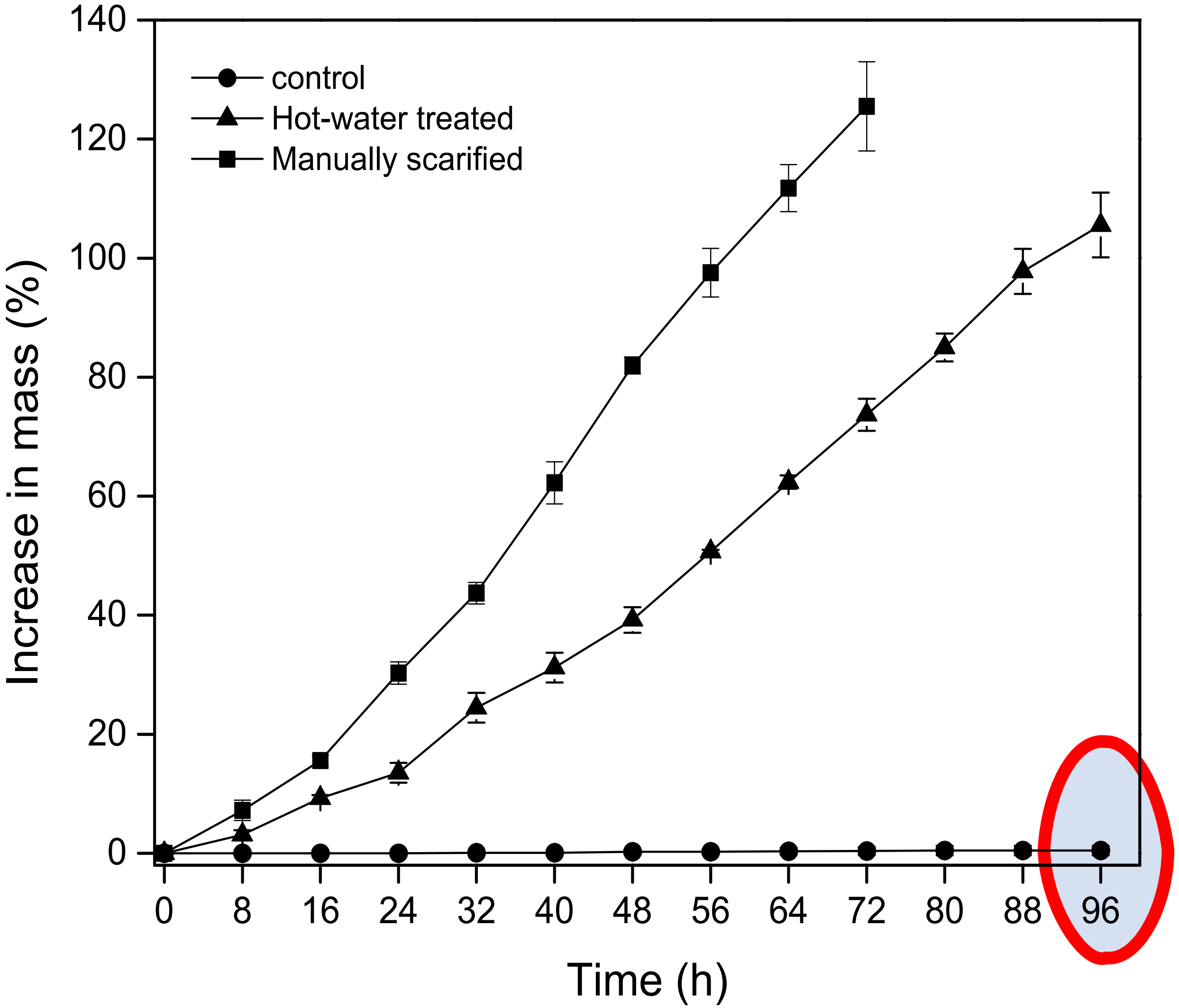


Structure of *Cinnamonum camphora* (a) collection of fruits showing different size; (b) a single fruit with attachments; (c) a single fruit without attachments; (d) cross-section of a fruit with pericarp; (e) cross-section of a fruit without pericarp and (f) close-up of seed coat. Sc, seed coat; COT, cotyledon, EMB, embryo, PER, pericarp; MS, micople side; D MS, distal micople side.



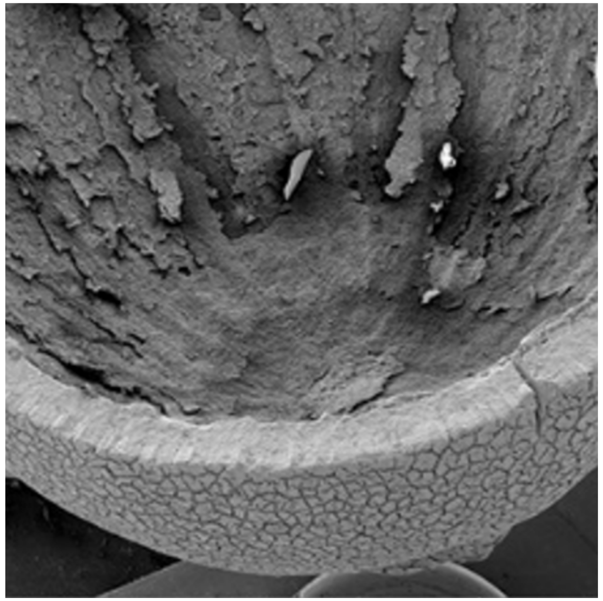
From Jaganathan et al. (2019) Bot Letters

The only way to confirm physical dormancy in a species is by conducting an imbibition test



Percentage increase in mass of non-treated intact (control), hot-water treated and mechanically scarified *Delonix regia* seeds on moist filter paper incubated at ambient conditions. Error bars represent the standard deviation of the mean.

From Jaganathan et al. (2018) Plant Biol.


In the past five decades…

(1) **environmental conditions/factors required for the development and breaking of PY**

- Rainfall
- Temperature
- Relative humidity
- Diurnal temperature fluctuation

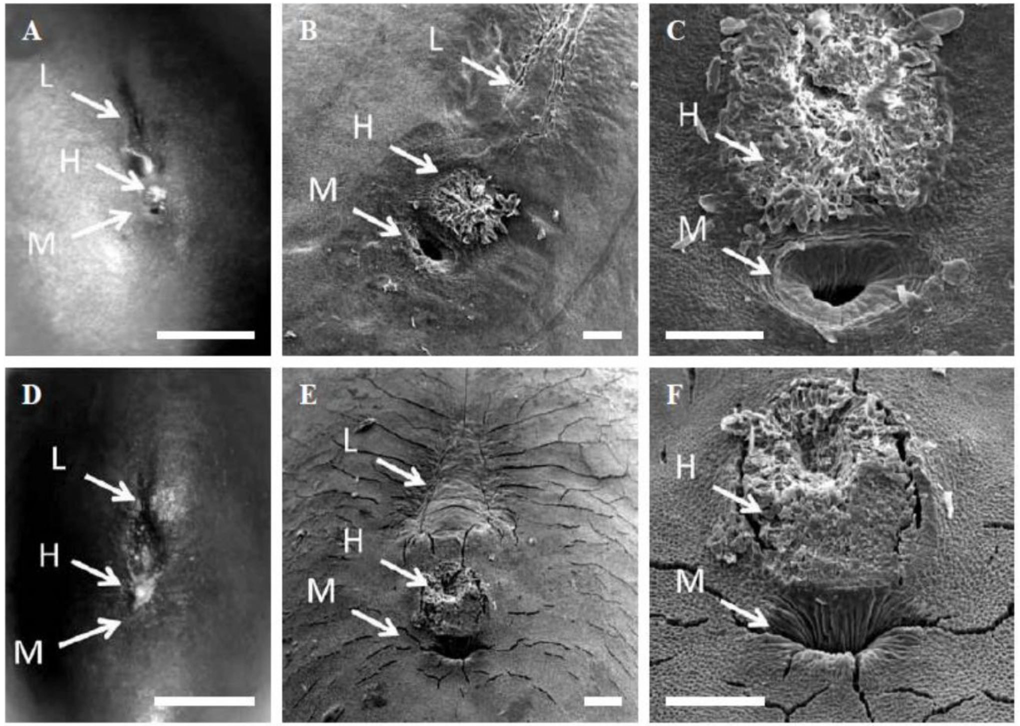
(2) **structures involved in the development and breaking of impermeable coats; and**

- Micropyle
- Hilum
- Light line
- Water-gap structures, e.g. Lens

(3) **association with other fitness traits such as desiccation-sensitivity (DS), predation and defense.**

- DS and PY are mutually exclusive traits
- PY invest little in chemical defense
- Impermeable seed coat offers protection against predation and persistence

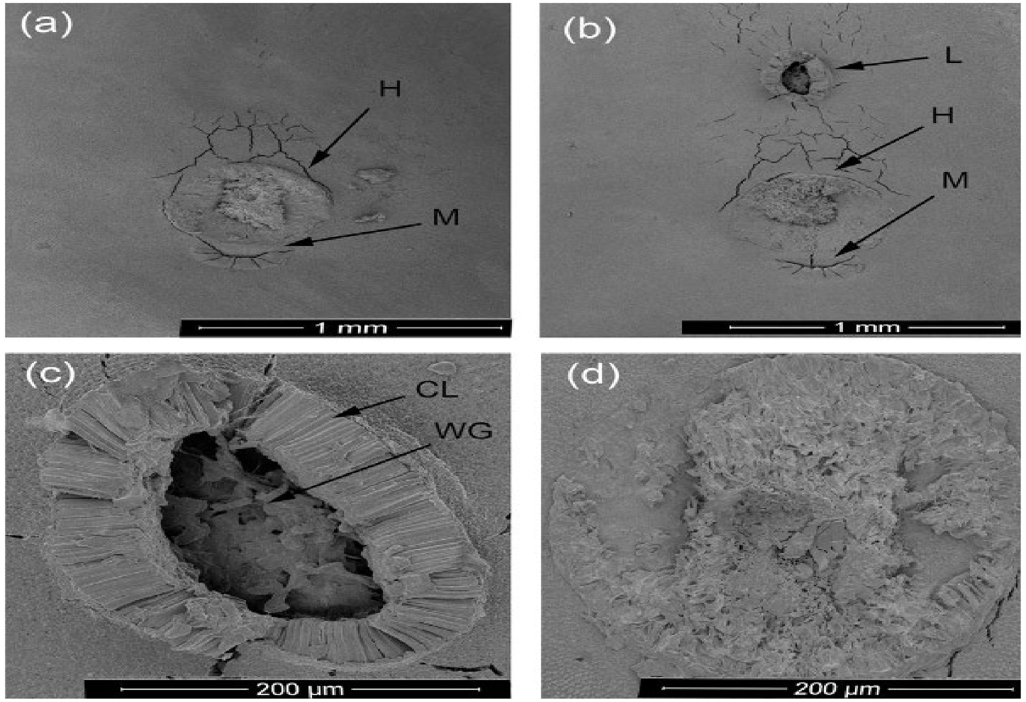
During development



Seed coat closes
Hilum closes (Lens become more distinct)
Micropyle closes

Seeds become impermeable

During dormancy-break



Water-gap opens
Water enters and hydrates embryo

Seeds become permeable

1) Evolutionary origin
2) Primary and secondary dormancy
3) Global distribution
4) Dormancy-cycling/subdivision

Some authors even proposed impermeable seed coat is not a form of dormancy

Conundrum 1

Evolutionary origin

Evolution of impermeable seeds

Factors	Support	Against
Fire	Keeley et al. (2011) Trends Plant Sci; Pausas and Lamont (2022) Biol Rev	Bradshaw et al. (2011) Trends Plant Sci; Also see Jaganathan (2015) Seed Sci Res
Endozoochory	Temple (1977) Science	Jaganathan (2016) Perpsp Plant Ecol Evol Syst
Crypsis	Paulsen (2014) J Ecology Paulsen (2015) Seed Sci Res	Jayasuriya et al. (2015) Seed Sci Res; Jaganathan (2018) Ecol Res
Protection during persistence	Brancalion (2010) Ann. Bot; Filip Vandelook (2021) ISSS conference	Jaganathan et al. (2018) Ann. Bot Plants

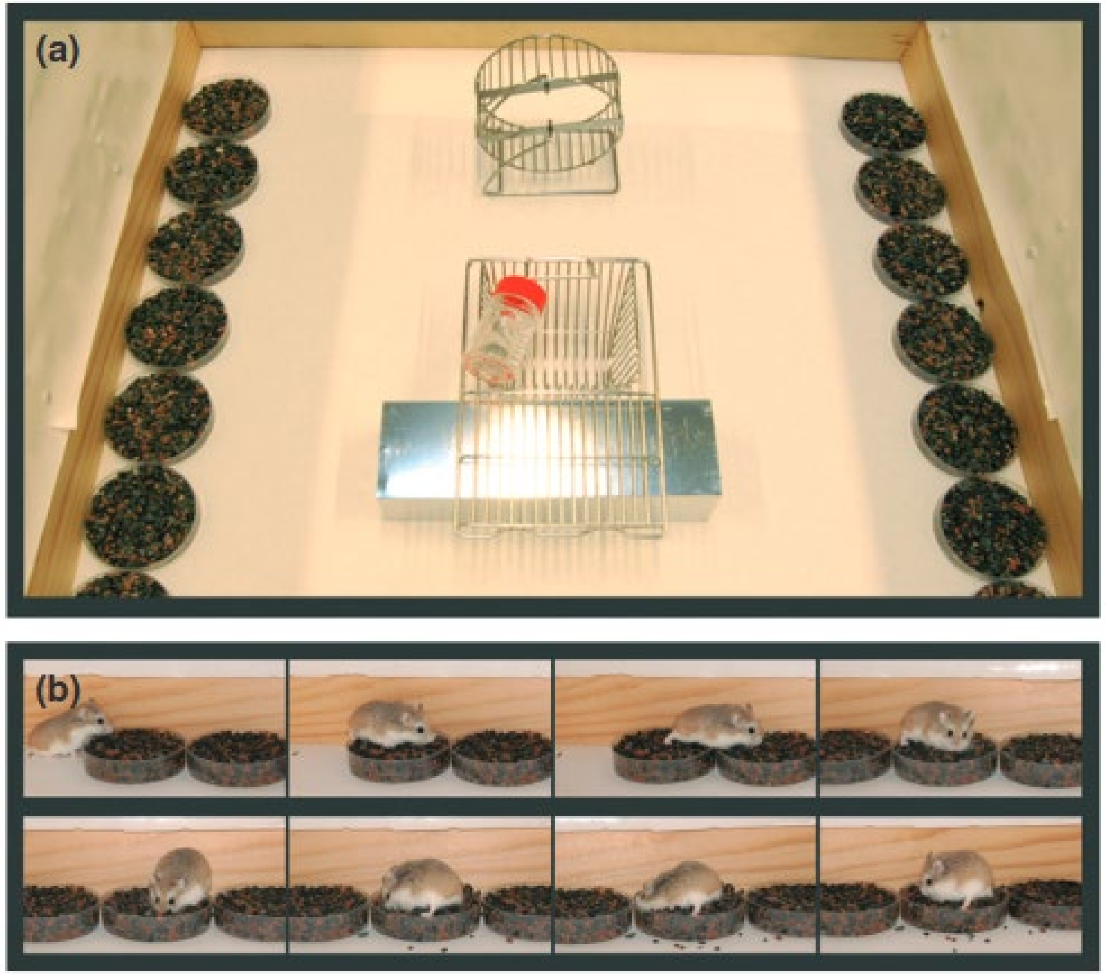


Fig. 1 The arena. (a) The set-up of the wooden arena in which the hamsters were offered seed caches and which included a nest box filled with nesting material, a running wheel, and a water bottle. (b) The hamsters easily find and harvest buried seed caches using olfaction.

Paulsen et al. (2014) New Phytologist

- Does not explain year-to-year variation
- Does not explain why other species did not evolve impermeable coats, e.g. pine
- Does not explain the long-term persistence
- <u>Chance event?</u>

The same applies to all factors

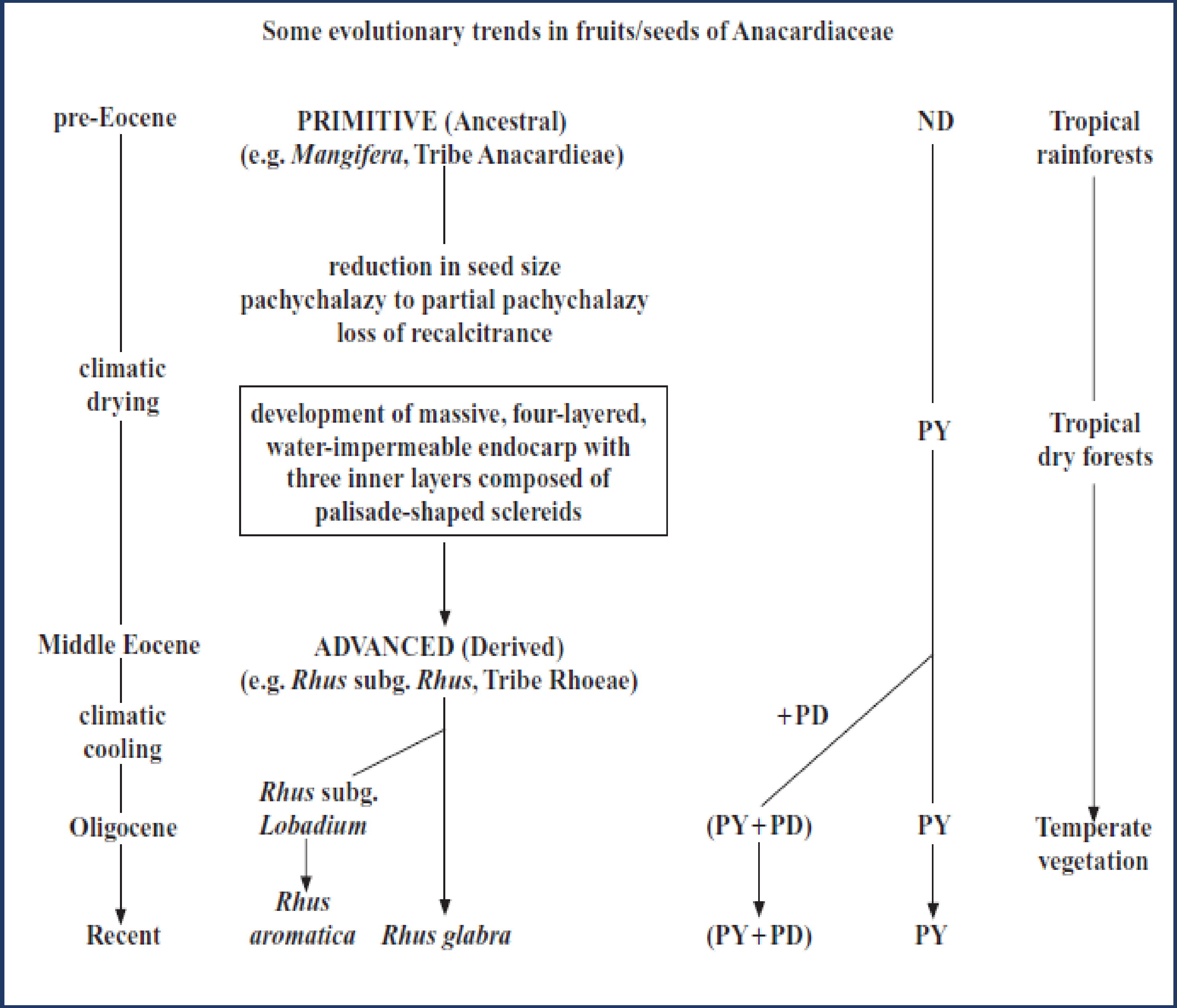
Byron B. Lamont

Since seed dormancy is usually considered as just under climate control, non-soil-stored seeds subject to frugivory or fire-caused heat release (serotiny) have been ignored in global syntheses, but there is a case for considering them as examples of physical dormancy.

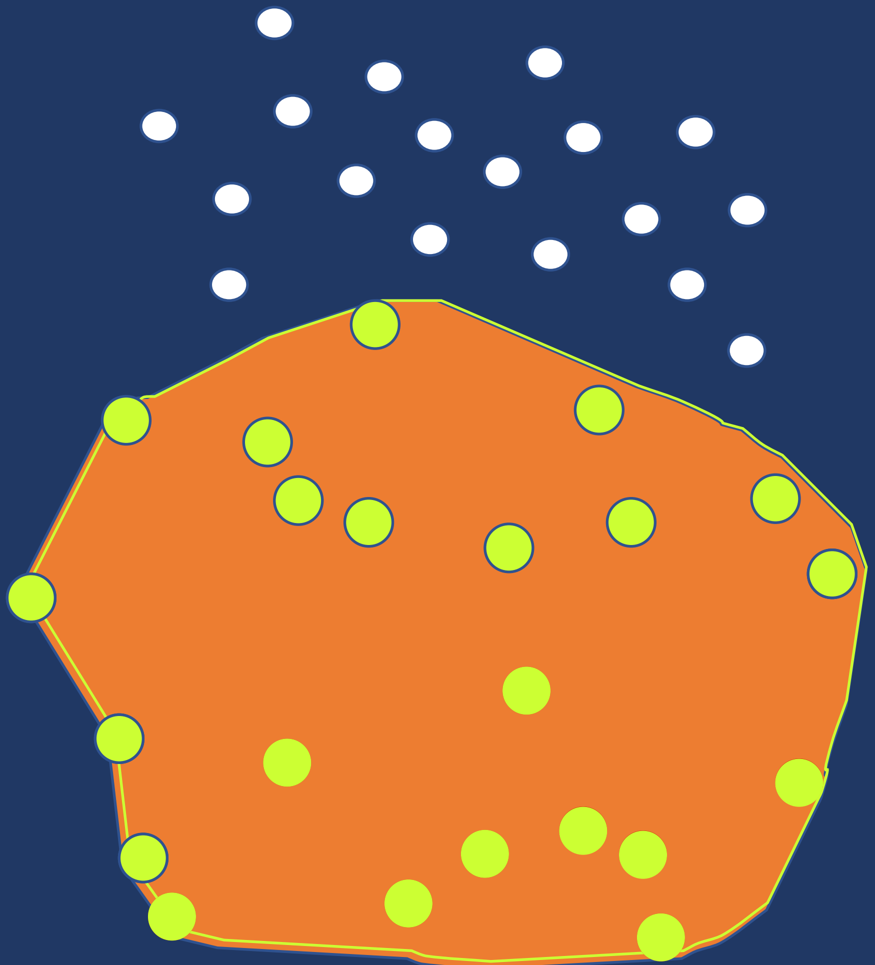
Juli G. Pausas

"Physical dormancy-break is not tied to fire in the Cerrado mosaic. " One limitation to serotiny is that when fire intervals are very long and plants die before the next fire, seeds are released but seldom recruit successfully in the unburned vegetation

Climate drying?



Baskin et al. (2000) Plant Species Biol

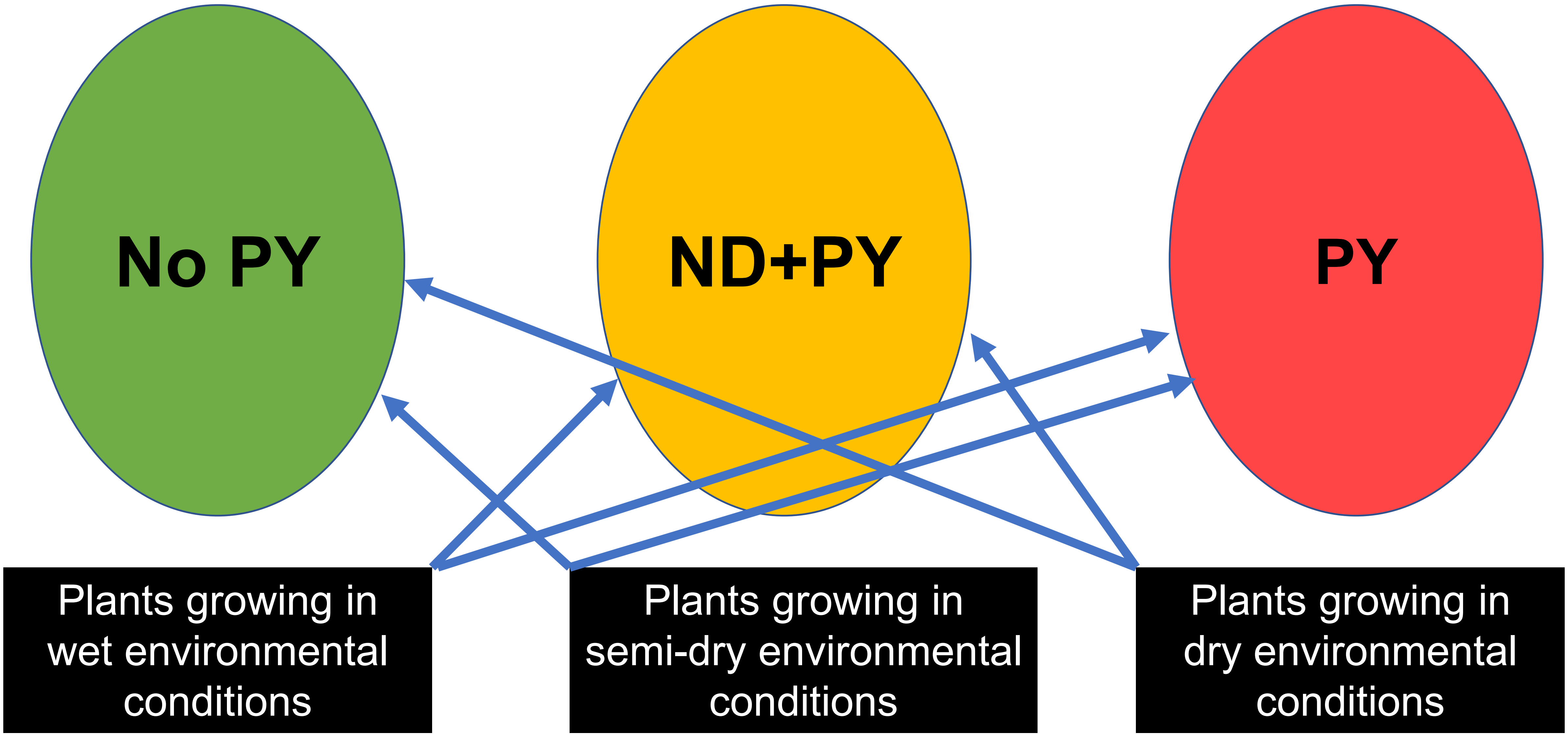


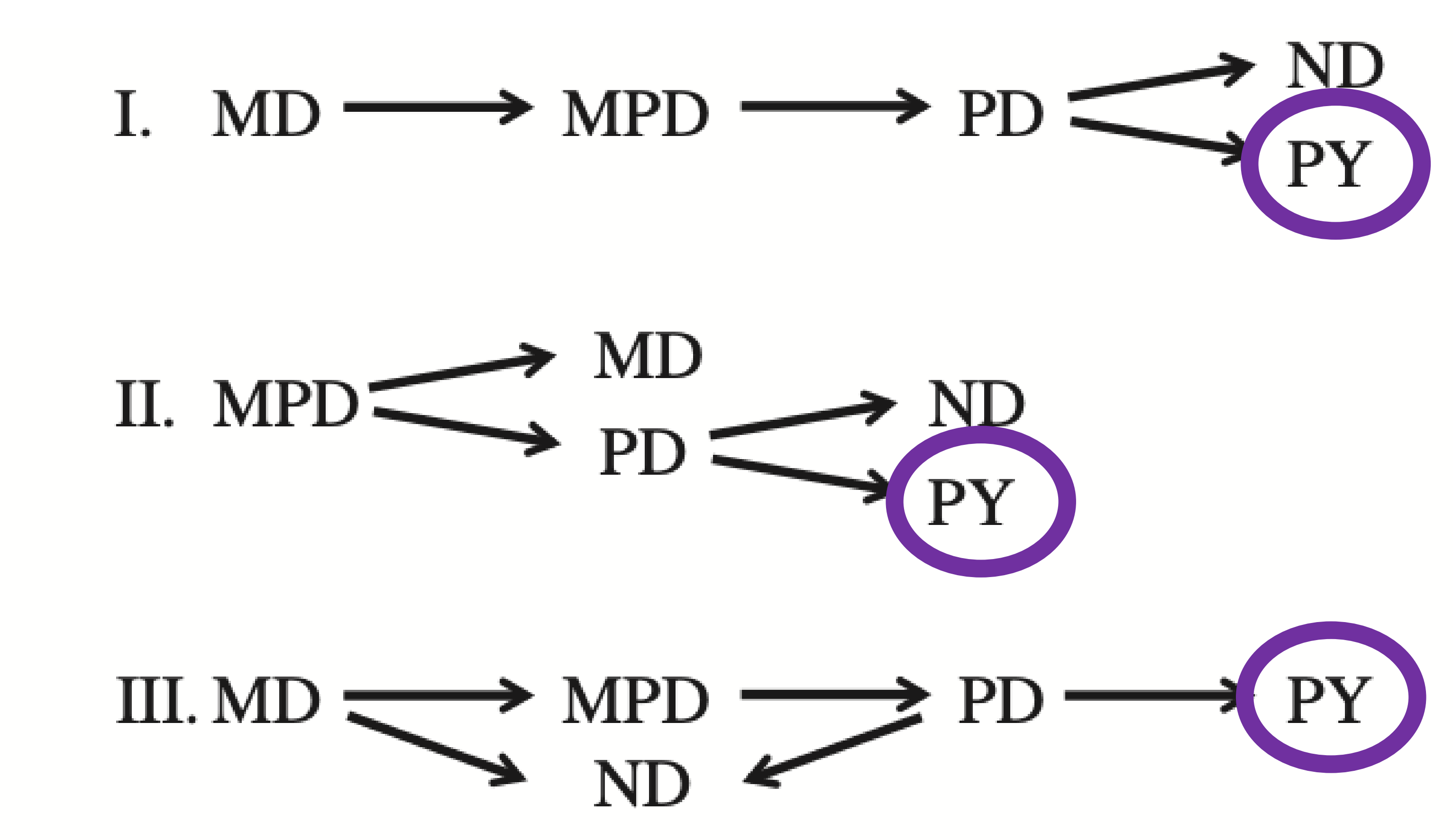
What about protection after dispersal

- PY seeds can persist in the soil for a long time
- Microorganisms cannot attack the internal parts of the seeds
- Can disperse to secondary environments
- Protect from acid environments of the animal intestine (gut).

Quinlivan states

The length of the growing period in the spring months appears to be a critical factor in the development of hardseededness. Environments with relatively long spring growing periods cause a higher proportion of hard seeds to form at field maturity, and increase the resistance which these hard seeds are capable of offering to the softening effects of the following summer environment. During the dry summer period the rate of softening of hard seeds is determined, not only by the previous growing season but also by the summer environment itself. Hot summer environments with wide soil surface temperature fluctuations are conducive to a relatively rapid rate of softening.


No PY
ND+PY
PY
Plants growing in wet environmental conditions
Plants growing in semi-dry environmental conditions
Plants growing in dry environmental conditions



From Willis et al. (2014) New Phytol

Regardless of the ancestral state, PY is definitely a derived trait, most likely evolved from PD

Resolving Conundrum 1

One of the main reasons to accept **climate change as the evolutionary factor of PY evolution** is the effect on all plants in a particular area. No other factor described as the driving force for the evolution of PY acts on all plants. Thus, only a proportion of seeds face those factors during seed maturation and dormancy break. For example, the fire could act on species only in fire-prone areas.

Conundrum 2

Redefining primary and secondary dormancy

Defining primary and secondary dormancy

Primary dormancy : Seeds that are dormant at the time of dispersal
Secondary dormancy: Seeds that are dormant at the time of dispersal, lose dormancy and re-enter dormancy

According to Soltani *et al*. (2019) there are no known cases of non-dormant seeds becoming dormant after dispersal. If any such cases are to be found, they should be referred to as 'enforced dormancy'.

Is this only for physiological dormancy? What about physical dormancy

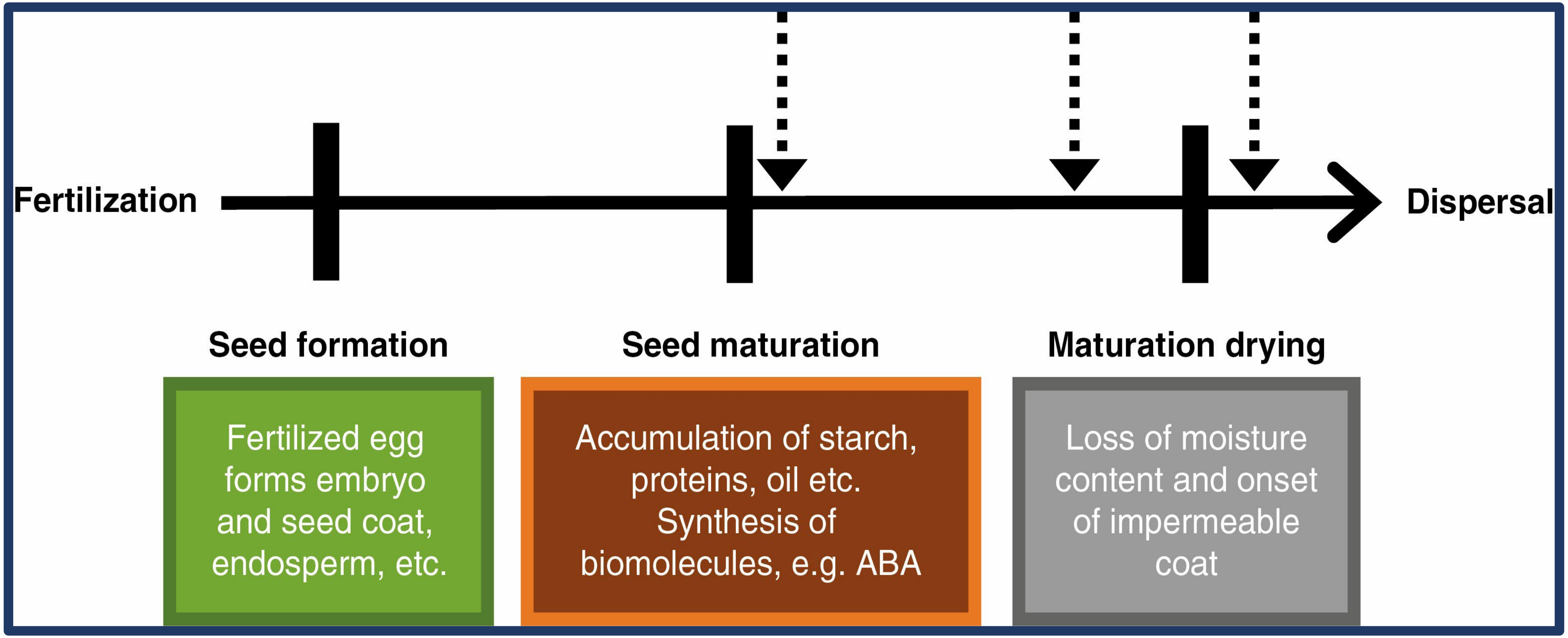
Elias Soltani

WEED RESEARCH
An International Journal of Weed Biology, Ecology and Vegetation Management

Review Paper

A review of the relationship between primary and secondary dormancy, with reference to the volunteer crop weed oilseed rape (*Brassica napus*)

E Soltani, J M Baskin, C C Baskin



Annals of Botany **130**: 121–129, 2022
https://doi.org/10.1093/aob/mcac084, available online at www.academic.oup.com/aob

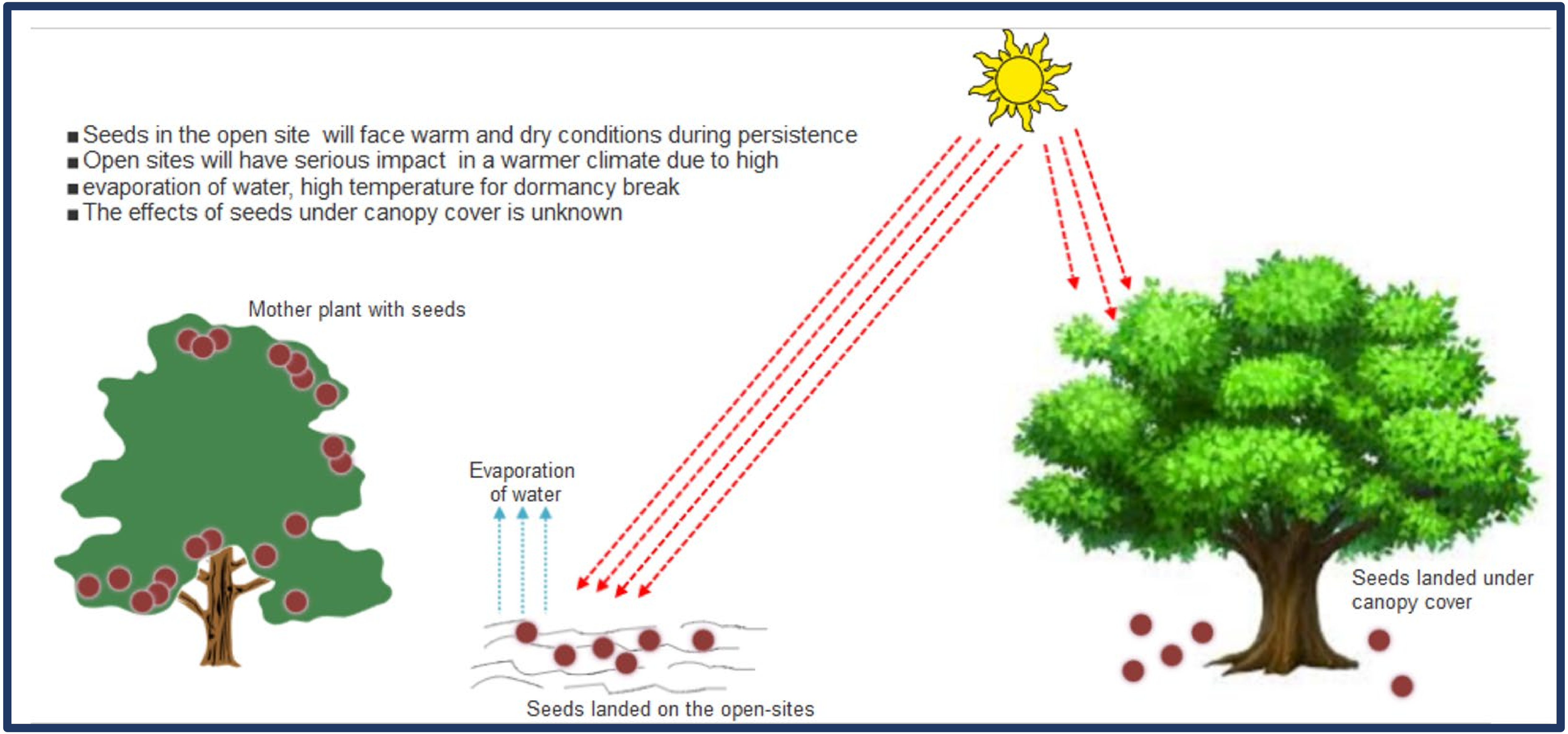
ANNALS OF BOTANY Founded 1887

VIEWPOINT

Unravelling the paradox in physically dormant species: elucidating the onset of dormancy after dispersal and dormancy-cycling

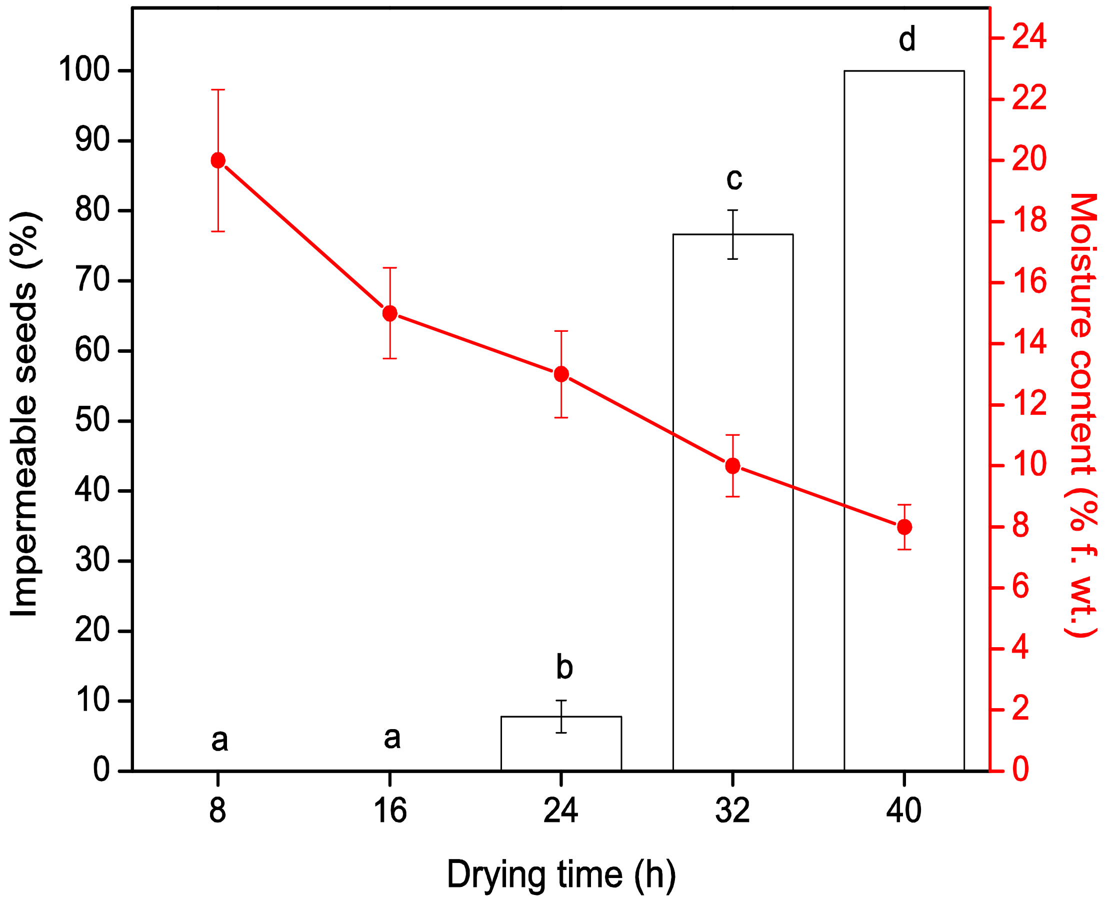
Ganesh K. Jaganathan*

Germplasm Conservation Laboratory, University of Shanghai for Science and Technology, Shanghai 200093, China
* *E-mail: jganeshcbe@gmail.com*

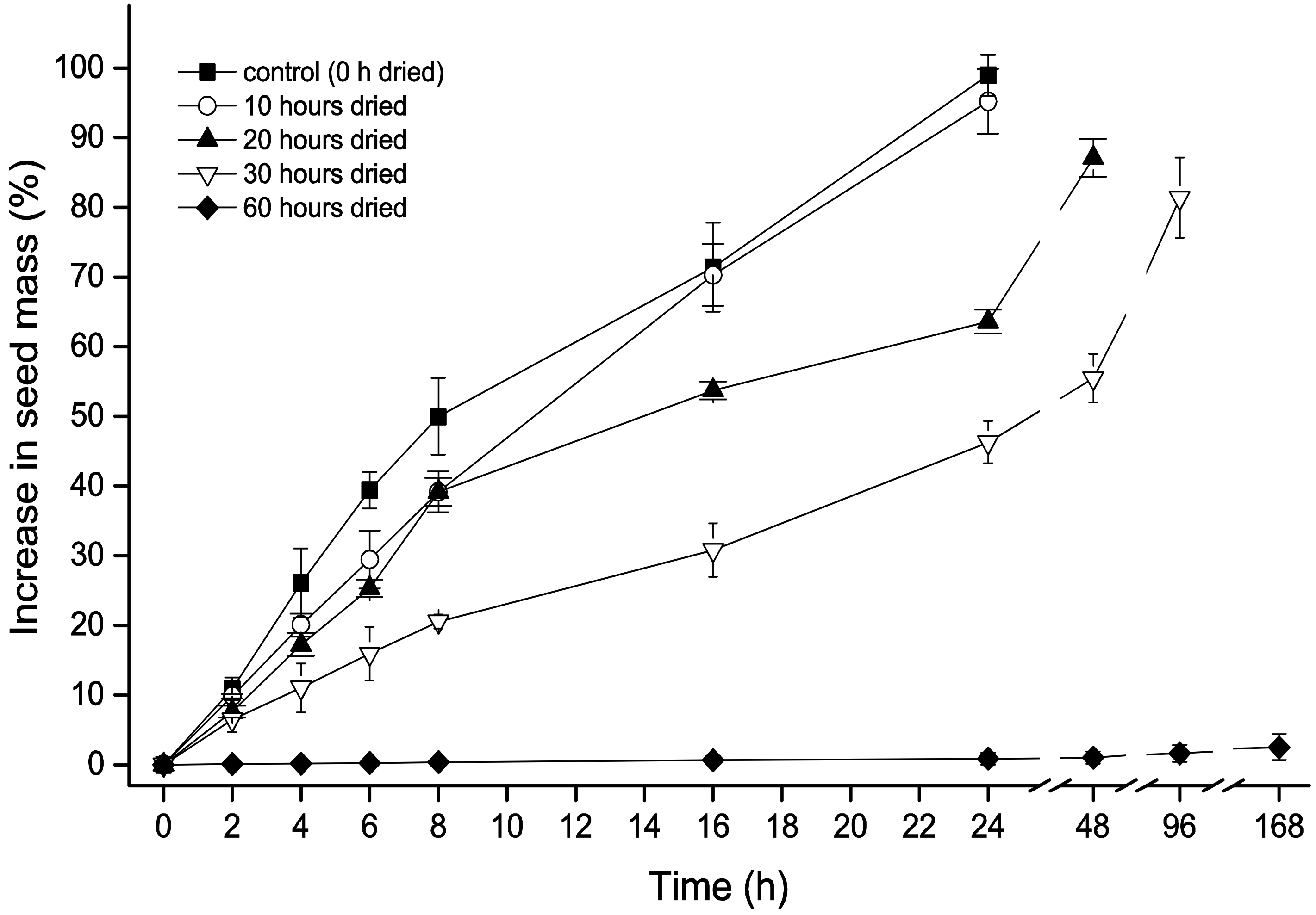


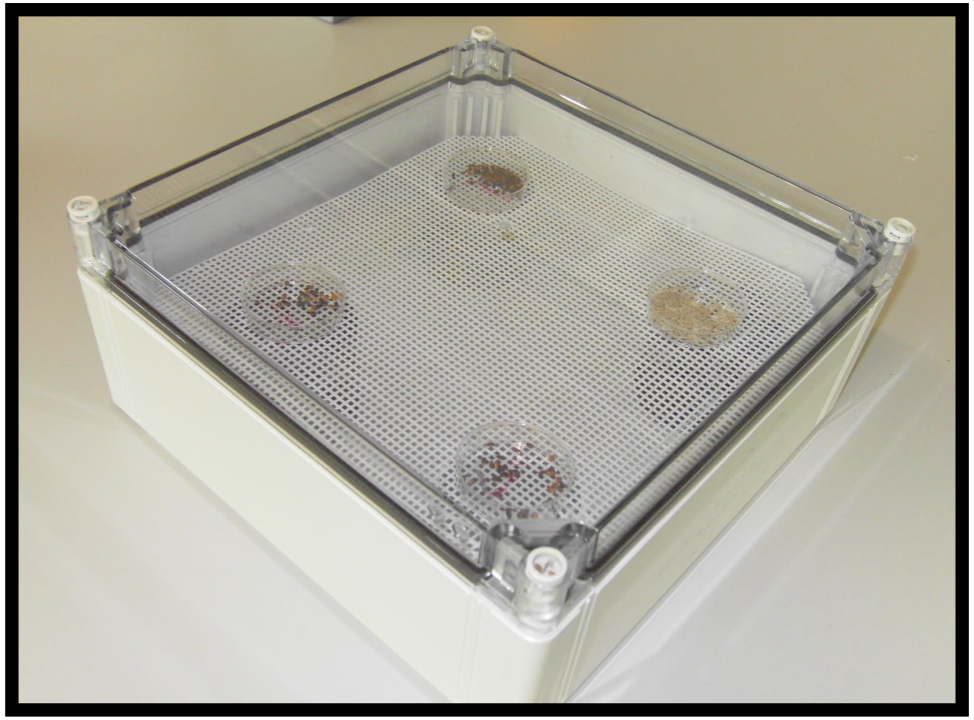
Jaganathan and Biddick (2021) J Trop Ecol.

Photographs of seed maturation temperature measurement in *Acacia chundra*. The pods are undergoing maturation drying, the thermocouples were fixed in a way they sit close to the pod (a), and these thermocouples are then attached to a data logger in the research station (b).



The proportion of impermeable *Nelumbo nucifera* seeds at different moisture contents. Different letters indicate a statistically significant difference in the number of impermeable seeds at the different moisture contents. Error bars indicate the standard deviation of the mean





Percentage increase in *Astragalus adsurgens* seed mass when placed in a moist environment after being dried to different periods above silica gel. Error bars represent the standard deviation

Robert L. Geneve

Anatomical observations suggest that the micropyle in all species except eastern redbud remains open late in seed development to aid in seed desiccation coincident with acquisition of physical dormancy.

This agrees with the previous and subsequent observations including Hyde (1954) Ann. Bot., Gladstone (1958) Aus J Agri Res.

Resolving Conundrum 2

Permeable seeds can become impermeable after dispersal. Therefore, **primary dormancy is not a requirement for the development of dormancy subsequently**. Consequently, ‘enforced dormancy’ is a known case, perhaps, much more common than previously thought. But some refinement is needed to define dormancy.

This ability to dry and become dormant after dispersal may affect how the species with physical dormancy survive any future change in climate.

Conundrum 3

Global distribution

Analyses of a large data set of legumes (n = 216 000 observations of 532 species) revealed a clear association between seed dormancy, seed size and seasonality. Dormancy was prevalent in temperate, seasonal environments, while nondormant seeds were concentrated in the tropics.

Rubio de Casas et al. (2017)

- **Our findings for species with physically dormant seeds (both PY and PYPD) corresponded with those of Rubio de Casas et al. (2017): these species produce small seeds, and occur predominantly outside of the tropics, where there are comparatively low minimum temperatures and high frequencies of frosts**
- **For the Fabaceae, it appears that PY may be disadvantageous in tropical habitats, and so PD seems to be the 'solution' to precipitation seasonality in those environments.**

Wyse and Dickie New Phytologist (2018) 217: 477–479

List of species with confirmed physical dormancy in alpine regions

Seed Science Research (2013) **23**, 257–269 doi:10.1017/S0960258513000214

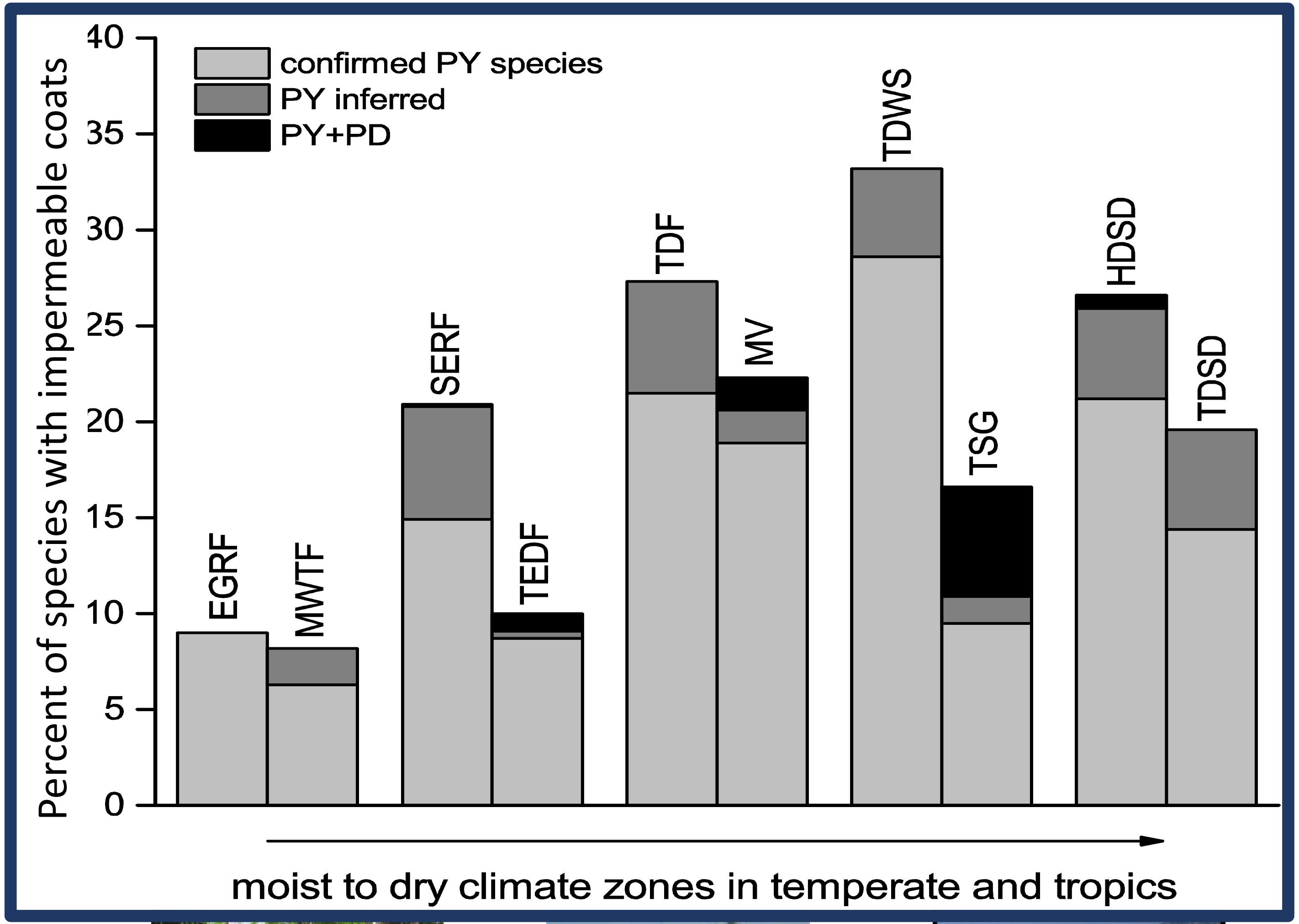
Seed dormancy and storage behaviour in tropical Fabaceae: a study of 100 species from Sri Lanka

K.M.G. Gehan Jayasuriya[1]*, Asanga S.T.B. Wijetunga[2], Jerry M. Baskin[3] and Carol C. Baskin[3,4]

[1]Department of Botany, University of Peradeniya, Peradeniya, Sri Lanka; [2]Department of Biology, Rajarata University of Sri Lanka, Mihintale, Sri Lanka; [3]Department of Biology, University of Kentucky, Lexington, Kentucky 40506-0225, USA; [4]Department of Plant and Soil Sciences, University of Kentucky, Lexington, Kentucky 40546-0321, USA

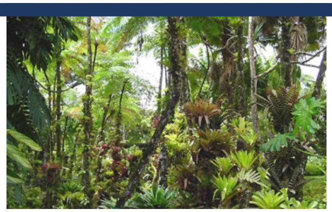
Out of 100 Fabaceae species tested, 86 had physical dormancy

Species	Family	Dormancy type
Anthyllis alpicola	Fabaceae	PY
A. subpolaris	Fabaceae	PY
Astragalus cottonii	Fabaceae	PY
Geranium albiflorum	Geraniaceae	PY
Hedysarum arcticum	Fabaceae	PY
H. occidentale	Fabaceae	PY
Lupinus latifolius	Fabaceae	PY
Luzula spicata	Juncaceae	(PY?) +PD*
Oxytropis sordida	Fabaceae	PY
O. viscida	Fabaceae	PY
Trifolium nanum	Fabaceae	PY
T. pallescens	Fabaceae	PY
Vicia amoena	Fabaceae	PY
V. unijuga	Fabaceae	PY
V. angustifolia	Fabaceae	PY



Tropical and sub-tropical zones
EGRF-evergreen rain forest
SEGRF-semi-evergreen rain forest
TDF-tropical deciduous forest
TDWS-tropical dry woodland and savanna
HDSD-hot desert and semi-desert

Temperate zones
MWTW-moist, warm temperature woodland
TDW-temperate deciduous woodland
MV-matorral vegetation
TDSD-temperate desert and semi-desert



Distribution of physical dormancy in various life-forms across tropical and temperate ecosystems. Values given in parenthesis are the percentage of inferred species. NDE- no details exist.

Life form	Tropical Ecosystem	Temperate Ecosystem
Trees	15.2 (5)	6.8 (0.9)
Shrubs (and bamboos)	27.8 (6.2)	18.9 (0.2)
Lianas and vines	22.3 (3)	20 (3.4)
Herbs and epiphytes	21.7 (4)	10.5 (2.4)
Weeds	18.2 (0)	26.9 (0)
Annuals	23.5 (1.3)	NDE
Non-weeds	NDE	8.8 (1.2)
Forbs	NDE	19.8 (1.7)
Graminoids	NDE	0

Resolving Conundrum 3

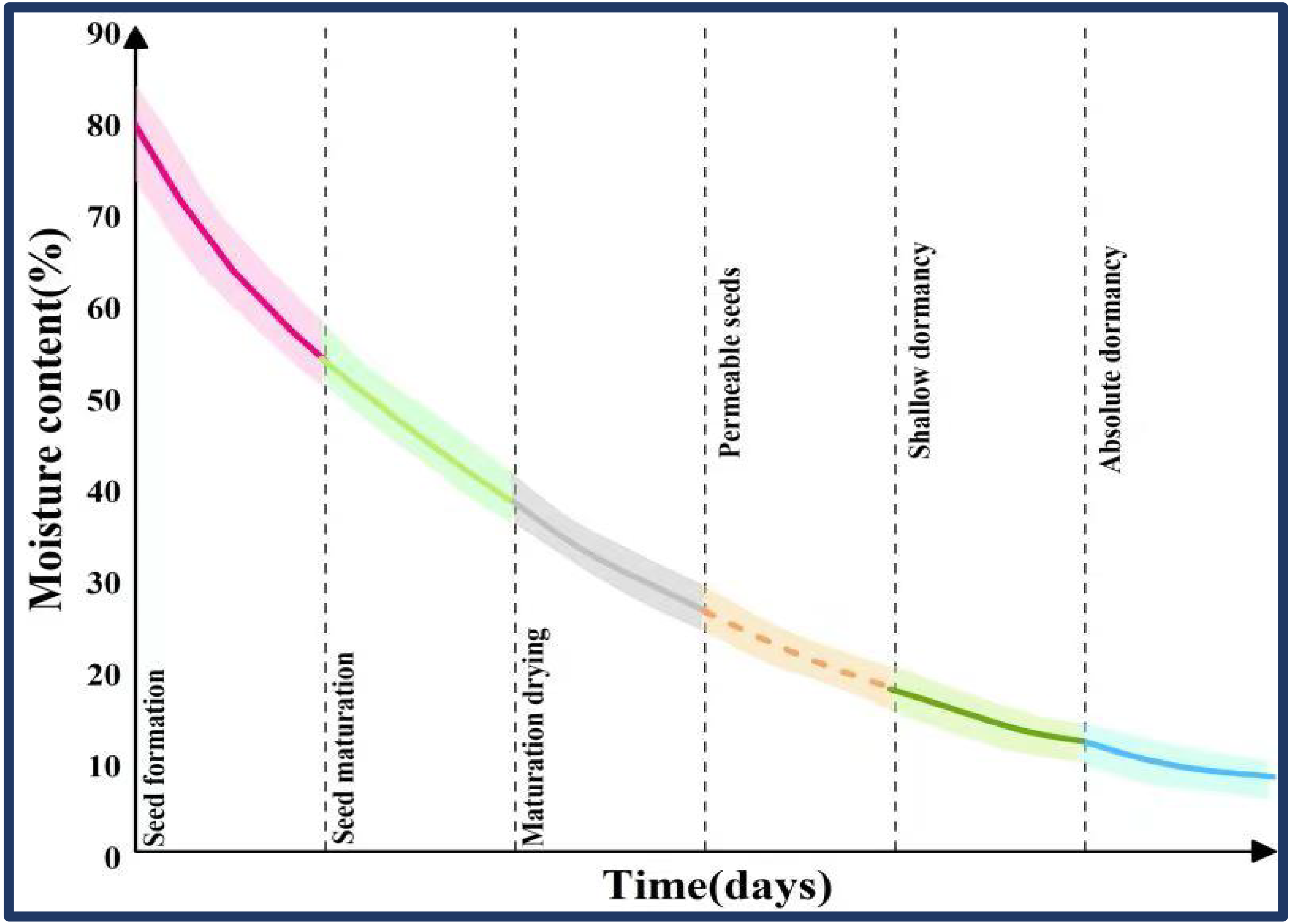
Physical dormancy is arguably more common in the tropics, particularly in tropical drylands. Contradictory to previous claims, temperate ecosystems may have less physical dormant species. Claiming physical dormancy ‘*may be*’ disadvantageous in the tropics is redundant.

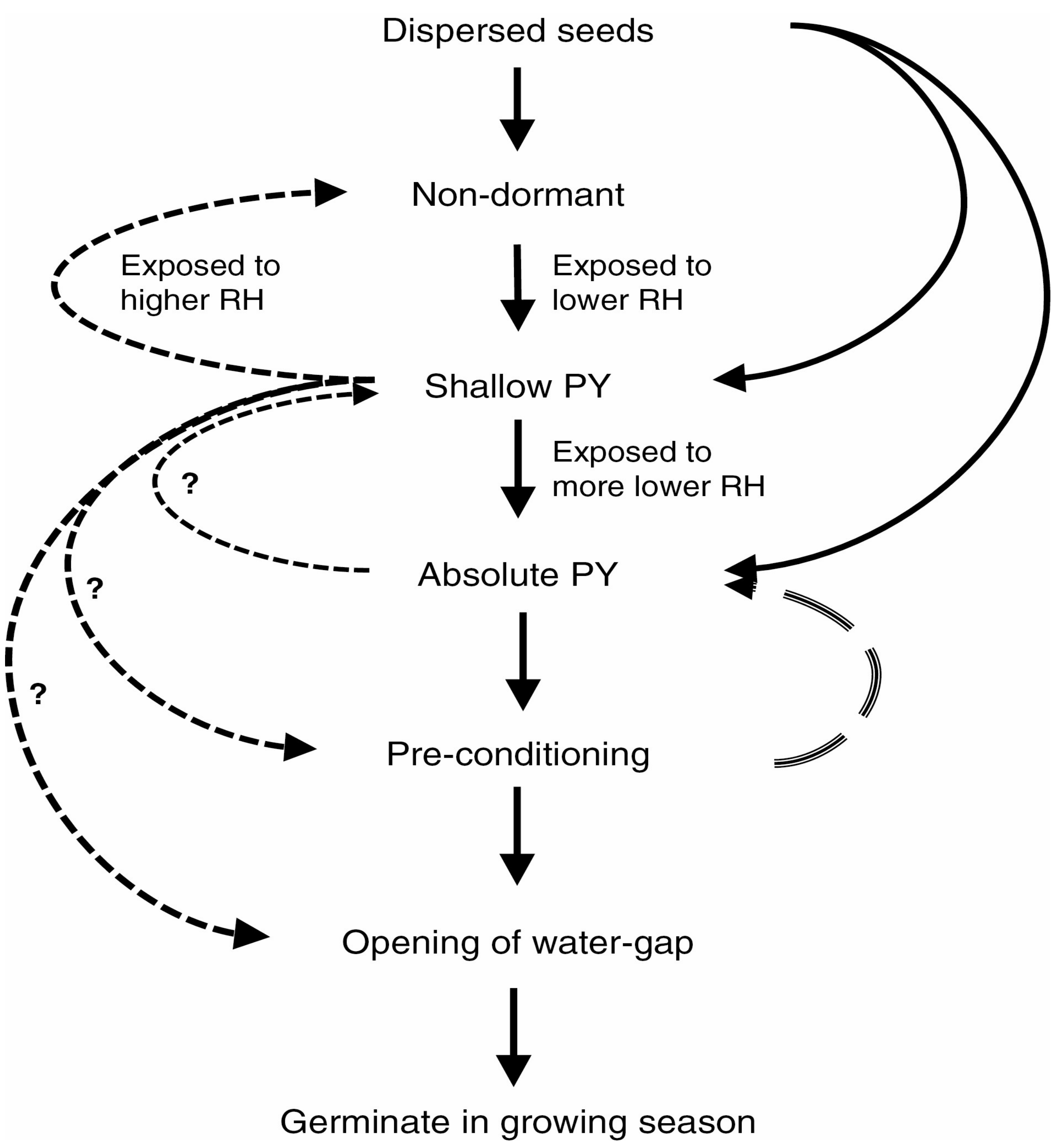
More studies on Africa, South America, and Asia are required to document the presence of physical dormancy. However, Global Biodiversity Information Facility (GBIF) is highly biased.

Conundrum 4

Dormancy-cycling/sub-division

Subdivision of physical dormancy





Conceptual model showing PY seeds dispersed at different levels due to the variation in maternal environment drying seeds to different moisture content. Disentangling dormancy-cycling and sensitivity-cycling.

From Jaganathan (2022) Ann Bot.

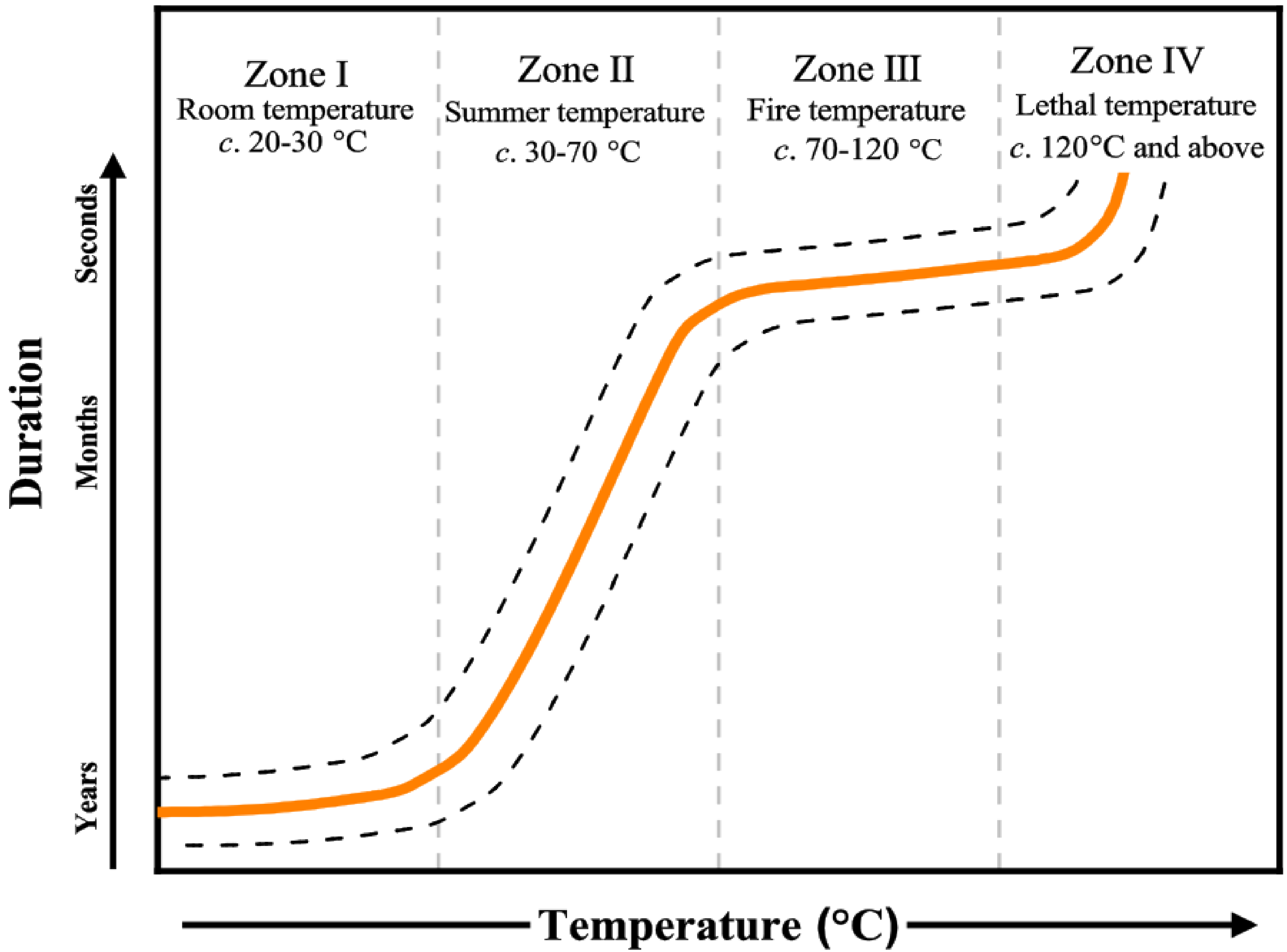
Resolving Conundrum 4

Dormancy-cycling, which is the change in permeable to impermeable state (and impermeable to permeable state), **is different from sensitivity-cycling**, where in impermeable nature of the coat is maintained but the seeds cycle between a dormancy-breaking state and an insensitive state.

This certainly needs more detailed studies.

Towards clarity

Dormancy breaking and moisture content



Conceptual model showing the relationship between duration required for physical dormancy break at different temperatures. The dashed lines signify considerable variation between and within species resulting from moisture content differences.

Moisture content plausibly (definitely) interacts with temperature explaining why some seeds come out of dormancy

Plant Ecol
DOI 10.1007/s11258-015-0560-y

CrossMark

Influence of maternal environment in developing different levels of physical dormancy and its ecological significance

Ganesh K. Jaganathan

Journal of Ecology

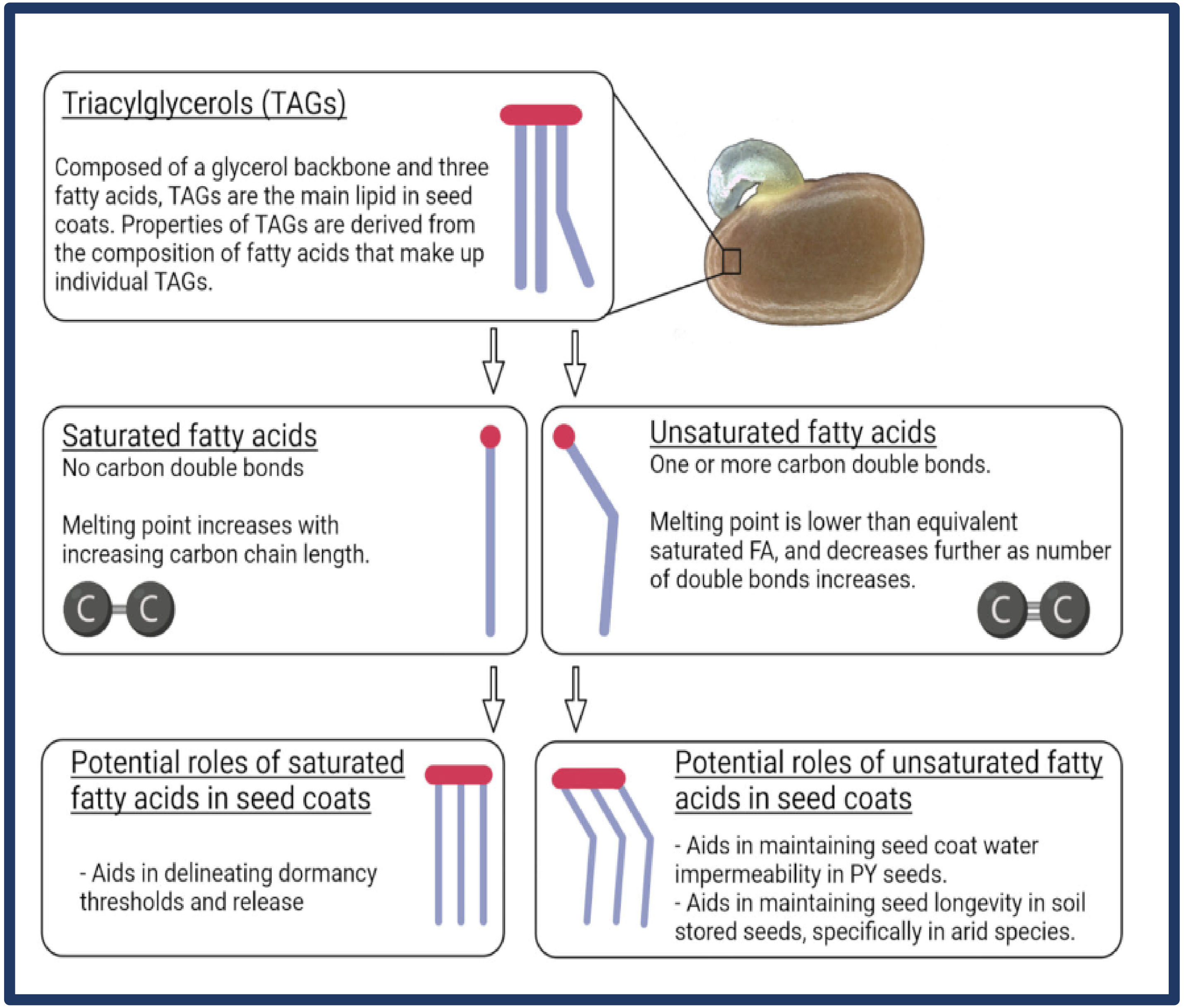
BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE | Free Access

Seed moisture content as a primary trait regulating the lethal temperature thresholds of seeds

Ryan Tangney, David J. Merritt, Joseph B. Fontaine, Ben P. Miller

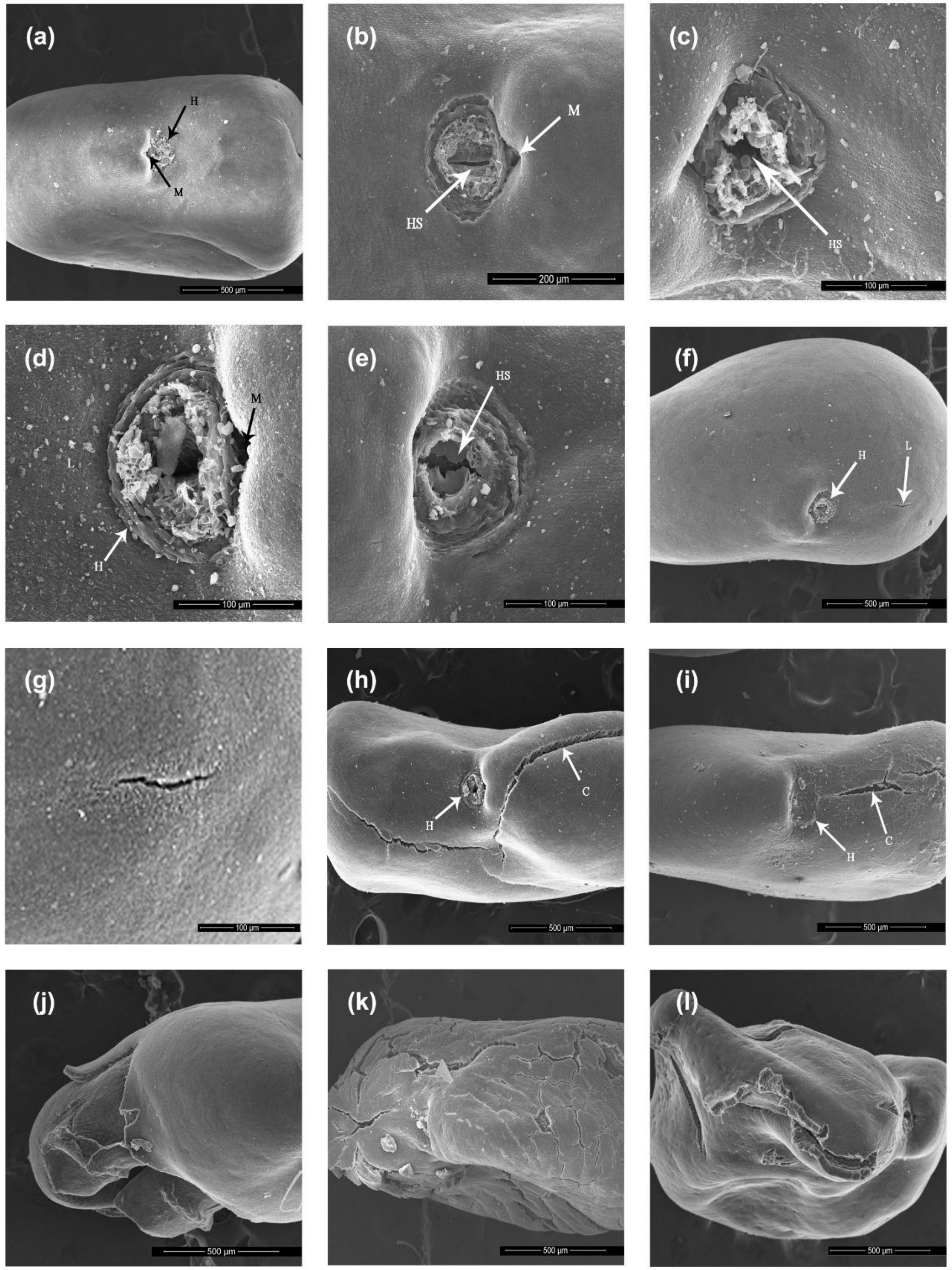
Seeds with elevated moisture contents have lower lethal temperature thresholds, leading to increased seed mortality during fire events when seeds (and soils) are moist. Thermal tolerance varied among coexisting species within this fire-prone system.



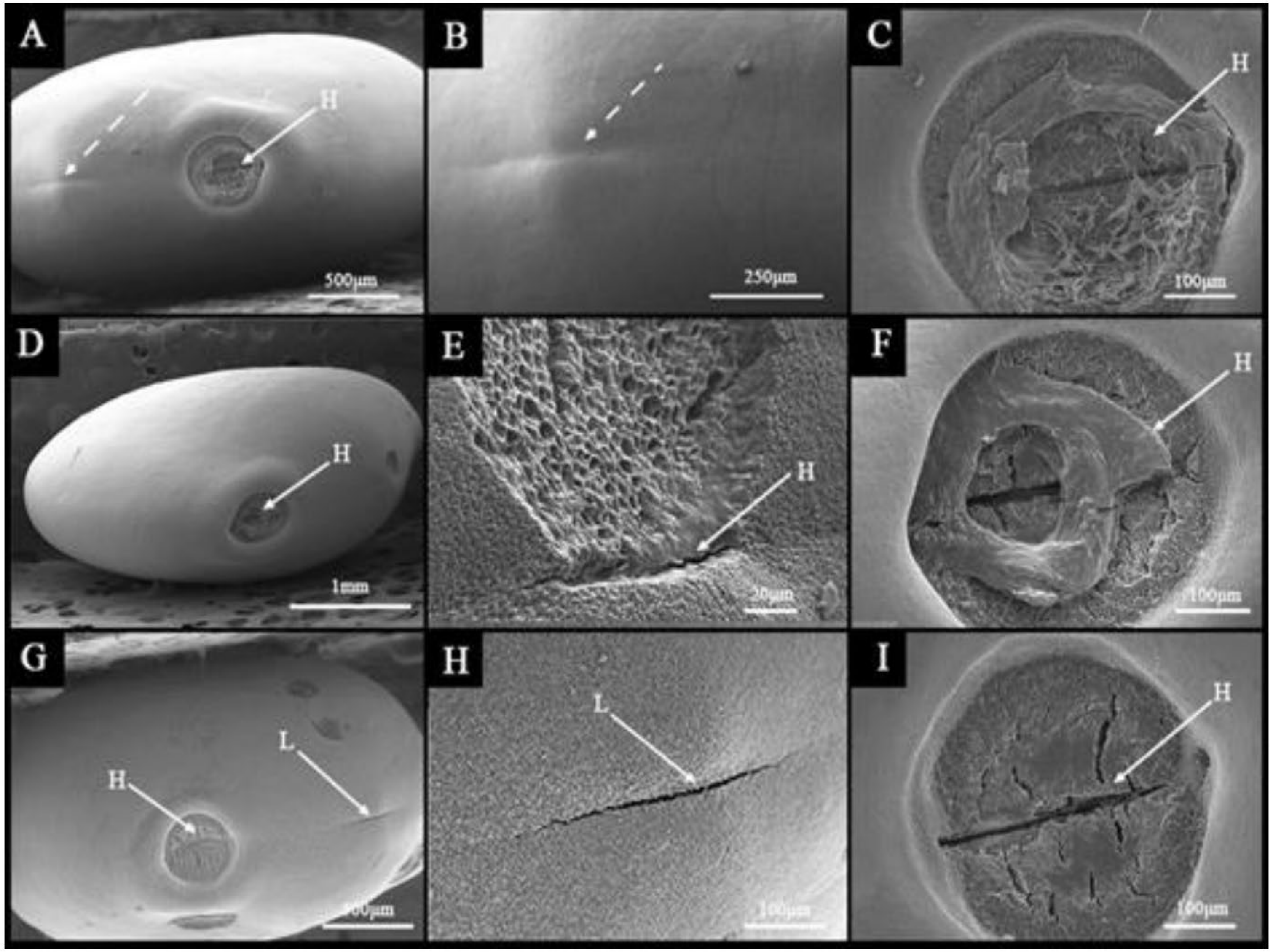
From McInnes et al. 2023, Plant Biology

The hydrolysis of lipids to fatty acids in the seed coat requires free water.

Jaganathan and Harrision, unpubl.



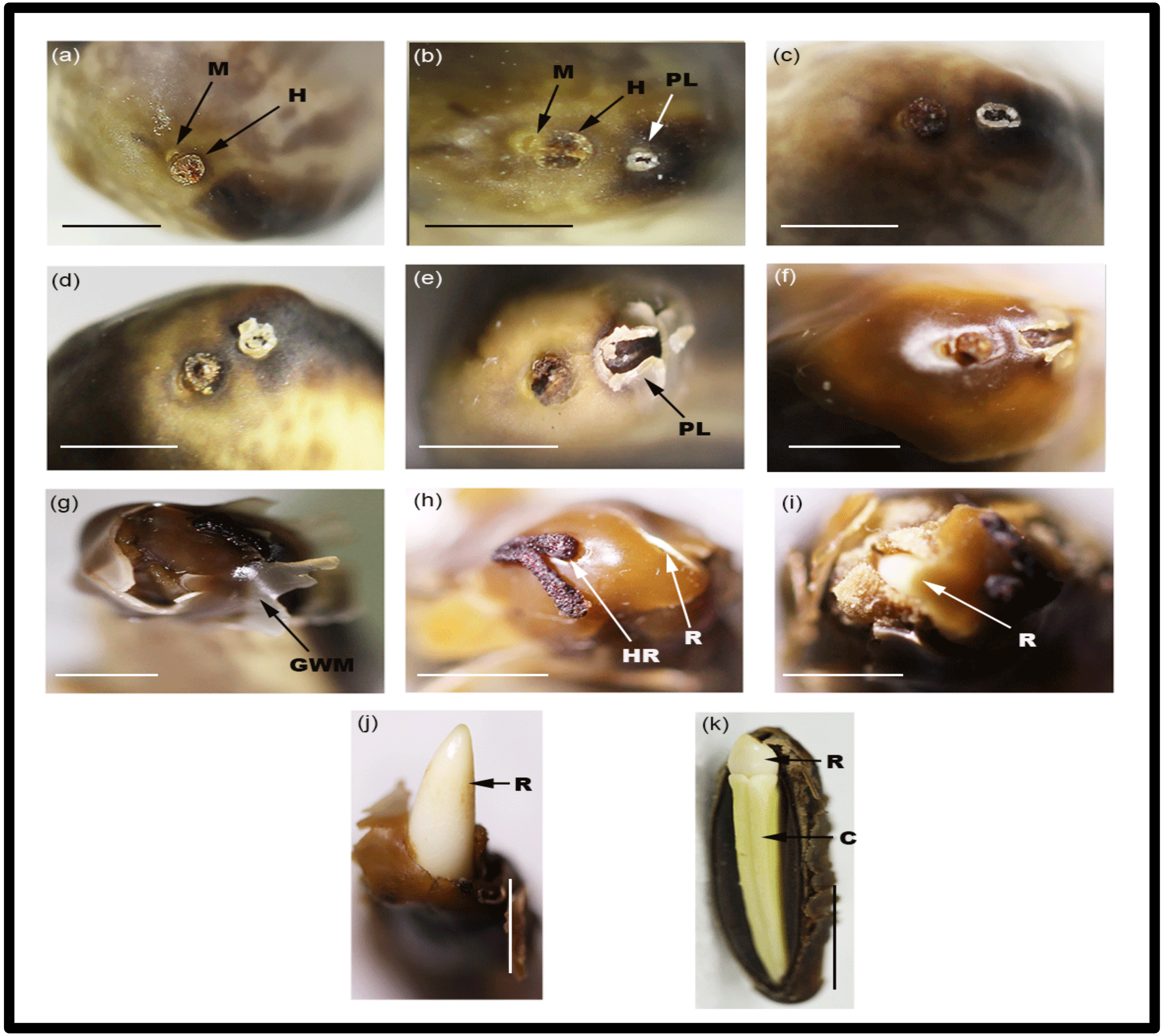
- Water-gap opens only during seasonal temperature fluctuation and fire
- Dry and wet heat opens water-gap similar to fire.
- Other natural and empirical factors such as acid treatment or liquid nitrogen mostly result in seed coat cracks.
- Whether the water-gap can open at room temperature storage is unknown.
- Why some species have two water-gaps (water-gap complex) and others have only one remains a mystery. It may vary between treatment.



Scanning electron micrograph of *Glycyrrhiza uralensis* seeds after treating with concentrated sulfuric acid for 30 minutes, control seeds (A); enlarged lens area (B); seed hilum enlarged (C); after 45 minutes of concentrated sulfuric acid treatment, whole seed (D); seed lens area enlarged (E) and seed hilum enlarged (F); After 60 min of conc. Sulfruic acid treatment, the whole seeds (G), crack in lens area (H), enlargement of hilum (I); L, lens; H, hilum

Jaganathan unpubl.

Seed coat morphology of a dormant seed (a); immediately after dipping in hot-water treatment (b); after 12 h (c), 24 h (d), 32 h (e), 48 h (f), 60 h (g), 72 h (i), 80 h (j) into germination; cross section of 80 h germinated seeds (k). C, cotyledons; GWM, glue like white matter; H, hilum; HR, hilar region; M, micropyle; L, lens; R, radicle. Scale – 5 mm.



From Jaganathan et al. (2018) Plant Biol.

Because moisture content is an important component, future studies are expected to study this…

But, how to determine moisture content in physical dormant species

Previously, several studies have used
130 °C for 4 hours
130 °C for 2 hours
105 °C for 6 hours
105 °C for 72 hours
105 °C for 24 hours
130–133 °C for 1 hour
105 °C for 12 hours
103 °C for 17 hours
80 °C for 24 hours

Most PY seeds will open the water-gap or result in seed coat crack within a few minutes after exposed to fire-like temperature

SUMMARY: 1

(1) Climate drying during the middle Eocene or earlier is proposed as the driving force for physical dormancy evolution

(2) Adaptation to fire, endozoochory, and protection during persistence are more likely the by-products.

(3) Maternal environments leading to moisture content determine the state of seeds at dispersal- permeable or impermeable

(4) Seeds with impermeable coats are more common in the dry tropical ecosystem, but wet ecosystems select desiccation-sensitive seeds

SUMMARY: 2

(5) Moisture content variation within a seed lot explains why some seeds break dormancy, but others do not at a given temperature.

(6) Dormancy-cycling and sensitivity-cycling are two different things; yet empirical evidence is still lacking on a wide range of species.

(7) Fatty acid is proposed to be involved in dormancy-breaking, but more studies are required.

Many thanks to...

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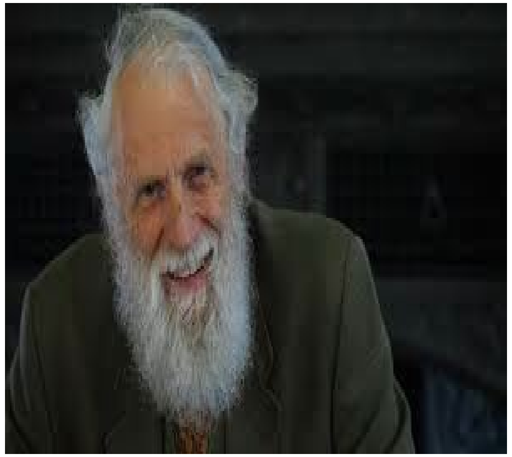
Brilliant students

Collaborators, teachers, seed collectors and professors all over the world

Thank you

Questions?



"In an informal and unpublished presentation to the British Ecological Society in 2004, Peter Grubb expressed some dissatisfaction that progress in ecology was often hampered by our failure to reject wrong ideas and faulty interpretations. I agree with this conclusion and suggest that this problem is, in part, a consequence of specialization and fragmentation of ecological research. In the absence of agreed protocols and overarching theory, Ecology with its numerous subdisciplines, can sometimes resemble an amorphous, postmodern hotel or rabbit warren with separate entrances, corridors and rooms that safely accommodate the irreconcilable."

Grime (2007) J of Ecol.