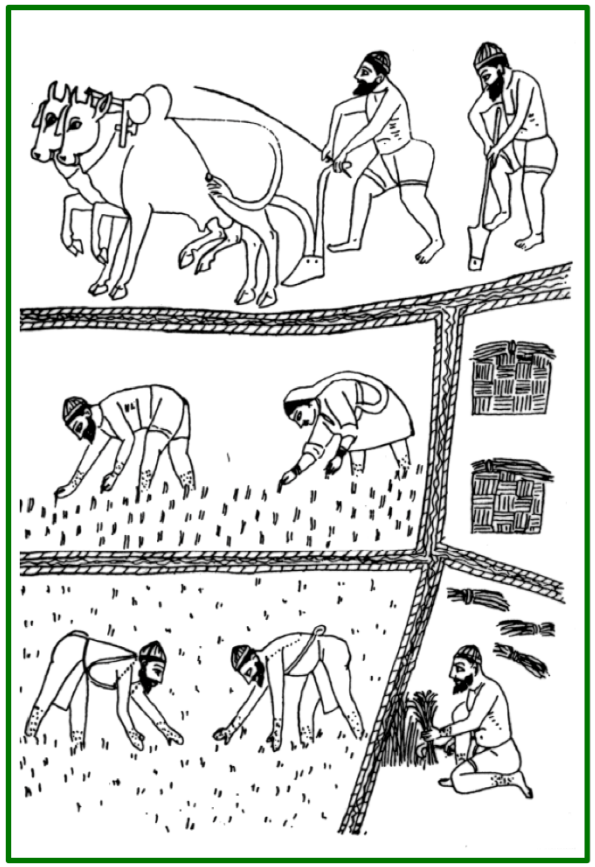
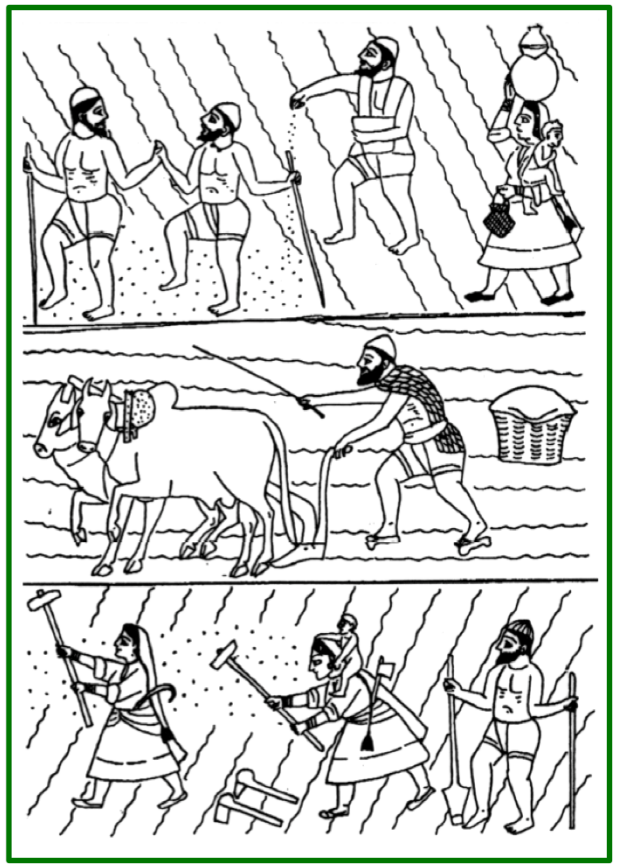
Don’t let seed dormancy be a headache: how to understand, classify and overcome it

Carol C. Baskin, University of Kentucky (USA)

Early interest in seed dormancy and germination





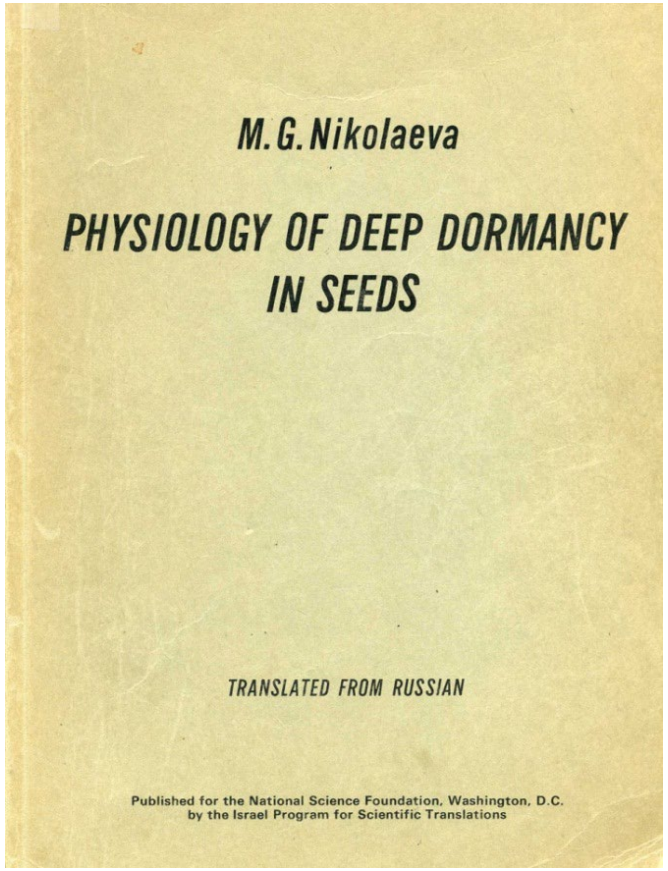
Theophrastus (c.372-287 B.C.)

(The Father of Botany)

Noted that germination can be influenced by climatic factors, inhibitors, seed age and seed coats

CCB – first seed germination study in 1966

Organizing seed dormancy



1967 [1969]

Dr. Marianna G. Nikolaeva
Russian Seed Physiologist/Biologist

A classification scheme for seed dormancy modified from Nikolaeva

A. **Class** - **Physiological dormancy** (PD)
   Levels - deep, intermediate, nondeep
      Types - 1, 2, 3, 4, and 6 (of nondeep PD)

B **Class** - **Morphological dormancy** (MD)

C. **Class** - **Morphophysiological dormancy** (MPD)
   Levels- nondeep simple, intermediate simple, deep simple, nondeep simple epicotyl, deep simple epicotyl, deep simple double, nondeep complex, intermediate complex, and deep complex

D. **Class** - **Physical dormancy** (PY)
   (probably needs to be subdivided)

E. **Class** - **Combinational dormancy** (PY + PD)
   Level - nondeep PD (probably both Type 1 and Type 2 are represented)

Mechanical dormancy is an aspect of PD, *i.e.*, mechanical restraint by (a) covering layer(s) of an embryo with low growth potential**.**

Evidence for **chemical dormancy** is equivocal.

(Baskin and Baskin, 2004)

We want to germinate seeds that we know very little about.

Are they ‘seeds’ or things that look like seeds? Were they fully matured when they were harvested?

Cedar Sedge, *Carex eburnea*

Can you break the dormancy and germinate fresh seeds?

Maybe not if seeds were picked ‘green’

Make sure that seeds going into gene banks can be germinated

Do nonscarified seeds imbibe water?

- Increase in size
- Best to weigh the seeds
- May take several days/weeks for seeds to imbibe fully

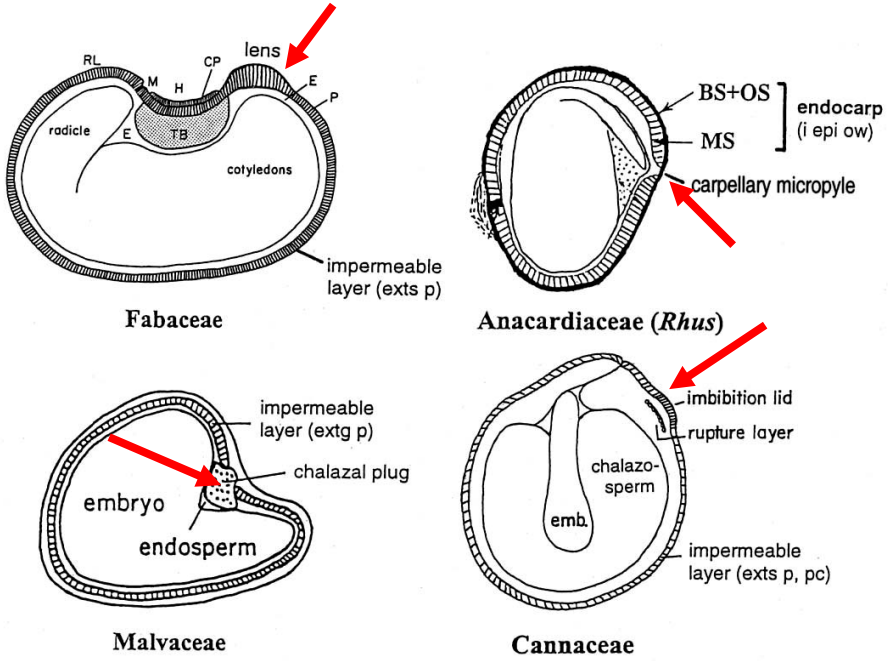
Physical Dormancy (PY)

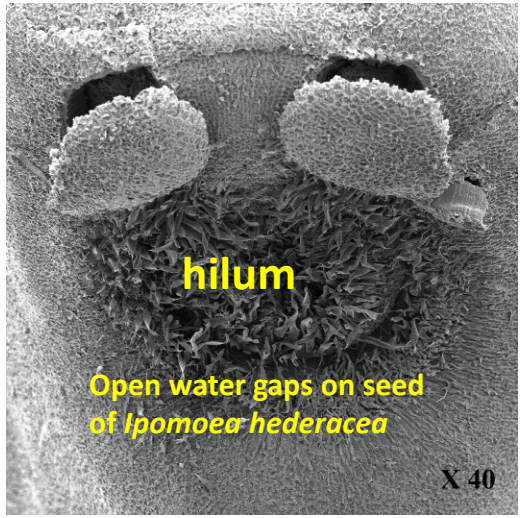
(can not be recalcitrant)

- Water-impermeable seed (or fruit) coat
- Embryo fully developed
- If seed (or fruit) becomes water- permeable,

  germination occurs in less than about 4 weeks, usually within a few days.

Water gap on seed or fruit coat: it serves as environmental signal detector





[from Gehan Jayasuriya's Ph.D. thesis (2008)]

Orders and families of angiosperms with physical dormancy

(Baskin, Baskin, and Li, 2000; Baskin *et al*., 2006)

Order	Family	Dormancy class
Fabales	Fabaceae	PY water-impermeable seed coat
	Surianaceae	PY water-impermeable endocarp
Geraniales	Geraniaceae	PY
Malvales	Bixaceae	PY
	Cistaceae	PY
	Cochlospermaceae	PY
	Dipterocarpaceae[a]	PY
	Malvaceae[b]	PY
	Sarcolaenaceae	PY
	Sphaerosepalaceae	PY
Proteales	Nelumbonaceae	PY
Rosales	Rhamnaceae	PY
Sapindales	Anacardiaceae	PY
	Sapindaceae	PY
Solanales	Convolvulaceae[c]	PY
Zingiberales	Cannaceae	PY

For most of these families, not all members of the family have PY.

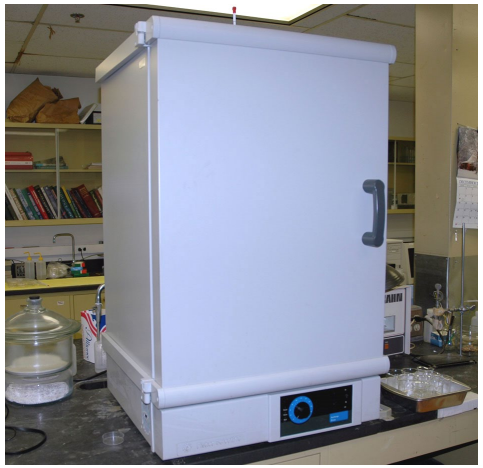
[a]including subfamilies Monotoideae and Pakaraimoideae but not subfamily Dipterocarpoideae
[b]including Bombacaceae, Sterculiaceae, and Tiliaceae; [c]including Cuscutaceae

Breaking physical dormancy in the laboratory

(mechanical scarification)

(acid scarification)

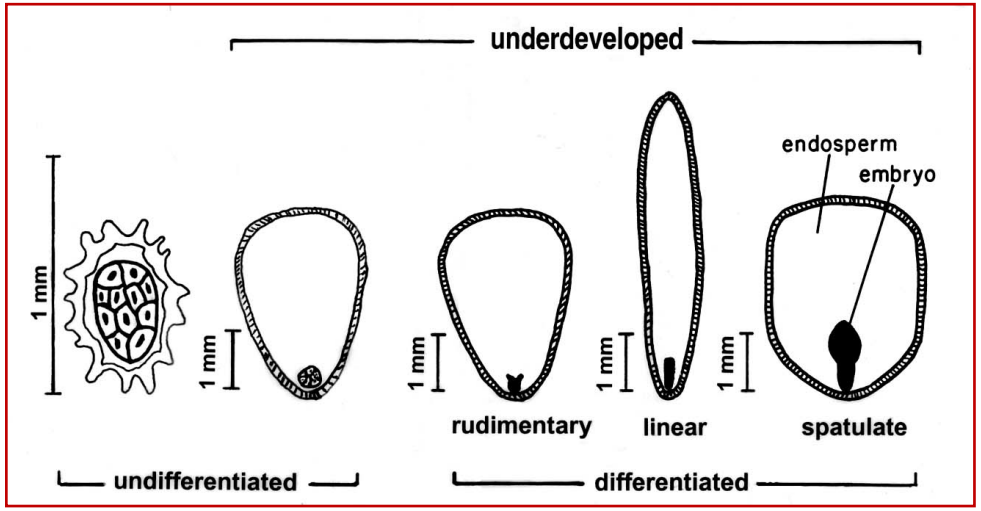
(wet heat)



(dry heat)

Do seeds have a small embryo?

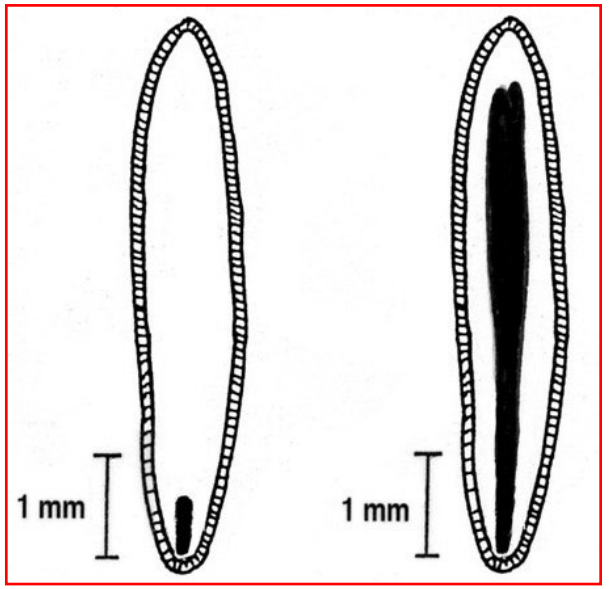
- Seeds imbibe water.
- Seeds germinate within about 7-30 days.
- Seeds have an underdeveloped embryo.
- "Dormancy" period is the time required for embryo to grow.



Kinds of small embryos

Morphological Dormancy (MD)

(could be either recalcitrant or orthodox)



Example of embryo growth

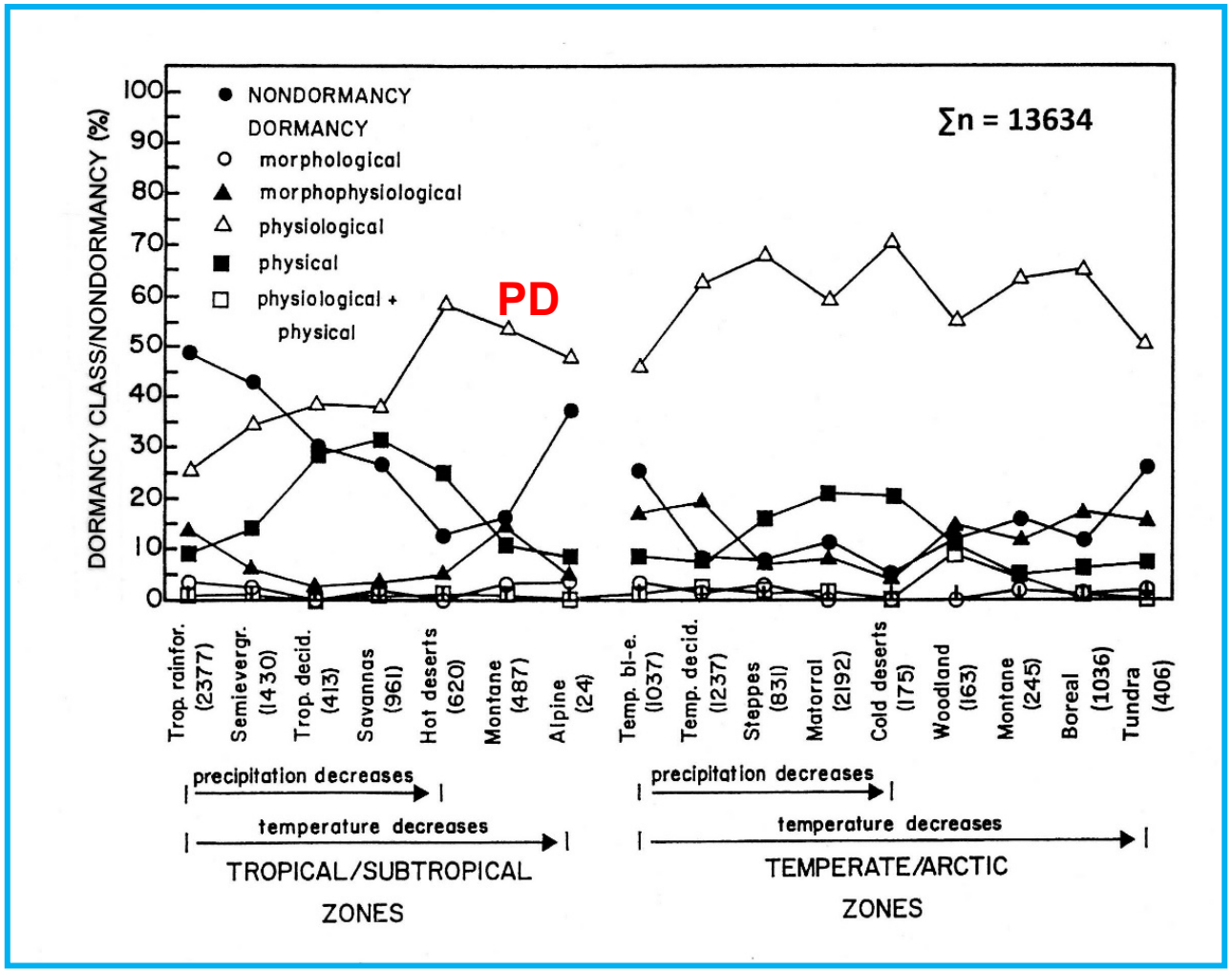
Physiological Dormancy (PD)

(could be either recalcitrant or orthodox)

- **Seeds imbibe water.**
- **Seeds have fully developed embryos.**
- **Germination takes longer than about 30 days.**
- **Physiological inhibiting mechanism in embryo (PIM)**
- **PIM results in low growth potential of embryo.**
- **Sometimes, scarified seeds with PD will germinate because the mechanical restriction has been released.**

- **Moist warm (≥ 15 °C) and/or moist cold (c. 0-10° C) stratification is (are) required to increase growth potential of the embryo.**

World biogeography of nondormancy and the five classes of seed dormancy



(Baskin and Baskin, 2014)

What proportion of the dormant seeds has PD?

Rainforest	49.3%
Semievergreen	60.8
Dry	54.2
Savanna	51.0
Hot desert	66.9
Montane	63.6
Alpine	57.8
Broadleaf	62.1
Deciduous	66.3
Steppes	73.2
Matorral	65.6
Cold desert	74.9
Woodland	61.8
Montane	74.4
Boreal	69.1
Tundra	66.8

Physiological dormancy in angiosperms

435 families of angiosperms

61.4% have PD

20.5% MD/MPD

4.1% PY

2.3% Nondormant (ND)

10.8% no information [47 families – no data]

PD + ND in 151 of 435 families (34.7%)

Why is there so much PD?

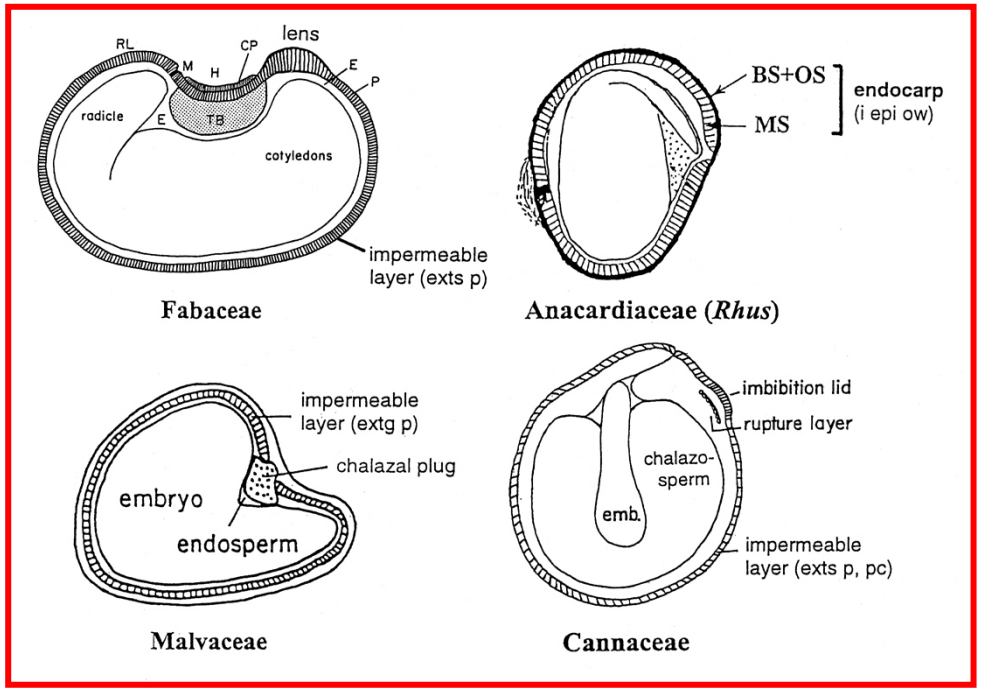
Fine-tuning of the species to its environment

- Three different levels of PD: nondeep, intermediate and deep
- Six types of nondeep PD
- Dormancy-breaking: warm and/or cold stratification
- Afterripening (breaking of PD) in dry storage
- AFTER PD IS BROKEN:
  - Temperatures and light/dark requirements for germination
  - Chemical stimulation of germination: smoke, ethylene, chemicals from host plant

Combinational Dormancy (PY+PD)

(cannot be recalcitrant)

- Seeds (or fruits) do not imbibe water.
- Embryo is fully developed.
- Embryo has some degree of nondeep physiological dormancy.
- Seeds have both physical and physiological dormancy.



+ PD = **(PY+PD)**

Combination of PY +PD

- Seed (or fruit) coat is water impermeable
- Embryo has physiological dormancy
- Two kinds in KY:

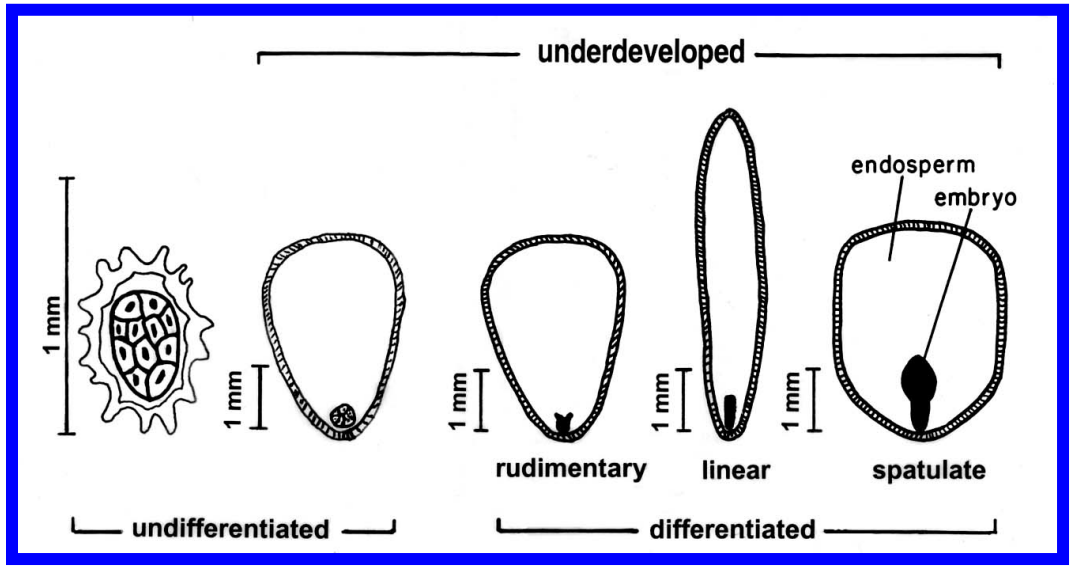
1 PY broken in summer --- PD broken in winter
germinates in spring [redbud]

2 PD broken in summer --- PY broken in autumn
germinates in autumn [wild geranium]

Morphophysiological Dormancy (MPD)

(could be either recalcitrant or orthodox)

- Seeds imbibe water.
- Germination takes longer than about 4 weeks.
- Seeds have underdeveloped embryos.
- Embryos are physiologically dormant.
- There are 9 described levels of MPD.



+ PD = **MPD**

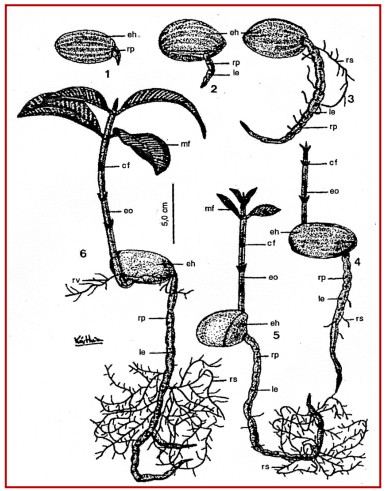
Classification of physiological dormancy

(Baskin and Baskin, 2014)

Class 3. Physiological [C]
- Subclass 1. Regular
  - Level 1. Nondeep (C_1) **Most !!**
    - Type 1. C_{1a} or C_{1b}
    - Type 2. C_{1a} or C_{1b}
    - Type 3. C_{1a} or C_{1b}
    - Type 4. C_{1b}
    - Type 5. C_{1a} or C_{1b}
  - Level 2. Intermediate (C_2)
    - Type 1. (C_{2b}) [not confirmed]
    - Type 2. (C_{2a}) [not confirmed]
  - Level 3. Deep (C_3)
    - Type 1. (C_{3b})
    - Type 2. (C_{3a})

- Subclass 2. Epicotyl
  - Level 1. Nondeep
    - Type 1. C_{1b}(root) - C^{p}_{1a}(shoot)
    - Type 2. C_{nd}(root) - C^{p}_{1b} (shoot)
    - Type 3. C_{nd}(root) - $C^{p'}_{1b}$ (shoot)
    - Type 4. C^{u}_{1b}(root) - C^{u}_{3b} (shoot)
  - Level 2. Deep
    - Type 1. C_{nd} (root) - C_{3a}(shoot)
    - Type 2. C_{nd} (root) - C^{p}_{3b}(shoot)

Epicotyl PD in *Platonia insignis* (Clusiaceae)



(Mourão and Beltrati, 1995)

Nondeep physiological dormancy

- Excised embryo may grow normally.
- Scarification may promote germination.
- GA_3 may promote germination.
- Dormancy-break and germination could require very different conditions, especially temperature.

- Important question: Where does the species grow?

Breaking nondeep physiological dormancy: temperate regions

Dormancy-break		Germination
Hot summer	→	**Cool autumn**
dry or wet/dry		**moist**

Temperate region (Kentucky): Winter annuals a few monocarpic and polycarpic perennials

Mediterranean regions: Winter annuals and many monocarpic and polycarpic perennials perennials

Breaking nondeep physiological dormancy: temperate regions

Dormancy-break		Germination
Cold winter moist	→	**Cool/warm spring moist**

Summer annuals and many monocarpic and polycarpic perennials

Breaking nondeep physiological dormancy: subtropical/tropical regions

- **Hot/warm and wet all year**

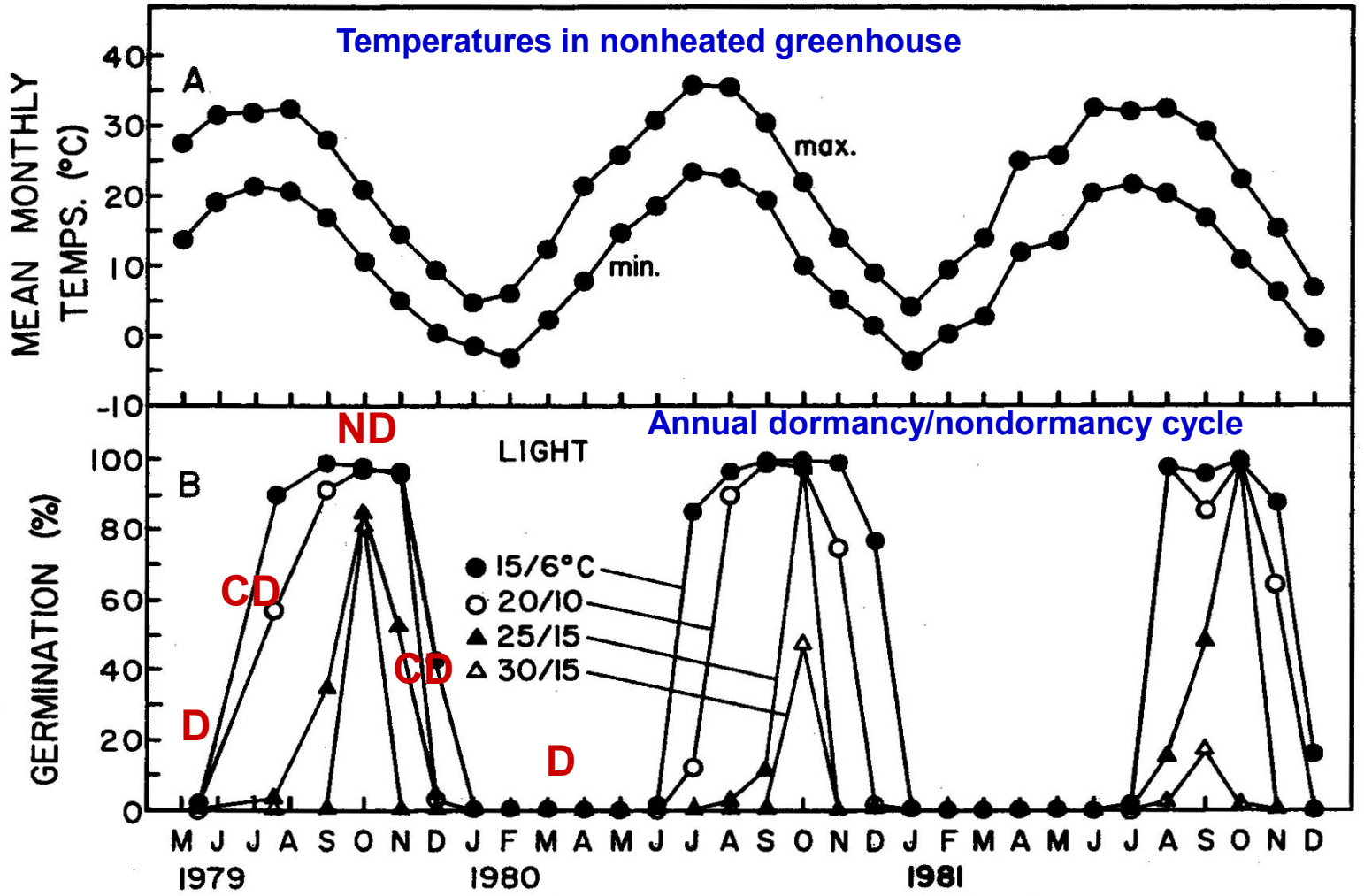
  Nondormant seeds?

  Slow breaking of dormancy → immediate germination

- **Hot/warm all year, with dry and wet seasons**

  dormancy-break in hot dry season → germination in wet season

Germination of *Arabidopsis thaliana* seeds after various periods of burial in soil



No germination in darkness

(Baskin and Baskin, 1983)

Three levels of physiological dormancy (PD)

Nondeep

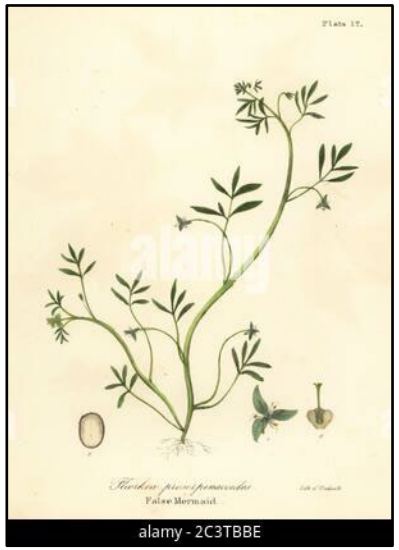
Intermediate – seeds require cold stratification

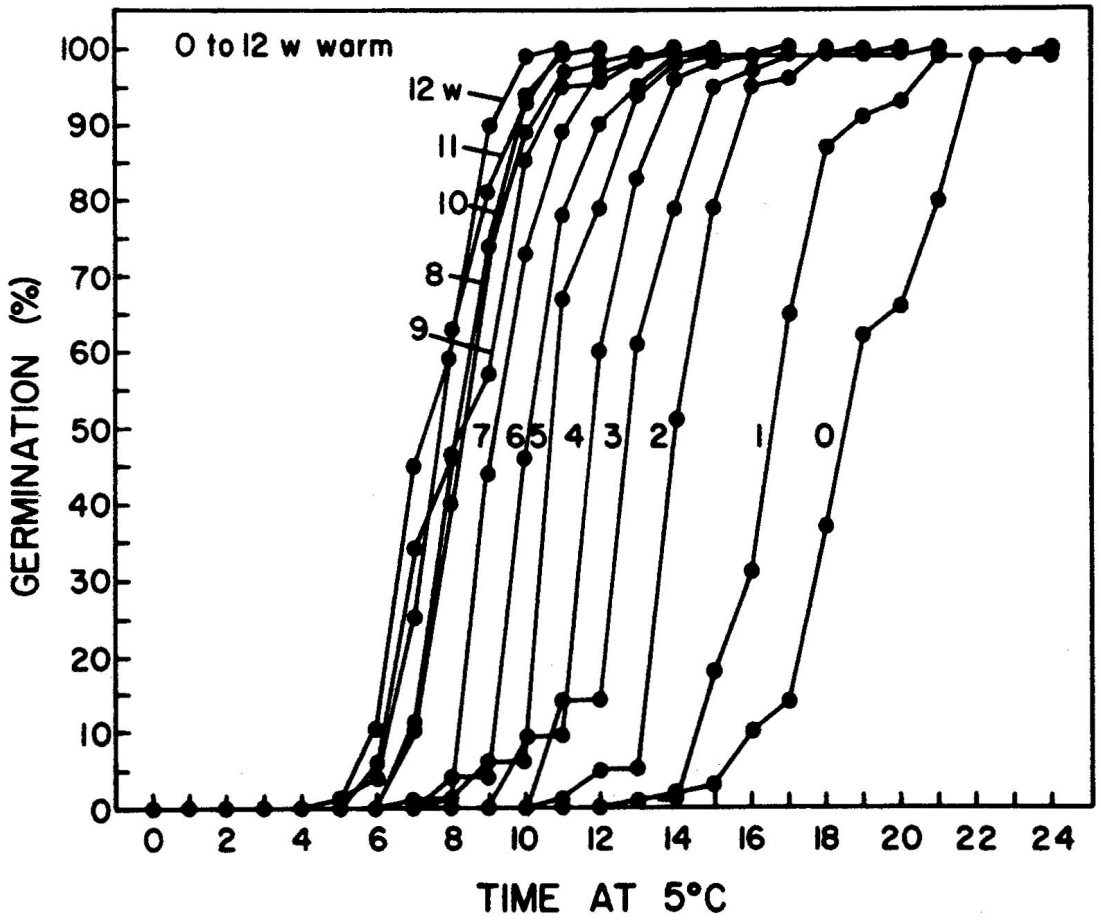
Deep

Intermediate PD

- Excised embryos will grow normally
- GA_3 may (or may not) promote germination
- Dormancy-break in lab is slow; long periods of cold stratification are required
- Dormancy-break and germination at same (low) temperatures (e.g. 5°C)
- Warm stratification (or dry storage) may decrease the length of the cold stratification period required to break dormancy

Germination of *Floerkea proserpinacoides* Limnanthaceae) seeds at 5°C after 0-12 weeks of warm stratification at 30/15°C





Warm stratification prior to cold stratification decreases the amount of cold stratification required to break dormancy.

Temperature requirements for dormancy-break and germination are the same

(Baskin *et al.*, 1988)

Intermediate PD

[80 species, 20 studied in detail]

Amaranthaceae, Berberidaceae, Betulaceae, Brassicaceae, Cucurbitaceae, Cupressaceae, Ericaceae, Fagaceae, Lamiaceae, Limnanthaceae, Oleaceae, Rosaceae and Sapindaceae

Does intermediate PD occur in subtropical and tropical regions??

[Would a brief period of low temperatures (in the subtropics) greatly reduce the length of the warm stratification period needed to break dormancy?]

Three levels of physiological dormancy (PD)

Nondeep

Intermediate

Deep

seeds require a long period (3-6 mo) of cold stratification

However

seeds require a long period of (4-16 mo) warm stratification

discovered in an ericaceous shrub in Hawaii

Deep PD

- Excised embryos either do not grow, or the plant is deformed (nanism).
- GA3 does not work.
- Dormancy-break and germination occur at same temperature regime.

- About 20 temperate species in the Balsaminaceae, Celastraceae, Rosaceae and Sapindaceae (require cold stratification)

- It took 3 to 8 months before seeds of species of Burseraceae, Clusiaceae, Combretaceae, Euphorbiaceae, Fagaceae, Flacourtiaceae, Hernandiaceae, Lecythidaceae, Meliaceae, Menispermaceae, Myrtaceae, Rhizophoraceae, Rutaceae, Symplocaceae and Verbenaceae began to germinate in phenology studies of tropical trees in Malaysia (Ng,1991, 1992),

Design for move-along experiment

(Baskin and Baskin, 2004)

Temperature Regime (°C)		Time at Each Temperature in Series (weeks)	Controls[a]			
summer Series A	winter Series B		5	15/6[b]	20/10	30/15
30/15	5	12	Winter	e. spring or l. aut.	late spr. or e. autumn	summer
↓	↓		↓	↓	↓	↓
20/10	15/6[b]	4				
↓	↓		↓	↓	↓	↓
15/6[b]	20/10	4				
↓	↓		↓	↓	↓	↓
5	30/15	12				
↓	↓		↓	↓	↓	↓
15/6[b]	20/10	4				
↓	↓		↓	↓	↓	↓
20/10	15/6[b]	4				
↓	↓		↓	↓	↓	↓
30/15	5	12				
↓	↓		↓	↓	↓	↓
20/10	15/6[b]	4				
↓	↓		↓	↓	↓	↓
15/6[b]	20/10	4				
↓	↓		↓	↓	↓	↓
5	30/15	12				

[a]Controls are seeds that remain on a wet substrate at 5°C, 15/6°C, 20/10°C, and 30/15°C for the duration of the experiment.

[b]If number of seeds is limited, 15/6°C can be omitted and time at 20/10°C increased to 6 weeks.

Cumulative time (wk) at each control	Control temperature regimes: Early spring[a]	Late spring[b]	Summer	Winter	Time (wk) at each phase of "move along"	"Move along": Start summer	Start winter
12	(0)	(0)	(0)	(0)	12	(0)	(0)
						↓	↓
						early autumn	early spring
16	(0)	(0)	(0)	(0)	4	(0)	(0)
						↓	↓
						late autumn	late spring
20	(0)	(0)	(0)	(0)	4	(0)	(0)
						↓	↓
						winter	summer
32	(1±1)	(0)	(0)	(0)	12	(93±2)	(0)
						↓	↓
						early spring	early autumn
34	(7±1)	(0)	(0)	(0)	4	(93±2)	(0)
						↓	↓
						late spring	late autumn
38	(19±3)	(0)	(0)	(1±1)	4	(93±2)	(0)
						↓	↓
						summer	winter
52	(33 ±3)	(1±1)	(0)	(1±1)	12	(93±2)	(83±4)

[a]Same as late autumn

[b]Same as early autumn

Move-along experiment

to determine if the water-permeable seeds require warm and/or cold stratification for dormancy-break and germination

Germination percentages are in parentheses

Erythronium americanum

nondeep complex MPD

(Baskin and Baskin 2005)

A special concern: effects of long-term drying on seed dormancy and germination

- **Fresh seeds of *Arthropodium cirratum* (Asparagaceae) did not germinate, but after 6 mo of dry storage they germinated to about 95%.**
- **After 9 mo of dry storage only about 55% of the seeds germinated; 95% of them were viable (Conner and Conner, 1988).**

- **“Low germination after seed banking due to reinforced seed dormancy rather than seed mortality” (Logeswaran and Ensslin in the S*amara*, December 2022)**

Questions:

Questions

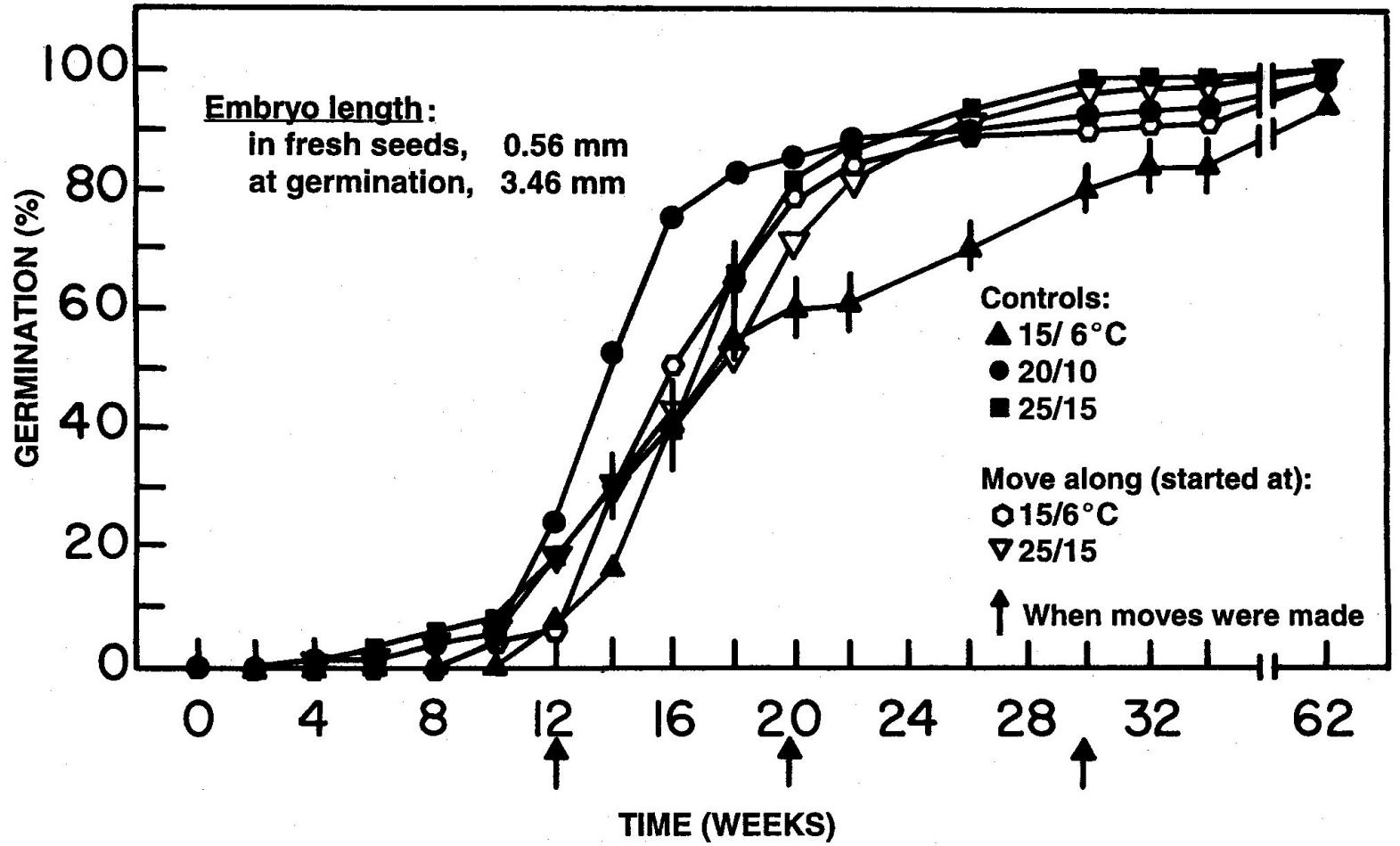
- **Is this a deeper level of PD?**
- **How can this dormancy be broken?**
- **Are we seeing dormancy cycling?**

- **Cycling at constant conditions**
  (p. 87 in Baskin & Baskin 2014 “Seeds”)

Finally, if seeds are viable don't throw them away! Keep moving them to new conditions or simply wait

- Think about what might happen to the seeds in the field (i.e. 'think like a seed')
- New temperature regimes
- Wetting and drying
- Keep waiting/watching

Germination of *Cheirodendron trigynum* seeds



Nondeep simple MPD

Seeds require many weeks of warm moist conditions before the embryo grows and the radicle emerges.

(Baskin et al., 2015)

Thank you

Tropical montane forest, Kauai, Hawaii, USA

Carol.baskin@uky.edu