Photoinhibition of seed germination: occurrence, ecology and phylogeny

Article *in* Seed Science Research · May 2017

DOI: 10.1017/S0960258517000137

Seed Science Research (2017) **27**, 131–153 doi:10.1017/S0960258517000137

REVIEW PAPER

Photoinhibition of seed germination: occurrence, ecology and phylogeny

Angelino Carta[1]*, Evangelia Skourti[2], Efisio Mattana[3], Filip Vandelook[4] and Costas A. Thanos[2]

[1]Department of Biology, University of Pisa, Italy; [2]Department of Botany, National and Kapodistrian University of Athens, Greece; [3]Natural Capital and Plant Health Department, Royal Botanic Gardens, Kew, UK; [4]Botanic Garden Meise, Belgium

Abstract

Light conditions provide important information about the best time and place for seedling establishment. Photoinhibition of seed germination (PISG), defined as the partial or complete suppression of germination under white light, has been interpreted as a physiological adaptation to avoid germination at or near the soil surface. This review is the first report of an all-inclusive, fully quantitative analysis of PISG in seed plants. Pertinent data available from the published literature for 301 taxa from 59 families and 27 orders were assessed. The association of PISG with several plant and seed traits allowed us to consider the adaptive significance of PISG in relation to plant life histories and the natural environments. As no gymnosperm has been found to be truly photoinhibited, it seems that PISG is apomorphic to flowering plants (especially monocots). Seeds of most taxa with PISG have a dark colour and intermediate mass, mostly in the range 1 to 27 mg. PISG is absent from humid tropical regions and from cold climates, but it is strongly associated with open, disturbed and dry habitats. An intriguing implication of PISG is the formation of a soil-surface seed bank. Taken together, these results clearly indicate that PISG is a physiological adaptation to avoid germination on the soil surface, where conditions are not suitable for seedling establishment. PISG is probably much more frequent in seed plants than previously thought. Thus, laboratory experiments should be conducted under well-characterized light and dark conditions.

Keywords: adaptation, climate, habitat, life history, light, photoinhibition, phylogeny, seed traits

* Correspondence
Email: acarta@biologia.unipi.it

Introduction

Plant species exhibit different sensitivities to light environments for seed germination. Seeds of many species are indifferent to light conditions, whereas others can germinate only in light, only in the darkness or to higher percentages in light than in darkness and vice versa (Baskin and Baskin, 2014). Light conditions provide important information about the optimal time and place for seedling establishment. The chances of successful establishment may be determined by whether the germinating seed is buried in the soil or is on the soil surface. If seeds are buried, the precise depth is crucial for seedling emergence (Bond *et al*., 1999). Seed mass may represent a constraint for seedling emergence of small-seeded species. Small seeds are therefore more likely to require light for germination, which ensures that germination does not occur too deep in the soil for seedling emergence (Pons, 2000). Thus light response and seed mass could have co-evolved (Milberg *et al*., 2000). However, solar irradiance penetrates to only 4–5 mm into the soil in physiologically significant quantities (Tester and Morris, 1987).

Photoinhibition of seed germination (PISG) refers to the suppression or retardation of germination under white (day) light conditions, with a high photon flux density (PFD) and it is considered to be a high irradiance response (HIR) *sensu* Górski and Górska (1979). The inhibitory effect of a high PFD on seed germination has been demonstrated in a number of species, even those that are otherwise positively photoblastic (Pons, 2000). Indeed, the inhibitory effect on seed germination in light-requiring species may be particularly effective under extremely high levels of natural lighting (Corbineau and Côme, 1982). In this context, PISG has been traditionally interpreted as a physiological adaptation to avoid germination at or near the soil surface, which protects seedlings from dehydration and exposure to extremely high temperatures (Koller *et al*., 1964; Thanos *et al*., 1991). An interesting implication of this adaptation is the formation of a third seed bank type apart from the well-established canopy and soil seed banks: the soil-surface seed bank (Thanos *et al.*, 2005). As a result, non-dormant seeds of photoinhibited species may persist at the soil surface and eventually germinate only when incorporated in the soil (Fenner and Thompson, 2005). Not only light quantity but also light quality may influence the seeds' responses to light. Irradiance is attenuated by the plant canopy and/or by the leaf litter, leading to light enriched in far red (FR; Vazquez-Yanes *et al.*, 1990). Hence, from an ecological point of view PISG under white light or natural daylight conditions occurs only in seeds exposed to direct, rather than transmitted, daylight (Pons, 2000).

PISG has been known for over a century (Heinricher, 1903; Remer, 1904). Kinzel (1913–1926) found that out of the 964 species he studied, light favoured seed germination in 672 species and inhibited germination in 258. However, despite the importance from evolutionary, ecological and agricultural perspectives, inhibition of seed germination under artificial white light or natural, non-shaded daylight has received little attention. This shortage of studies is in sharp contrast to the extensive literature concerning the other two major light germination responses, namely promotion by light in the laboratory or in the field (e.g. on the soil surface; Milberg *et al.*, 2000) and inhibition by plant canopy-filtered light (Pons, 2000 and literature cited therein). Therefore, in this review the occurrence of PISG at seed, species and environmental levels has been explored and analysed from a physiological, ecological and evolutionary perspective.

Materials and methods

Data source

A dataset was compiled based on information in the Baskin and Baskin (2014) book and on information from a literature search that was electronically conducted within the ISI Web of Science and Google Scholar databases, using the following keywords: 'dark germination', 'seed germination photoinhibition', 'seed germination light inhibition', 'soil emergence'. Studies were included in the analysis only when it was clear that a source of (white) light was used and if the germination percentage or rate in darkness was statistically significantly higher than that in light. Only data for optimal or near-optimal conditions for germination were used. A 30% final germination limit under dark conditions was applied to retain only records with a reasonably good germination response and are listed in Table 1. The discarded records are listed in supplementary Table S1.

For each taxon, final germination percentage and, when available, rate in light and in darkness were recorded, as well as optimal temperature for germination, dormancy type, seed mass, life form, phylogeny, plant height, habitat type, climate and biogeographic range, all of which are known to more or less influence responses of seeds to light. Moreover, as the photoreceptors (phytochromes) are located in the embryo, the optical properties of the seed-covering structures were taken into account. Thus, in this review, seed colour was also recorded and included in the analysis. Most of this information was gathered from the original publications, but when not available it was retrieved from the literature (e.g. Tutin *et al.*, 1964–1980; Western Australian Herbarium, 1998; Flora of China Editorial Committee, 1994+; Flora of North America Editorial Committee, 1993+).

Taxonomic information was standardized against The Plant List (2013), and phylogenetic classification followed Angiosperm Phylogeny Group (APG) IV (Stevens, 2001; APG, 2016). Biogeographical range followed the Floristic Regions of Takhtajan (1986), and climate was defined according to the terrestrial ecoregions of the world (Olson *et al.*, 2001). Plant species richness per ecoregion was derived from the estimates made by Kier *et al.* (2005). The Seed Information Database (Royal Botanic Gardens Kew, 2016) was queried for information on a specific seed trait, when this was not available in the original publication, and for the seed mass for the world flora.

Data analysis

The PISG index (P_i) was defined as:

$$P_i = (GD - GL)/GD,$$

where GD is final germination percentage in darkness and GL is final germination percentage in light. Thus, P_i can have values between 0 and 1, with 0 corresponding to equal germination percentages in light and darkness, and 1 to germination occurring only in the dark.

For analytical purposes, we classified the species into three levels of habitat moisture (dry = 1, moist = 2, wet = 3) and light (shaded = 1, semi-shaded = 2, open = 3) conditions. Then, we fitted generalized linear models (GLMs, logit link function, binomial distribution) to analyse the effect of seed germination conditions (mean temperature and temperature regimes), environmental traits (habitat moisture and light) and plant traits (height and seed mass) on P_i. The analyses were also run for the subgroup of taxa with final germination ≥ 70%, but since the results were similar only those from the entire dataset (final germination ≥ 30%) are presented here.

The frequency distribution of seed mass in our dataset was compared with that of the world flora by means of a Kolmogorov–Smirnov two sample test.

Table 1. Photoinhibited taxa, seed properties, plant traits and PISG index (P_i).

No.	Order	Family	Taxon	Bio-geography	Climate	Habitat type	Life form	Plant height (cm)	Seed mass (mg)	Seed colour	Dormancy	P_i	Group	Reference(s)
1	**Alismatales**	Araceae	*Arum maculatum* L.	Cb	H	W	G	30	120.00	L	PD	**0.21**	Pw	130
2			*Arum purpureospathum* P.C. Boyce	Me	S	M	G	45	44.19	L	PD	**1.00**	Ps	56
3	**Apiales**	Apiaceae	*Bupleurum gaudianum* Snogerup	Me	S	M	T	7	0.10	D	MPD	**0.20**	Pw	56
4			*Bupleurum ranunculoides* L.	EA	H	H	H	50	1.80	D	MPD	0.22	Pw	151
5			*Bupleurum rotundifolium* L.	Cb	H	R	T	40	2.68	D	MPD	**0.38**	Pw	11
6			*Echinophora spinosa* L.	Me	S	M	H	50	24.00	L	ND	**0.44**	R	44
7			*Eryngium creticum* Lam.	SA	D	D	T	60	1.60	L	MPD	**0.31**	Pw	68
8			*Eryngium maritimum* L.	Me	S	M	G	40	26.10	D	PD	**0.17**	R	44
9			*Foeniculum vulgare* Mill.	Me	S	R	H	80	18.53	L	MD	**0.29**	Pw	158
10			*Ligusticum scoticum* L.	Cb	H	M	H	60	3.70	L	MPD	0.17	Pw	124
11	**Arecales**	Arecaceae	*Phoenix theophrasti* Greuter	Me	S	G	P	1500	362.20	D	ND	**0.00**	R	56, 131, 166
12	**Asparagales**	Amaryllidaceae	*Acis autumnalis* (L.) Sweet	Me	S	S	G	15	11.29	D	MPD	**0.06**	R	105
13			*Allium altissimum* Regel	IT	D	G	G	150	6.44	D	PD	**0.05**	R	83
14			*Allium aschersonianum* Barbey	SA	S	D	G	80	3.59	D	PD	**0.15**	Pw	Kd
15			*Allium bourgeaui* subsp. *creticum* Bothmer	Me	S	M	G	115	2.84	D	ND	**0.81**	Ps	35
16			*Allium curtum* Boiss. & Gaill.	SA	S	D	G	45	0.61	D	PD	**0.24**	Pw	Kd
17			*Allium decipiens* Fisch. ex Schult. & Schult. f.	IT	D	G	G	80	2.00	D	PD	0.15	Pw	83
18			*Allium karataviense* Regel	IT	D	D	G	20	6.22	D	PD	0.17	Pw	83
19			*Allium negevense* Kollmann	SA	S	S	G	25	1.93	D	PD	**0.75**	Ps	Kd
20			*Allium polyrhizum* Turcz. ex Regel	IT	D	G	G	30	4.03	D	PD	0.55	Ps	137
21			*Allium rothii* Zucc.	SA	S	D	G	15	3.95	D	PD	**0.55**	Ps	67
22			*Allium sphaerocephalon* L.	Me	S	G	G	75	1.36	D	PD	**0.16**	Pw	Kd
23			*Allium staticiforme* Sm.	Me	S	M	G	35	0.50	D	PD	**0.26**	Pw	164
24			*Allium trachyscordum* Vved.	IT	D	D	G	30	2.82	D	PD	**1.00**	Ps	Kd
25			*Allium truncatum* (Feinbrun) Kollmann & D. Zohary	SA	S	D	G	115	2.51	D	PD	**0.30**	Pw	67
26			*Allium ursinum* L.	Cb	H	G	G	30	5.98	D	PD	**1.00**	Ps	u3
27			*Galanthus nivalis* L.	Cb	H	W	G	15	7.73	L	PD	**0.80**	Ps	52, 120
28			*Leucocoryne purpurea* Gay	CP	S	S	G	30	1.59	D	MPD	**0.30**	Pw	Kd
29			*Narcissus cavanillesii* Barra & G. López	Me	S	S	G	20	1.30	D	MPD	**0.12**	Pw	105
30			*Narcissus confusus* Pugsley	Me	S	S	G	20	1.29	D	MPD	**0.96**	Ps	34
31			*Narcissus hispanicus* Gouan	Me	S	S	G	50	6.14	D	MPD	**0.41**	Pw	75
32			*Narcissus longispathus* Degen & Hervier ex Pugsley	Me	S	S	G	70	7.88	D	MPD	0.72	Ps	74
33			*Narcissus pseudonarcissus* L.	Cb	H	G	G	35	5.06	D	PD	**0.49**	Pw	120
34			*Narcissus radinganorum* Fern. Casas	Me	S	S	G	35	4.76	D	MPD	**0.68**	Ps	76
35			*Narcissus rupicola* Dufour	Me	S	S	G	25	3.47	D	MPD	**0.29**	Pw	Kd
36			*Narcissus serotinus* L.	Me	S	S	G	25	2.60	D	MPD	**0.11**	Pw	105
37			*Nothoscordum bivalve* (L.) Britton	Md	S	G	G	30	2.48	D	MPD	0.70	Ps	12
38			*Pancratium maritimum* L.	Me	S	M	G	40	46.40	D	MD	**0.13**	Pw	4

Continued

Table 1. *Continued*

No.	Order	Family	Taxon	Bio-geography	Climate	Habitat type	Life form	Plant height (cm)	Seed mass (mg)	Seed colour	Dormancy	P_i	Group	Reference(s)
39		Asparagaceae	*Arthropodium cirrhatum* (G.Forst.) R.Br.	Nz	H	W	G	80	2.03	D	MPD	**0.94**	Ps	32
40			*Bellevalia brevipedicellata* Turrrill	Me	S	M	G	18	9.50	D	ND	**0.00**	R	44, 56
41			*Bowiea volubilis* Harv.	SZ	S	S	G	20	3.06	D	MPD	**0.36**	Pw	95
42			*Drimia maritima* (L.) Stearn	Me	S	G	G	110	8.59	D	ND	**0.03**	R	105, u2
43			*Eucomis autumnalis* (Mill.) Chitt.	SZ	S	S	G	50	8.70	D	MPD	**0.60**	Ps	96
44			*Fusifilum capitatum* (Hook.f.) Speta	SZ	S	G	G	80	2.42	D	MPD	**0.46**	Pw	95
45			*Leopoldia weissii* Freyn	Me	S	S	G	30	4.70	D	ND	**0.44**	Pw	47
46			*Maianthemum bifolium* (L.) F.W. Schmidt	Cb	H	W	G	25	11.00	L	MPD	**0.33**	Pw	94
47			*Maianthemum stellatum* (L.) Link	Md	S	W	G	45	16.27	L	MPD	**0.95**	Ps	114
48			*Muscari neglectum* Guss. ex Ten.	Me	S	S	G	30	4.30	D	ND	**0.20**	Pw	47
49			*Polygonatum biflorum* (Walter) Elliott	NAA	H	W	G	150	24.20	L	MPD	0.59	Ps	9, 114
50			*Prospero autumnale* (L.) Speta	Me	S	S	G	30	2.09	D	PD	**0.06**	R	105
51			*Schoenolirion croceum* (Michx.) Alph. Wood	Md	S	G	G	45	10.25	D	PD	**0.33**	Pw	174
52			*Scilla hyacinthoides* L.	SA	S	G	G	60	11.12	D	PD	**0.08**	R	150
53		Asphodelaceae	*Asphodeline lutea* (L.) Rchb.	Me	S	S	G	80	15.80	D	ND	**0.87**	Ps	u2
54			*Asphodelus microcarpus* Salzm. & Viv.	SA	D	S	G	100	3.10	D	ND	**0.04**	R	68
55			*Asphodelus tenuifolius* Cav.	Me	S	S	G	40	1.47	D	MPD	0.71	Ps	Kd
56			*Bulbine abyssinica* A.Rich.	Cp	S	S	G	45	1.77	D	MPD	0.30	Pw	Kd
57			*Bulbinella latifolia* Kunth	Cp	S	S	H	60	4.35	D	MPD	**0.11**	Pw	Kd
58			*Eremurus anisopterus* (Kar. & Kir.) Regel	IT	D	D	G	80	7.21	D	MPD	**1.00**	Ps	104
59			*Xanthorrhoea australis* R.Br.	NEA	H	S	H	180	12.74	D	ND	**0.13**	Pw	Kd
60			*Xanthorrhoea bracteata* R.Br.	NEA	H	S	H	50	6.91	D	ND	**0.16**	Pw	Kd
61			*Xanthorrhoea gracilis* Endl.	SWA	S	S	G	90	12.07	D	ND	**0.56**	Ps	17
62			*Xanthorrhoea johnsonii* A.T.Lee	NEA	H	S	G	190	18.05	D	PD	0.63	Ps	31
63		Iridaceae	*Crocus biflorus* Mill. subsp. *alexandri* (Velen.) B. Mathew	Cb	H	S	G	10	4.10	D	PD	**0.93**	Ps	152
64			*Crocus biflorus* Mill. subsp. *melantherus* B. Mathew	Me	S	S	G	10	3.80	L	PD	0.72	Ps	152
65			*Crocus biflorus* Mill. subsp. *stridii* (Papan. & Zacharof) B. Mathew	Cb	H	S	G	10	2.90	D	PD	0.82	Ps	152
66			*Crocus boryi* J. Gay	Me	S	S	G	15	3.40	D	PD	**1.00**	Ps	152
67			*Crocus cancellatus* Herb. subsp. *mazziaricus* (Herb.) B. Mathew	Me	S	S	G	15	9.90	D	PD	**1.00**	Ps	152
68			*Crocus cartwrightianus* Herb.	Me	S	S	G	7	14.90	D	PD	**0.92**	Ps	152
69			*Crocus chrysanthus* (Herb.) Herb.	Me	S	S	G	7	4.60	L	PD	**1.00**	Ps	152
70			*Crocus fleischeri* J. Gay	Me	S	S	G	5	6.20	D	PD	**1.00**	Ps	152
71			*Crocus goulimyi* Turrill	Me	S	S	G	21	14.00	D	PD	**1.00**	Ps	152
72			*Crocus hadriaticus* Herb.	Me	S	S	G	9	15.00	D	PD	**0.82**	Ps	152
73			*Crocus laevigatus* Bory & Chaub. in Bory	Me	S	S	G	8	3.50	D	PD	**0.32**	Pw	152
74			*Crocus neglectus* Peruzzi & Carta	Me	S	G	G	15	5.60	L	MPD	**0.33**	Pw	25

75			*Crocus nivalis* Bory & Chaub.	Me	S	S	G	7	4.00	L	PD	**0.92**	Ps	152
76			*Crocus niveus* Bowles	Me	S	S	G	18	15.10	D	PD	**0.98**	Ps	152
77			*Crocus olivieri* J. Gay subsp. *balansae* (Baker) B. Mathew	Me	S	S	G	7	6.30	D	PD	1.00	Ps	152
78			*Crocus olivieri* J. Gay subsp. *olivieri*	Me	S	S	G	7	6.00	D	PD	**0.98**	Ps	152
79			*Crocus oreocreticus* B.L. Burtt	Me	S	S	G	5	15.00	D	PD	**0.71**	Ps	152
80			*Crocus orphei* Karamplianis & Constantin	Cb	H	S	G	6	5.30	D	PD	**0.39**	Pw	152
81			*Crocus sieberi* J. Gay	Me	S	S	G	5	3.60	D	PD	**0.96**	Ps	152
82			*Crocus tournefortii* J. Gay	Me	S	S	G	10	3.60	D	PD	**0.94**	Ps	152
83			*Crocus veluchensis* Herb.	Cb	H	H	G	10	3.70	D	PD	**0.59**	Ps	152
84		Orchidaceae	*Anacamptis morio* (L.) R.M.Bateman, Pridgeon & M.W. Chase	Cb	H	G	G	35	0.00	D	MD	1.00	Ps	173
85			*Calypso bulbosa* (L.) Oakes	Cb	H	W	G	20	0.00	L	PD	**0.33**	Pw	3
86			*Cyrtopodium punctatum* (L.) Lindl.	Cr	H	T	G	80	0.00	L	PD	**0.71**	Ps	50
87			*Dactylorhiza purpurella* (T.Stephenson & T.A. Stephenson) Soó	Cb	H	G	G	25	0.00	D	MD	**0.77**	Ps	71
88			*Dactylorhiza sambucina* (L.) Soó	Cb	H	G	G	30	0.00	D	MD	0.98	Ps	173
89			*Dactylorhiza viridis* (L.) R.M.Bateman, Pridgeon & M.W. Chase	Cb	H	G	G	30	0.00	D	MD	**0.99**	Ps	71
90			*Galearis spathulata* (Lindl.) P.F.Hunt	EA	S	H	G	15	0.00	D	MD	**0.22**	Pw	175
91			*Gymnadenia conopsea* (L.) R.Br.	Cb	H	G	G	60	0.00	D	MD	0.97	Ps	173
92			*Ponerorchis chusua* (D. Don) Soó	EA	S	G	G	45	0.00	D	MD	**0.25**	Pw	175
93	**Asterales**	Asteraceae	*Anthemis tomentosa* Boiss.	Me	S	M	T	30	0.25	D	PD	0.60	Ps	44
94			*Artemisia campestris* subsp. *inodora* Nyman	IT	D	G	P	200	0.76	L	PD	**0.09**	R	168
95			*Artemisia sphaerocephala* Krasch.	IT	D	D	P	120	0.70	L	PD	**0.11**	Pw	168
96			*Artemisia halodendron* Turcz. ex Besser	EA	H	D	H	60	6.10	L	ND	**1.00**	Ps	99
97			*Carlina diae* (Rech. fil.) Meusel & Kästner	Me	S	C	H	60	5.70	L	ND	**0.00**	R	56
98			*Centaurea alexandrina* Delile	SA	D	D	H	30	5.41	L	ND	**0.43**	Pw	68
99			*Centaurea pumilio* L.	Me	S	M	H	15	4.85	D	ND	**0.71**	Ps	35, 146
100			*Cirsium pitcheri* (Torr. ex Eaton) Torr. & A.Gray	NAA	H	M	H	30	9.98	L	PD	0.75	Ps	69
101			*Dimorphotheca tragus* (Aiton) B.Nord.	Cp	S	D	C	50	4.30	L	PD	**0.14**	Pw	40, 41
102			*Echinops spinosissimus* Turra	SA	D	D	H	50	27.70	L	PD	**0.15**	Pw	68
103			*Gazania leiopoda* (DC.) Roessler	Cp	S	D	H	50	2.40	L	PD	**0.22**	Pw	40, 41
104			*Ixeris chinensis* subsp. *versicolor* (Fisch. ex Link) Kitam.	IT	D	G	H	50	0.16	D	ND	**0.10**	Pw	175
105			*Lactuca sativa* L.	Cb	H	R	T	30	1.00	D	PD	**0.89**	Ps	20, 63
106			*Lactuca tatarica* (L.) C.A.Mey.	IT	D	D	H	40	0.78	D	PD	**0.73**	Ps	175
107			*Otanthus maritimus* Hoffmanns. & Link	Me	S	M	H	40	0.83	L	PD	**0.83**	Ps	164
108			*Podotheca gnaphalioides* Graham	SWA	S	G	T	30	0.64	D	PD	**0.66**	Ps	144
109			*Solidago litoralis* Savi	Me	S	M	H	40	0.40	L	PD	**0.30**	Pw	u1
110			*Stenachaenium campestre* Baker	Br	H	G	H	40	0.10	D	PD	0.30	Pw	54
111			*Tagetes minuta* L.	Br	H	G	T	80	0.98	D	PD	**0.26**	Pw	54
112			*Tragopogon lassithicus* Rech. fil.	Me	S	H	H	8	10.00	D	PD	**0.00**	R	56
113			*Ursinia anthemoides* (L.) Poir.	Cp	S	S	T	50	35.00	L	PD	0.45	Pw	144

Continued

Table 1. *Continued*

No.	Order	Family	Taxon	Bio-geography	Climate	Habitat type	Life form	Plant height (cm)	Seed mass (mg)	Seed colour	Dormancy	P_i	Group	Reference(s)
114		Campanulaceae	*Howellia aquatilis* A.Gray	RM	S	A	G	100	1.00	L	PD	**0.03**	R	100
115	**Boraginales**	Boraginaceae	*Alkanna tinctoria* (L.) Tausch	Me	S	R	H	30	3.63	L	ND	**0.29**	Pw	44
116			*Cynoglossum officinale* L.	Cb	H	G	H	35	28.00	L	PD	**0.68**	Ps	171
117			*Echium angustifolium* subsp. *sericeum* (Vahl) Klotz	SA	D	D	H	30	2.50	L	PD	0.68	Ps	68
118			*Nemophila menziesii* Hook. & Arn.	Md	S	G	T	15	2.80	D	PD	**0.58**	Ps	36
119			*Nemophila menziesii* subsp. *insignis* (Benth.) Brand	Md	S	G	T	60	1.20	D	PD	**0.49**	Pw	26, 136
120			*Phacelia tanacetifolia* Benth.	Cb	H	R	T	100	1.70	D	PD	**0.19**	Pw	27, 128, 129, 135
121	**Brassicales**	Brassicaceae	*Alliaria petiolata* (M.Bieb.) Cavara & Grande	Cb	S	R	H	80	3.04	D	PD	0.23	Pw	13
122			*Alyssum akamasicum* Burtt	Me	S	S	C	25	0.57	D	PD	**0.09**	R	81, 82
123			*Alyssum fragillimum* (Bald.) Rech.f.	Me	S	H	C	30	0.71	L	PD	**0.15**	Pw	56
124			*Alyssum sphacioticum* Boiss. & Heldr.	Me	S	H	C	10	3.51	D	PD	**0.41**	Pw	56
125			*Brassica tournefortii* Gouan	Me	S	M	T	50	1.31	D	PD	**1.00**	Ps	40, 41, 44, 164
126			*Cakile edentula* (Bigelow) Hook.	NAA	H	M	T	60	11.10	D	PD	**0.21**	Pw	1, 107, 108
127			*Cakile maritima* Scop.	Me	S	M	T	25	17.40	D	PD	0.80	Ps	7, 139, 164
128			*Descurainia pinnata* (Walter) Britton	Md	D	D	T	60	0.10	L	PD	**0.21**	Pw	55
129			*Enarthrocarpus strangulatus* Boiss.	SA	D	D	T	20	0.60	D	ND	**0.80**	Ps	68
130			*Erucaria microcarpa* Boiss.	SA	D	D	T	20	3.00	L	PD	**1.00**	Ps	68
131			*Malcolmia flexuosa* (Sm.) Sm.	Me	S	M	T	30	0.55	D	ND	**0.02**	R	44
132			*Malcolmia littorea* (L.) R.Br.	Me	S	M	C	30	0.14	L	PD	0.99	Ps	42
133			*Matthiola tricuspidata* (L.) R.Br.	Me	S	M	T	25	0.85	D	ND	**0.86**	Ps	165
134			*Raphanus raphanistrum* subsp. *sativus* (L.) Domin	Cb	H	R	T	50	19.00	D	PD	**0.47**	Pw	110, 117
135		Cleomaceae	*Cleome gynandra* L.	SZ	S	S	H	60	0.90	D	PD	**0.27**	Pw	122
136		Resedaceae	*Reseda lutea* L.	Me	S	S	H	100	0.80	D	PD	**0.23**	Pw	46
137	**Caryophyllales**	Aizoaceae	*Conicosia pugioniformis* (L.) N.E.Br.	Cp	S	D	H	20	0.90	D	PD	0.43	Pw	40, 41
138		Amaranthaceae	*Agriophyllum squarrosum* (L.) Moq.	IT	D	D	T	25	1.52	L	PD	**0.63**	Ps	183
139			*Amaranthus albus* L.	Md	S	R	T	50	0.30	D	PD	0.95	Ps	161
140			*Amaranthus caudatus* L.	SZ	S	R	T	150	0.50	D	PD	**0.01**	R	86
141			*Amaranthus dubius* Mart. ex Thell.	Cr	S	R	T	100	0.23	D	PD	0.40	Pw	172
142			*Atriplex centralasiatica* Iljin	IT	D	D	T	20	0.01	D	PD	0.22	Pw	182
143			*Atriplex dimorphostegia* Kar. & Kir.	SA	D	D	T	50	0.85	L	PD	**0.95**	Ps	92
144			*Haloxylon salicornicum* (Moq.) Bunge ex Boiss.	SA	D	D	C	60	5.99	L	ND	0.75	Ps	68
145			*Suaeda vermiculata* Forssk. ex J.F. Gmel.	SZ	D	D	C	150	0.79	D	PD	**0.30**	Pw	87, 148, 180
146		Caryophyllaceae	*Dianthus xylorrhizus* Boiss. & Heldr.	Me	S	S	C	15	2.03	D	ND	**0.01**	R	56
147			*Minuartia wettsteinii* Mattf.	Me	S	S	C	15	1.42	D	ND	**0.02**	R	56
148			*Silene aethiopica* Burm. f.	Cp	S	M	T	25	0.30	D	PD	1.00	Ps	84
149			*Silene ammophila* Boiss. & Heldr. subsp. *carpathae* Chowdhuri	Me	S	M	T	15	0.34	D	PD	**0.81**	Ps	56

150			*Silene colorata* Poir.	Me	S	M	T	40	0.26	D	PD	**0.30**	Pw	44
151			*Silene gallica* L.	Me	S	M	T	45	0.33	D	PD	**0.61**	Ps	44
152			*Silene glaucifolia* Lag.	Me	S	S	H	20	0.62	D	PD	**0.11**	Pw	118
153			*Silene kotschyi* Boiss.	Me	S	M	T	20	0.15	D	PD	**0.73**	Ps	153
154			*Silene laxipruinosa* Mayol & Rosselló	Me	S	S	H	30	0.65	D	PD	**0.34**	Pw	118
155			*Silene succulenta* Forssk.	Me	S	M	H	20	0.54	D	ND	**0.98**	Ps	44, 56
156		Molluginaceae	*Pharnaceum aurantium* Druce	Cp	S	D	H	80	0.13	L	PD	**0.52**	Ps	40, 41
157		Polygonaceae	*Calligonum comosum* L'Hér.	SA	S	D	P	150	25.60	L	ND	**0.79**	Ps	89
158			*Rumex patientia* L.	IT	D	D	H	150	3.12	D	PD	**0.11**	Pw	175
159		Tamaricaceae	*Reaumuria soongarica* (Pall.) Maxim.	IT	D	G	C	60	1.24	D	ND	**0.15**	Pw	179
160	**Cucurbitales**	Cucurbitaceae	*Citrullus colocynthis* (L.) Schrad.	SA	D	D	H	60	35.97	D	PD	**0.89**	Ps	91
161			*Citrullus lanatus* (Thunb.) Matsum. & Nakai	SZ	D	D	T	60	83.00	D	PD	**0.73**	Ps	117, 162
162			*Cucumis anguria* L.	SZ	D	D	T	20	9.40	D	PD	**0.92**	Ps	121
163			*Cucumis melo* L.	SZ	D	D	T	30	14.06	L	PD	**0.73**	Ps	5
164			*Cucurbita maxima* Duchesne	CP	S	D	T	60	240.90	L	PD	**0.67**	Ps	117
165			*Cucurbita pepo* var. *texana* (Scheele) D.S.Decker	Md	D	G	T	100	91.26	L	PD	**0.18**	Pw	125
166			*Lagenaria siceraria* (Molina) Standl.	SZ	S	R	T	600	154.00	D	ND	**0.30**	Pw	117
167	**Dioscoreales**	Dioscoreaceae	*Dioscorea communis* (L.) Caddick & Wilkin	Me	S	W	G	400	18.89	L	MPD	**0.32**	Pw	Kd
168			*Dioscorea japonica* Thunb.	EA	H	W	G	200	4.07	L	MPD	**0.47**	Pw	123
169			*Dioscorea quinquelobata* Thunb.	EA	H	W	G	200	6.53	L	MPD	0.85	Ps	123
170			*Dioscorea septemloba* Thunb.	EA	H	W	G	150	8.75	L	MPD	**0.28**	Pw	123
171			*Dioscorea tokoro* Makino ex Miyabe	EA	H	W	G	200	15.64	L	MPD	**0.15**	Pw	123
172	**Dipsacales**	Caprifoliaceae	*Centranthus ruber* (L.) DC.	Me	S	G	H	70	1.80	L	ND	**0.38**	Pw	106
173	**Ericales**	Ericaceae	*Epacris stuartii* Stapf	NEA	H	S	C	80	0.03	L	PD	0.52	Ps	85
174		Primulaceae	*Ardisia quinquegona* Blume	EA	H	W	P	200	39.01	D	PD	**0.16**	Pw	28
175			*Cyclamen persicum* Mill.	Me	S	W	G	14	6.84	D	PD	**0.53**	Ps	23, 119
176			*Jacquinia armillaris* Jacq.	Br	H	M	C	200	101.43	D	ND	**0.92**	Ps	59, 60
177			*Rapanea divaricata* (A. Cunn.) W.R.B. Oliv.	Nz	H	W	P	300	8.70	L	PD	**0.02**	R	22
178	**Fabales**	Fabaceae	*Acacia drummondii* subsp. *candolleana* (Meissner) Maslin	SWA	S	S	P	75	22.50	L	PY	**0.98**	Ps	17
179			*Acacia extensa* Lindl.	SWA	S	S	P	150	12.93	D	PY	0.63	Ps	17
180			*Acacia pulchella* var. *glaberrima* Meissner	SWA	S	S	P	150	8.50	D	PY	**0.92**	Ps	17
181			*Aeschynomene aspera* L.	In	H	A	C	200	12.00	L	PY	**0.15**	Pw	39
182			*Astragalus sieberi* DC.	SA	D	D	C	40	2.00	D	PY	0.57	Ps	68
183			*Bossiaea aquifolium* Benth.	SWA	S	S	P	200	10.60	D	PY	0.80	Ps	16, 17, 97
184			*Bossiaea ornata* Benth.	SWA	S	S	C	100	3.00	D	PY	0.60	Ps	15, 17, 18, 97
185			*Caragana erinacea* Kom.	IT	D	D	C	150	9.63	D	PY	**0.15**	Pw	175
186			*Caragana korshinskii* Kom.	EA	H	D	P	200	49.90	D	ND	**1.00**	Ps	99
187			*Caragana microphylla* Lam.	EA	H	D	P	250	38.44	D	ND	1.00	Ps	99
188			*Cytisus scoparius* (L.) Link	Me	S	S	P	300	9.00	D	PY	**0.07**	Pw	101
189			*Erythrophleum fordii* Oliv.	EA	H	W	P	1000	762.00	D	ND	**0.22**	Pw	28
190			*Genista triacanthos* Brot.	Me	S	S	C	100	1.70	D	PY	0.32	Pw	101
191			*Genista tridentata* L.	Me	S	S	C	100	4.20	D	PY	0.14	Pw	101

Continued

Table 1. *Continued*

No.	Order	Family	Taxon	Biogeography	Climate	Habitat type	Life form	Plant height (cm)	Seed mass (mg)	Seed colour	Dormancy	P_i	Group	Reference(s)
192			*Genista umbellata* (L'Her.) Poir.	Me	S	S	C	100	3.40	D	PY	**0.20**	Pw	101
193			*Gompholobium knightianum* Lindl.	SWA	S	S	C	40	3.46	D	PY	1.00	Ps	17
194			*Kennedia prostrata* R.Br.	SWA	S	S	C	30	29.70	D	PY	0.60	Ps	16, 17
195			*Medicago polymorpha* L.	Me	S	S	T	60	30.10	L	PY	**0.63**	Ps	78
196			*Medicago sativa* L.	EA	H	D	H	100	2.00	L	ND	**0.19**	Pw	99
197			*Melilotus suaveolens* Ledeb.	EA	H	D	H	150	2.50	L	ND	0.66	Ps	99
198			*Mimosa scabrella* Benth.	Br	H	T	P	1500	9.78	D	PY	0.34	Pw	45
199			*Psoralea esculenta* Pursh	Md	S	G	G	50	20.75	D	PY	**0.41**	Pw	156, 157
200			*Racosperma lateriticola* (Maslin) Pedley	SWA	S	S	P	100	5.80	D	PY	1.00	Ps	15, 17, 19
201			*Spartium junceum* L.	Me	S	S	P	200	14.50	D	PY	**0.07**	R	101
202			*Sphaerolobium vimineum* Sm.	SWA	S	S	P	80	1.83	D	PY	0.67	Ps	17, 19
203			*Trifolium riograndense* Burkart	Br	H	G	H	30	1.50	L	PY	0.24	Pw	159
204	**Fagales**	Fagaceae	*Quercus robur* L.	Cb	H	W	P	2500	3378.00	L	ND	**0.00**	R	185
205	**Gentianales**	Apocynaceae	*Catharanthus roseus* (L.) G.Don	Mg	S	T	P	200	1.40	D	PD	**0.29**	Pw	24
206			*Cryptostegia grandiflora* Roxb. ex R.Br.	SZ	D	D	C	200	8.58	L	PD	**0.40**	Pw	147
207			*Gomphocarpus fruticosus* (L.) W.T. Aiton	SZ	S	G	P	150	6.71	D	PD	0.51	Ps	177
208			*Pergularia daemia* (Forssk.) Chiov.	SZ	D	D	H	100	8.00	L	PD	**0.83**	Ps	147
209			*Periploca laevigata* subsp. *angustifolia* (Labill.) Markgr.	Me	S	M	P	200	6.50	D	ND	**0.12**	Pw	56
210		Gentianaceae	*Gentianella campestris* (L.) Börner	Cb	H	G	H	30	0.18	L	MPD	0.80	Ps	112
211		Rubiaceae	*Asperula rigida* Sibth. & Sm.	Me	S	M	C	30	1.16	D	ND	**0.27**	Pw	35
212			*Crucianella maritima* L.	Me	S	M	C	40	1.87	L	ND	**0.72**	Ps	43, 146
213			*Galium spurium* L.	Cb	S	R	T	50	4.63	D	PD	**0.93**	Ps	103
214	**Lamiales**	Bignoniaceae	*Handroanthus impetiginosus* (Mart. ex DC.) Mattos	Br	H	T	P	3000	83.00	L	ND	**0.27**	Pw	45
215			*Zeyheria montana* Mart.	Br	S	G	P	300	30.00	L	ND	0.37	Pw	79
216		Lamiaceae	*Galeopsis speciosa* Mill.	Cb	H	R	T	70	4.23	D	PD	0.40	Pw	113
217			*Lamium amplexicaule* L.	Cb	S	R	T	25	0.61	D	PD	**0.34**	Pw	80
218			*Stachys sylvatica* L.	Cb	H	W	H	50	1.40	D	PD	**0.81**	Ps	154
219		Orobancaceae	*Aeginetia indica* L.	Ml	H	W	T	30	0.01	L	PD	**1.00**	Ps	57
220			*Orobanche minor* Sm.	Cb	H	G	T	15	0.00	L	PD	**0.51**	Ps	160
221			*Striga asiatica* (L.) Kuntze	SA	D	G	T	25	0.15	L	PD	0.58	Ps	98, 133
222		Verbenaceae	*Lippia filifolia* Mart. & Schauer	Br	H	T	H	30	0.98	D	ND	**0.64**	Ps	127
223	**Laurales**	Lauraceae	*Lindera melissifolia* (Walter) Blume	NAA	H	W	P	200	69.00	D	PD	**0.32**	Pw	72
224			*Ocotea catharinensis* Mez	Br	H	T	P	2000	80.00	D	PD	**0.03**	R	102, 151
225	**Liliales**	Colchicaceae	*Colchicum macrophyllum* B.L.Burtt	Me	S	S	G	15	3.73	D	MPD	**0.54**	Ps	2
226			*Colchicum montanum* L.	Me	S	G	G	15	1.91	D	MPD	1.00	Ps	33
227		Liliaceae	*Androcymbium rechingeri* Greuter	Me	S	M	G	10	1.90	D	ND	**0.00**	R	44
228			*Convallaria keiskei* Miq.	EA	H	G	G	30	2.90	L	MPD	**0.97**	Ps	93
229			*Leopoldia comosa* (L.) Parl.	Me	S	S	G	50	5.80	D	ND	**0.00**	R	47
230			*Muscari commutatum* Guss.	Me	S	S	G	20	2.60	D	ND	**0.00**	R	47
231			*Tulipa sylvestris* L.	Cb	H	G	G	45	2.86	L	MPD	**0.13**	Pw	Kd
232			*Tulipa sylvestris* subsp. *australis* (Link) Pamp.	Me	S	G	G	40	4.20	L	MPD	**0.14**	Pw	u1

233		Melanthiaceae	*Trillium camschatcense* Ker Gawl.	EA	H	W	G	60	11.93	L	MPD	**0.29**	Pw	92
234		Smilacaceae	*Smilax campestris* Griseb.	Br	H	T	P	2000	46.56	L	MD	**0.37**	Pw	138
235	**Malpighiales**	Clusiaceae	*Garcinia oblongifolia* Champ. ex Benth.	EA	H	W	P	1500	454.00	D	PD	**0.12**	Pw	28
236		Euphorbiaceae	*Euphorbia paralias* L.	Me	S	M	H	60	9.61	L	PD	**1.00**	Ps	44
237			*Manihot esculenta* Crantz	Am	H	T	C	150	114.00	L	PD	**0.17**	Pw	132
238			*Ricinus communis* L.	SZ	S	T	P	200	295.60	D	PD	**0.88**	Ps	53
239		Passifloraceae	*Passiflora edulis* Sims	Br	S	W	H	250	13.80	D	ND	**0.33**	Pw	19, 184
240		Phyllanthaceae	*Phyllanthus calycinus* Labill.	SWA	S	S	P	120	1.68	D	ND	1.00	Ps	17
241			*Phyllanthus virgatus* G.Forst.	NEA	H	S	H	50	1.20	L	PD	0.82	Ps	31
242		Violaceae	*Viola scorpiuroides* Coss.	Me	S	M	C	30	2.20	D	PD	**0.17**	Pw	56
243	**Malvales**	Malvaceae	*Ceiba speciosa* (A.St.-Hil.) Ravenna	Br	H	T	P	2500	57.67	D	ND	**0.66**	Ps	45
244			*Lavatera triloba* L.	Me	S	M	P	150	6.65	D	PY	**0.14**	Pw	141
245	**Myrtales**	Combretaceae	*Combretum bracteosum* (Hochst.) Engl. & Diels	Cp	S	G	C	400	840.00	D	PD	**0.07**	R	37
246		Myrtaceae	*Corymbia calophylla* (R.Br. ex Lindl.) K.D.Hill & L.A.S.Johnson	SWA	S	S	P	5000	93.89	D	ND	**0.30**	Pw	17
247			*Eucalyptus diversicolor* F.Muell.	SWA	S	S	P	8000	1.21	L	ND	**0.15**	Pw	17
248			*Eucalyptus marginata* Donn ex Sm.	SWA	S	S	P	4000	12.19	D	PY	0.79	Ps	17
249			*Eucalyptus youmanii* Blakely & McKie	NEA	H	S	P	2000	2.23	L	PD	0.58	Ps	31
250			*Eugenia rostrifolia* D.Legrand	Br	H	T	P	3000	130.00	L	ND	0.79	Ps	142
251		Thymeleaceae	*Aquilaria sinensis* (Lour.) Spreng.	EA	H	W	P	1000	68.40	D	ND	**0.15**	Pw	181
252	**Poales**	Cyperaceae	*Carex nigra* (L.) Reichard	Cb	H	G	G	50	0.69	L	PD	0.16	Pw	143
253		Poaceae	*Agropyron cristatum* (L.) Gaertn.	Cb	D	G	G	70	1.70	L	PD	**0.11**	Pw	137
254			*Ammophila arenaria* (L.) Link	Me	S	M	G	120	3.71	L	ND	**0.44**	Pw	44
255			*Brachypodium distachyon* (L.) P. Beauv.	Me	S	S	T	30	4.10	L	PD	**0.18**	Pw	8
256			*Bromus hordeaceus* L.	Cb	S	R	T	50	4.50	L	ND	**0.79**	Ps	51
257			*Bromus sterilis* L.	Cb	S	R	T	40	9.20	L	ND	**0.94**	Ps	51, 77
258			*Elymus dahuricus* Griseb.	EA	H	D	H	120	3.85	L	ND	**1.00**	Ps	99
259			*Elymus farctus* (Viv.) Runemark ex Melderis	Me	S	M	G	60	13.27	L	ND	**0.33**	Pw	44
260			*Elymus repens* (L.) Gould	Cb	H	G	G	100	4.04	L	PD	0.55	Ps	167
261			*Festuca hallii* (Vasey) Piper	Cb	H	G	H	85	1.40	L	ND	**0.89**	Ps	115
262			*Koeleria macrantha* (Ledeb.) Schult.	Cb	H	G	H	90	0.30	L	ND	**0.25**	Pw	115
263			*Leymus arenarius* (L.) Hochst.	Cb	H	C	G	76	11.00	L	PD	**0.63**	Ps	64, 65
264			*Nassella viridula* (Trin.) Barkworth	Md	S	G	H	120	2.80	L	PD	0.17	Pw	58
265			*Oryzopsis hymenoides* (Roem. & Schult.) Ricker ex Piper	Md	S	G	G	40	3.00	L	PD	0.63	Ps	30, 48
266			*Phleum sardoum* Hack. ex Franch.	Me	S	M	T	5	0.24	L	ND	**0.03**	R	140
267			*Poa alpina* L.	Cb	H	H	H	50	0.36	L	PD	**0.31**	Pw	145
268			*Poa pratensis* L.	Cb	H	G	G	80	0.30	L	PD	**0.26**	Pw	167
269			*Schismus arabicus* Nees	SA	S	D	T	15	0.16	L	PD	0.44	Pw	66
270			*Scolochloa festucacea* (Willd.) Link	NAA	H	A	G	150	1.10	L	PD	0.85	Ps	155
271			*Sesleria doerfleri* Hayek	Me	S	C	H	70	3.26	D	PD	**0.00**	R	56
272			*Sorghum leiocladum* (Hack.) C.E. Hubb.	NEA	H	S	H	70	3.00	L	PD	0.57	Ps	31
273			*Spinifex hirsutus* Labill.	NEA	H	M	G	30	10.77	D	PD	**0.78**	Ps	70
274			*Spinifex sericeus* R.Br.	NEA	H	M	G	40	13.85	L	PD	**0.36**	Pw	109, 139
275	**Ranunculales**	Papaveraceae	*Eschscholzia californica* Cham.	Md	S	S	H	70	1.50	D	MPD	**0.83**	Ps	62

Continued

Table 1. *Continued*

No.	Order	Family	Taxon	Bio-geography	Climate	Habitat type	Life form	Plant height (cm)	Seed mass (mg)	Seed colour	Dormancy	P_i	Group	Reference(s)
276			*Glaucium flavum* Cranz	Me	S	M	H	60	1.10	D	PD	**1.00**	Ps	163
277		Ranunculaceae	*Anemone coronaria* L.	Me	S	S	G	30	0.53	D	MD	**0.66**	Ps	21
278			*Consolida ajacis* (L.) Schur	Me	S	R	T	60	2.04	D	PD	**0.76**	Ps	38
279			*Consolida regalis* Gray	Cb	H	G	T	70	2.09	D	MPD	**0.32**	Pw	Kd
280			*Delphinium fissum* subsp. *sordidum* (Cuatrec.) Amich, E.Rico & J. Sánchez	Me	S	S	H	100	1.25	D	MPD	**0.11**	Pw	73
281			*Delphinium tricorne* Michx.	NAA	H	G	T	60	2.56	D	MPD	**0.28**	Pw	10
282			*Nigella damascena* L.	Cb	H	G	T	45	3.16	D	MPD	**0.64**	Ps	126, Kd
283	**Rosales**	Rhamnaceae	*Cryptandra arbutiflora* Fenzl	SWA	S	W	P	100	0.40	D	PY	**0.17**	Pw	169
284			*Spyridium globulosum* Benth.	SWA	S	S	P	500	1.35	D	PY	**0.14**	Pw	169
285	**Sapindales**	Anacardiaceae	*Sclerocarya birrea* (A.Rich.) Hochst.	SZ	S	G	P	2000	2975.00	L	PD	**0.27**	Pw	116
286		Rutaceae	*Ruta graveolens* L.	Me	S	C	C	50	1.98	D	ND	**1.00**	Ps	u2
287		Sapindaceae	*Acer tataricum* subsp. *ginnala* (Maxim.) Wesm.	Cb	H	W	P	1000	37.20	D	PD	**0.43**	Pw	49
288	**Solanales**	Convolvulaceae	*Merremia aegyptia* (L.) Urb.	Cr	S	R	T	600	54.20	D	PD	**0.13**	Pw	172
289			*Operculina hamiltonii* (G. Don) D.F. Austin & Staples	Br	H	T	P	200	150.00	D	PY	**0.57**	Ps	111
290		Solanaceae	*Hyoscyamus niger* L.	Cb	H	R	H	70	0.60	D	PD	0.84	Ps	29
291			*Lycopersicon esculentum* Mill.	Cr	S	R	T	200	1.97	L	PD	**1.00**	Ps	61, 178
292			*Nicandra physalodes* (L.) Gaertn.	An	H	R	T	100	0.80	L	PD	0.54	Ps	176
293			*Solanum lycopersicum* L.	An	S	R	T	300	3.34	L	PD	**0.04**	R	117
294			*Solanum melongena* L.	In	S	R	T	150	3.50	L	PD	**0.05**	R	117
295			*Solanum scuticum* M. Nee	Br	H	T	P	200	1.11	D	PD	**0.78**	Ps	170
296	**Zygophyllales**	Zygophyllaceae	*Larrea tridentata* (Sessé & Moc. ex DC.) Coville	Md	D	D	P	200	2.40	L	PD	**0.53**	Ps	6, 134
297			*Peganum multisectum* (Maxim.) Bobrov	IT	D	D	H	30	2.18	D	PD	0.89	Ps	175
298			*Tetraena alba* (L.f.) Beier & Thulin	Me	S	M	C	60	1.70	D	PD	0.83	Ps	44
299			*Zygophyllum coccineum* L.	SA	D	D	C	75	0.80	D	PD	**0.18**	Pw	14
300			*Zygophyllum dumosum* Boiss.	SA	S	D	C	90	1.00	D	PD	**0.18**	Pw	88
301			*Zygophyllum fabago* L.	IT	D	D	C	40	1.20	D	PD	**0.37**	Pw	175

Taxonomic information was standardized against The Plant List Database (http://www.theplantlist.org/). Biogeographical range follows the Floristic Regions of Takhtajan (1986): Am, Amazonian; An, Andean; Br, Brazilian; Cb, Circumboreal; Cp, Cape; CP, Chile-Patagonian; Cr, Caribbean; EA, Eastern Asiatic; In, Indian; IT, Irano-Turanian; Md, Madrean; Me, Mediterranean; Mg, Madagascan; Ml, Malesian; NAA, North American Atlantic; NEA, Northeast Australian; Nz, Neozeylandic; RM, Rocky Mountain; SA, Saharo-Arabian; SWA, Southwest Australia; SZ, Sudano-Zambezian. Climate: D, dry; H, humid; S, seasonal. Life forms: P, Phanerophytes; C, Chamaephytes; H, Hemicryprophytes; G, Geophytes (Cryptophytes); T, Therophytes. Habitats: A, freshwater; M, coastal; W, woodlands; T, tropical forests; G, grasslands; H, high-mountain vegetation; S, low-sized shrublands; C, cliffs and walls; D, deserts; R, agricultural and ruderal habitats. Seed colour: L, light; D, dark. Seed dormancy classes: MD, Morphological; MPD, Morphophysiological; PY, Physical; PD, Physiological; ND, Nondormancy. P_i: numbers in bold = final dark germination exceeds 70%. Group: Ps, strongly photoinhibited taxa (P_i exceeds 0.5); Pw, weakly photoinhibited taxa (P_i exceeds 0.1 but not 0.5); R: light reduces only the rate of germination. Reference (s): numbers in alphabetical order within Table 1 are represented in brackets at the end of each citation in References; Kd, Filip Vandelook, Rosemary Newton, Angelino Carta unpublished data; u1, Angelino Carta unpublished data; u2, Costas Thanos, unpublished data; u3, Filip Vandelook unpublished data.

Whether both samples follow a normal distribution was assessed using a Kolmogorov–Smirnov single sample test. For graphical and analytical purposes, we estimated the probability density function of both samples applying the Kernel density estimation. This function does not assume any underlying distribution for the variable (non-parametric technique) but is extremely helpful in evaluating the underlying distribution of a continuous variable as its definite integral over its support set (the area under the density estimate) must equal 1. Hence, the area between two given values under a Kernel density estimate curve returns an estimated probability of the variable.

To assess whether observed frequencies of categorical variables (taxonomic ranks, biogeography, climate, habitat type, life form, seed colour and seed dormancy) differed significantly from theoretical expectations, we used simple χ^2 tests. A χ^2 test of independence was applied to determine whether there was a significant association between two categorical variables. All analyses were performed with the software R (R Development Core Team, 2015).

Results and Discussion

Occurrence

Records were examined for a total of 413 taxa. The requirements for PISG were not met for 112 taxa (supplementary Table S1). Thus, the final dataset contains 301 photoinhibited taxa, belonging to 59 families and 27 orders. The clear majority of these plants germinated to >70% in darkness (232 taxa; their P_i values shown in bold in Table 1). In 46 taxa, final dark germination ranges from 50 to 70%, and in only 23 taxa final dark germination ranges between 30 and 50%. Of the 301 taxa, 141 were strongly photoinhibited, with a P_i >50% (Ps; Table 1) while for 31 taxa, light significantly reduced germination rate without affecting final germination (R; Table 1).

Although PISG is not confined to specific major clades or biogeographical regions and habitats, some patterns have been identified. In particular, most of the photoinhibited seeds are dark coloured and relatively larger than those of the world flora (Fig. 1). They belong to non-woody plants (74%) and occur in open and dry habitats (73%; Fig. 2) at mid-latitudes (non-tropical) under a seasonal or arid climate (Fig. 4). Overall, the data suggest that PISG occurs in most biogeographical realms (excluding the Oceanic and the Antarctic, Fig. 4). Furthermore, PISG is not a limited, monophyletic phenomenon but occurs in 27 angiosperm orders (40% of all APG orders, Fig. 3).

While compiling the database and assembling the available literature, a reasonable question arose. How many species in the world flora can be expected to exhibit PISG? To answer this inquiry, we need to know the approximate number of taxa with known germination behaviour. A reliable proxy for this is the 15,311 taxa in SID (Royal Botanic Gardens Kew, 2016). On the basis of the total number of taxa in Table 1, we estimate a frequency of 2% for PISG, a moderate estimate compared with the one (26.8%) reported by Kinzel (1913–1926). Furthermore, by simple extrapolation, we can expect a total number of *ca* 6000 taxa [i.e. 0.02 × *ca* 300,000 angiosperms according to Christenhusz and Byng (2016)] with PISG in the world flora.

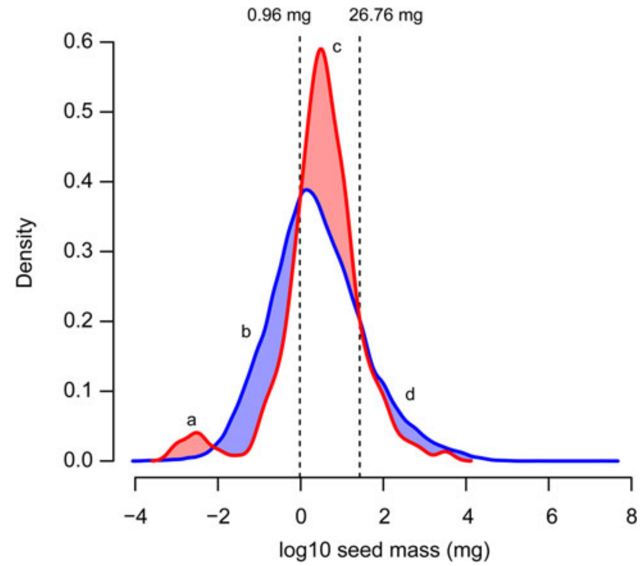

Figure 1. Kernel density estimates of seed mass for the world flora (blue line; Royal Botanic Gardens Kew, 2016) and for the photoinhibited flora (red line; present study). Both distributions are significantly different ($P < 0.001$ based on Kolmogorov–Smirnov two sample test). The vertical dashed lines correspond to seed mass thresholds separating seeds whose germination is light stimulated (<0.96 mg), photoinhibited (>0.96 and <26.76 mg) and indifferent to light (>26.76 mg). The red peak, coinciding approximately with 0.002 mg, corresponds to Orchidaceae and Orobanchaceae taxa. Red areas correspond to seed mass ranges where there is a higher representation of photoinhibited taxa than of the world flora, and blue areas to those where photoinhibited taxa are less represented.

Seed mass

Seed mass distributions for PISG (301 taxa) and the world flora (34,395 taxa; Royal Botanic Gardens Kew, 2016) are normal (Kolmogorov–Smirnov single sample test, $P < 0.001$), but their probability density estimates mostly do not overlap (Fig. 1). Indeed, the photoinhibited group has significantly (Kolmogorov–Smirnov two sample test, $P < 0.001$) larger seeds (mean 3.09 mg) than that of the world flora (mean 1.34 mg). Furthermore,

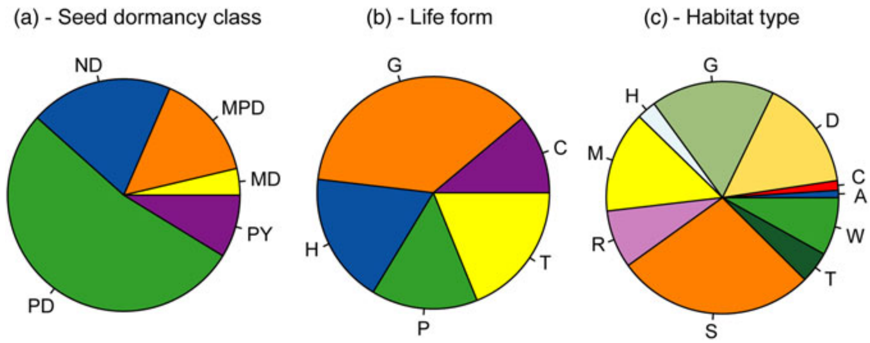

Figure 2. Proportion of photoinhibited taxa per seed dormancy class (a), life form (b) and habitat type (c). For explanation of the abbreviations see the footnote of Table 1.

seed mass has a standard deviation of 2.22 compared with 3.38 for the world flora and the probability for the photoinhibited seed mass curve in the range 0.96–26.76 mg (c in Fig. 1), is significantly higher (65.3%) than that of the world flora. Thus, while almost two-thirds of PISG taxa fall within this range, the corresponding value for the world flora is 45.9%. A secondary, minor peak of the PISG curve lies in the range 0.0003–0.0078 mg (a in Fig. 1). This 'hump' represents *ca* 3.4% of the PISG taxa and corresponds to members of Orchidaceae and Orobanchaceae listed in the dataset. Furthermore, within the ranges 0.0078–1 mg and >26.76 mg (b and d in Fig. 1, respectively), the PISG curve is lower than that of the world flora distribution. Thus, PISG is certainly under-represented in these particular ranges, arguably as the result of the well-known, relative predominance of light-requiring (e.g. Grime *et al.*, 1981; Pons, 2000) and light-indifferent (e.g. Milberg *et al.*, 2000; Pearson *et al.*, 2002) seeds, respectively.

Indeed, the lower value of the 0.96–26.76 mg range is consistent with the threshold of 1 mg, below which seeds are more likely to have a light-stimulated germination (Pons, 2000), and with the approximate cut-off (1.5 mg) between species that require light for germination and those that do not, which was identified by Jankowska-Blaszczuk and Daws (2007) while studying the impact of red:far red ratio on temperate forest herbs. The higher value of the 0.96–26.76 mg range suggests that seeds larger than *ca* 27 mg should be indifferent to light/dark conditions, since their seed mass may not represent a constraint for the emergence of germinated seeds. While studying the germination ecology of neotropical pioneers, Pearson *et al.* (2002) found that the maximum mass of species likely to show a significant positive germination response to irradiance was 0.7, whereas the mean seed mass of genera containing light indifferent species was 22.7 mg, confirming both thresholds identified in the present study.

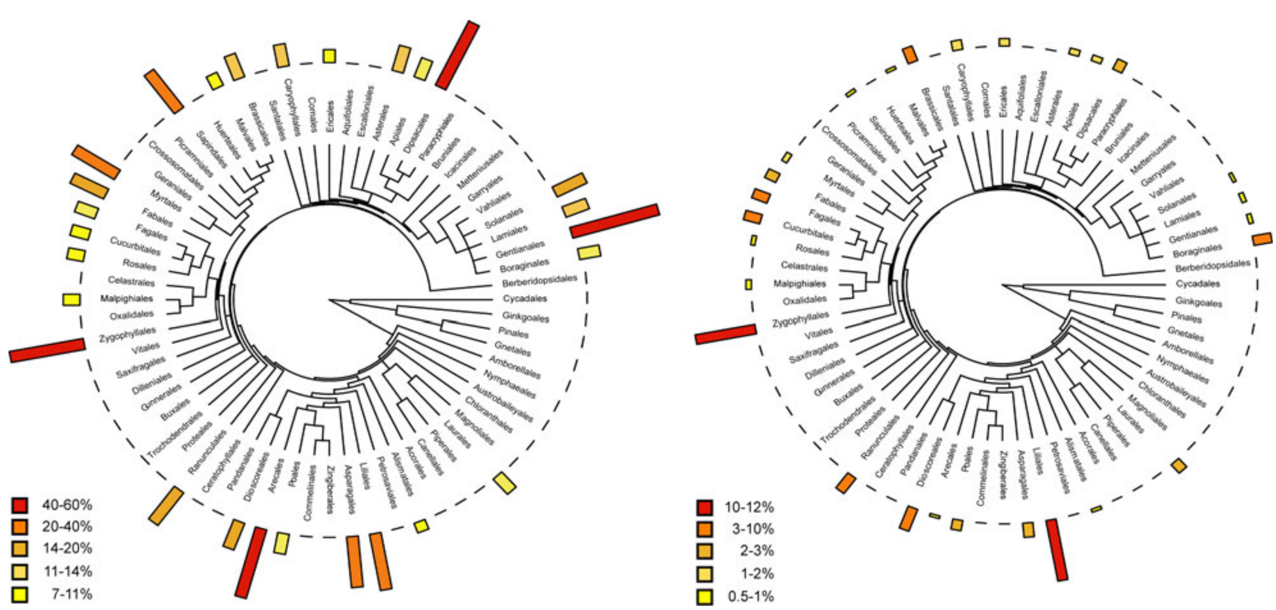

Figure 3. Photoinhibition of seed germination as percentage per order of families (left) and genera (right) with documented PISG. Phylogeny follows APG IV (Stevens, 2001; APG *et al.*, 2016).

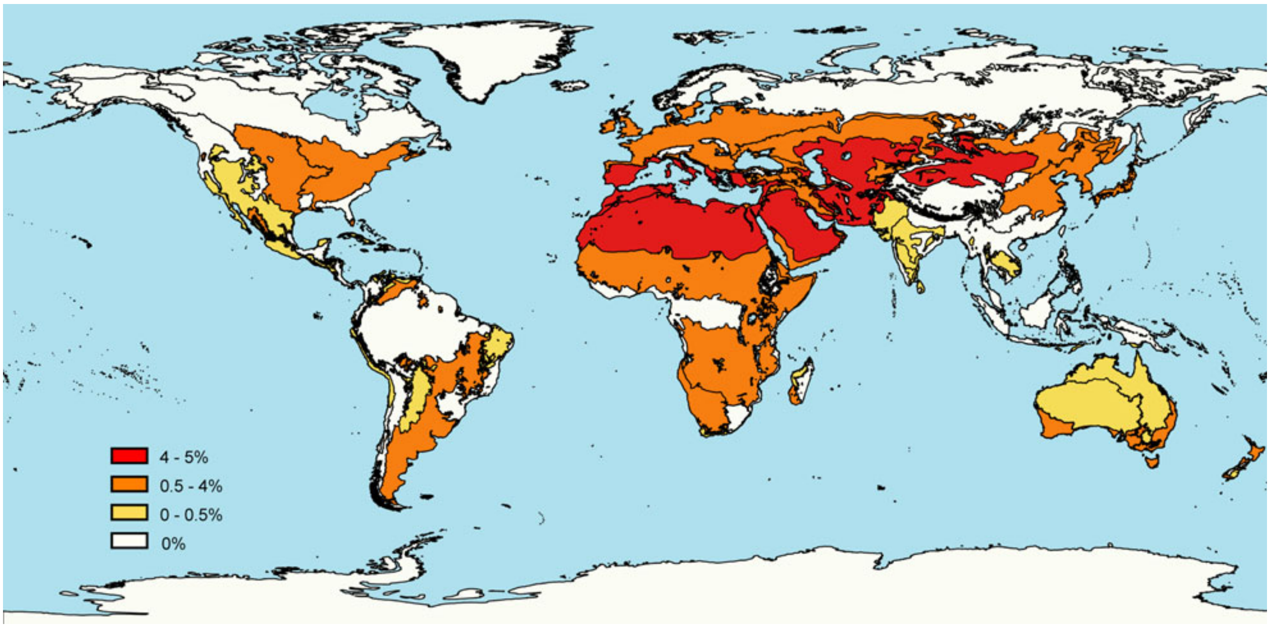

Figure 4. Percentage of photoinhibited taxa in each climatic region within each biogeographical realm (terrestrial ecoregions of the world; see Olson *et al*., 2001) calculated based on plant richness estimates from Kier *et al.* (2005). Realms: Australasia, Antarctic, Afrotropics, IndoMalay, Nearctic, Neotropics, Oceania, Palearctic. Climatic regions: tropical humid, tropical dry, temperate humid, temperate montane, cold, tropical semi-arid, temperate semi-arid, montane, polar, mediterranean, arid.

For species with relatively medium-sized seeds, in which seed mass is well above the assumed thresholds for light requirement, PISG is a rather more advantageous mechanism compared with a light requirement (Skourti and Thanos, 2015). This is because seedling emergence from burial depths below the upper 4–5 mm of the soil [where light is present in physiologically significant quantities (Tester and Morris, 1987)] can take place before the seed reserves are depleted. This might also explain why large seeds are correlated with dry and seasonal habitats, i.e. they can be buried as deeply as their particular seed reserves allow seedling emergence (Leishman *et al*., 2000; Daws *et al*., 2008; Vandelook *et al*., 2012). On the other hand, large seed size is also an adaptation to aseasonal and moist habitats (Tweddle *et al*., 2003), reducing the likelihood of desiccation-induced mortality in desiccation-sensitive or recalcitrant seeds (Daws *et al*., 2004). Large seed mass for recalcitrant seeds, which does not represent a constraint for emergence when buried and indifference to light for seeds larger than *ca* 27 mg or PISG for seeds with masses of between *ca* 1 and 27 mg, may therefore be adaptations to promote germination of buried seeds. It can thus be hypothesized that the ecological conditions that favour recalcitrance also select for large seed size.

Seeds of terrestrial orchids usually germinate better in darkness than in light (e.g. Waes and Debergh, 1986; Zettler and McInnis, 1994; Wang *et al*., 2009), although PISG in terrestrial orchids is by no means universal (e.g. Oliva and Arditti, 1984; Dutra *et al*., 2008). Orchids, and maybe other dust-seeded taxa as well, are clearly an exception to the 1 mg lower threshold of PISG. This is probably due to their specific germination ecology in association with fungi. Not only are seedlings from these dust-seeds less likely to run out of reserves before reaching the soil surface, but burial in the soil can also bring seeds into fungus-rich substrates (Zettler and McInnis, 1994). Light responses have been much less studied in epiphytic orchids, but at least one species, *Cyrtopodium punctatum*, is photoinhibited (Dutra *et al*., 2009). Much work is still needed to find general patterns in PISG in orchids. Also, most orchid seed germination experiments have been performed in asymbiotic and sterile laboratory conditions. However, burial experiments with seeds of *Dactylorhiza maculata*, *Epipactis helleberoni* (van der Kinderen, 1995) and *Cephalanthera damasonium* (Roy *et al.*, 2013) have shown that seeds of these orchids can germinate, in the absence of light, up to 7–10 cm deep in the soil. Both *D. maculate* and *E. helleborine* have been shown to germinate better in the dark than in light in laboratory conditions (Waes and Debergh, 1986), but a control experiment testing seed germination in exposed conditions in nature is missing.

Seed colour

Seed coats can be intensely pigmented, which reduces the PFD and alters the spectral composition of the light inside the seeds (Widell and Vogelmann, 1988). Most

 https://doi.org/10.1017/S0960258517000137

of the photoinhibited seeds were dark coloured (65%), confirming previous findings that PISG was related to black or dark-coloured seeds (Thanos, 1993; Thanos *et al*., 2005; Fournaraki, 2010). It has been reported that this optical property of the dark seed coat reduces light transmission to phytochrome in the embryo of seeds (Widell and Vogelmann, 1988). However, in our dataset, dark seeds were significantly over-represented in seasonal climates (χ^2 test of independence, $P < 0.001$) and it is possible that the 'abundance' of dark seeds could be a consequence of habitat selection ($P < 0.01$) or phylogenetic inheritance at the order, family and genus levels ($P < 0.001$, see also 'Phylogeny' section below), rather than a convergent evolution of seed coat colour and PISG. For example, the most important synapomorphy for Asparagales, first used by Huber (1969) as a unifying character in the order, is the characteristic black colour of the seeds caused by phytomelanin incrustation of the seed coat. This black substance is also common among seeds of Asteraceae (Stevens, 2001).

In Brassicaceae, seed colour seems to be related to geographical distribution through an association between high temperatures and light-coloured seed coats, with a few exceptions such as the brownish seeds of Mediterranean species (Van Deynze *et al*., 1992). If this is the case for other species, the high percentage of dark seeds may be due to the geographical distribution of photoinhibited seeds and not to the seed coat properties themselves. The above hypothesis is corroborated by results in *Arabidopsis* (Debeaujon *et al*., 2000), in which seed pigmentation mutants (less pigmented seeds) exhibit a higher capacity to germinate in darkness.

Seed germination

Plants in frost and drought conditions are more likely to have dormancy than species in milder and wetter environments (Jurado and Flores, 2005). In tropical rainforests, nondormancy is more frequent than in any other vegetation zone, and when temperate broad-leaved evergreen forests, deciduous forests, steppes, matorral and cold deserts are compared, non-dormancy decreases with a decrease of precipitation and temperature (Baskin and Baskin, 2014). The great majority of photoinhibited species included in the present study have been reported to be dormant, with only *ca* 20% of them being non-dormant (Fig. 2a). In particular, 52% of the photoinhibited species possess some degree of physiological dormancy (PD; Fig. 2a). These data are not surprising, since PD is the most common class of dormancy among seed plant species (Baskin and Baskin, 2014).

The percentage of photoinhibited species with morphophysiological dormancy (MPD) is relatively high (15%; Fig. 2a), and this is similar to the expected percentage of temperate, herbaceous species with MPD (Baskin and Baskin, 2014). A possible reason for this is that MPD is common among monocots and geophytes, which was the main photoinhibited life form in our dataset (Fig. 2b). Perhaps unexpectedly, some physically dormant (PY) species also have photoinhibited (9%) seeds. While there is emerging evidence that species with PY from fire-prone habitats show this kind of response to light (e.g. Turner *et al*., 2005), seed germination of species with PY is generally considered as neither suppressed nor promoted by the presence of light (Baskin and Baskin, 2014).

Some authors reported that PISG is stronger at higher germination temperatures (Thanos *et al*., 1989; Bell *et al*., 1995). However, the present review has not considered the possible dependence of photoinhibition on incubation temperature, i.e. promotion by light at certain temperatures and inhibition by others, in the same species and under similar light conditions (Fournaraki, 2010).

Life form and plant height

Non-woody species were the most common among the photoinhibited taxa, with most of them being geophytes (37%) followed by therophytes, i.e. annuals (19%) (Fig. 2b). These two life forms are significantly associated with arid and seasonal climates (χ^2 test of independence, $P < 0.05$). Geophytes are by far over-represented in the present study, considering that on a global scale they represent only 4% of the flora (Cain, 1950). Even in the Cape Floristic Region, the most geophyte-rich area on earth, they reach only about 23%. Also, it has been recently suggested that PISG is a common germination characteristic among geophytes from relatively dry habitats (Skourti and Thanos, 2015 and literature cited therein).

Phanerophytes (woody plants), which typically prevail in tropical semi-arid forests, are also represented in the dataset (14%), and this life form is most common in tropical semi-arid forests. A significant association between life forms and habitat types was also found (χ^2 test of independence, $P < 0.001$): with shrubs prevailing in scrubland (31%) and deserts (28%); geophytes in scrubland (40%) and grassland (25%); and annuals in ruderal (32%), maritime (22%), desert (20%) and grassland habitats (17%).

Logistic regression predicted a higher occurrence of PISG in relatively small plants (Table 2). However, Grime *et al*. (1981) detected no consistent relationship between germination in the dark and average height of seed release (i.e. plant height). Considering that plant height is also related to life form, and in relevance to the leaf-height-seed (LHS) strategy scheme proposed by Westoby (1998), further analyses are needed to confirm whether seedling establishment of

Table 2. Simple generalized linear models (GLMs, logit link function and binomial distribution) results for the effect of alternating temperature and mean temperature used in the germination experiments, plant height, seed mass, habitat light and habitat moisture on the P_i

	Estimate	SE	*z*	*P*
Testing conditions				
Alternating temperature	0.028	0.026	1.067	0.28
Mean temperature	−0.001	0.001	−0.047	0.962
Habitat traits				
Light	0.188	0.021	8.680	<0.001
Moisture	−0.021	0.022	−0.965	0.334
Plant traits				
log (plant height)	−0.253	0.009	−26.360	<0.0001
log (seed mass)	−0.048	0.005	−9.468	<0.0001

For analytical purposes, we classified the species into three categories according to habitat moisture (dry = 1; moist = 2; wet = 3) and habitat light (shaded = 1; semi-shaded = 2; open = 3).

smaller plants benefits from photoinhibition of seeds. Although an elaborate analysis of the relationship of plant height, leaf area and seed mass, under the light of photoinhibition may be promising, it is beyond the scope of this review.

Phylogeny

Gymnosperms have not been unequivocally proven to include photoinhibited taxa, despite a limited number of reports (on *Abies amabilis*, *A. lasiocarpa* and *Pinus monticola*, Li *et al*., 1994; *Tsuga mertensiana*, Edwards and El-Kassaby, 1996; *Podocarpus latifolius*, Bussmann and Lange, 2000). They are not included in the dataset because the PISG or the methodology were either not clearly explained or were dubious. Therefore, we can postulate that PISG seems to be apomorphic to flowering plants. Moreover, there are no published photoinhibition reports for the ANA grade and only few records in the Magnoliids (specifically in the Laurales), while PISG is quite widespread in eudicots and especially in monocots.

The percentages of families and genera with photoinhibited taxa, superimposed onto the phylogenetic framework, showed that the distribution of PISG across the seed plants occurs more frequently in certain lineages than others (Table 1, Fig. 3). The single most represented order is Asparagales (27%), followed by Fabales (9%), Asterales (7%), Caryophyllales (7%) and Poales (7%). The most represented families are Amaryllidaceae (9%), Fabaceae (8%), Asteraceae (7%), Iridaceae (7%), Poaceae (6%) and Asparagaceae (5%). Four of these families are monocots and three belong to Asparagales. The total number of monocot taxa is 122, or 40.5% among plants with PISG, a considerable divergence from the estimated 26.1% of monocots in the world flora (of eudicots plus monocots; Christenhusz and Byng, 2016).

Overall, PISG is clearly not monophyletic and shows a large degree of homoplasy across seed plants. Thus, this trait is shared by taxa belonging to distinct clades, due to convergence, parallelism or reversal. Consequently, while seed germination behaviour may often be inferred from embryo morphology (Baskin and Baskin, 2004) and other conservative seed morphological traits (Corner, 1976), a summarization based on shared morphological and functional seed characteristics by taxa belonging to the same lineage is not possible for PISG.

At present, the ancestral PISG state is not known. In particular, it is unclear whether PISG is ancient or a recent acquisition. Our understanding of the molecular mechanisms is incomplete, but there is evidence that, as for seed dormancy (Willis *et al*., 2014), most of the molecular pathways controlling PISG are common among seed plants. Thus, the information gained to date, suggests that PISG is likely to have evolved independently in different lineages (homoplasy).

Habitat and climate

Logistic regression revealed that P_i is strongly associated with open habitats (Table 2). Scrubland is the most represented habitat type overall (27%; Fig. 2c), mainly in Southwest Australian (75% of taxa) and Mediterranean regions (45%). However, scrublands consist primarily of a mosaic of habitats with different degree of vegetation cover. Thus, many (herbaceous) species reported as growing in scrublands could perhaps generally be defined as species growing in open habitats. In fact, grassland is the third most represented habitat category (14%) after deserts (16%). These results are not unexpected, since light-inhibited germination traditionally has been interpreted as an adaptive mechanism for plants inhabiting sandy, coastal habitats (Thanos *et al*., 1989, 1991; Bell *et al*., 1993; Delipetrou, 1996), deserts (Koller, 1956; Barbour, 1968; Gutterman, 2006) and semi-arid and open disturbed habitats (Thanos *et al*., 2005). In scrublands, grasslands and deserts (61% of taxa in our dataset), and in open and dry habitats in general (73% of taxa), water availability is limited, even temporarily, thus making germination strategies that avoid seedling desiccation, crucial for successful germination and subsequent seedling establishment in these environments. Additionally, Carta *et al*. (2014) argued that PISG coupled with epicotyl dormancy protects seedlings of *Crocus neglectus* growing in Mediterranean montane grasslands from frost damage in early winter.

Interestingly, a significant association between habitat types and plant orders has been found: deserts (Asparagales, Asterales, Caryophyllales and Cucurbitales), grasslands (Asparagales, Asterales, Boraginales, Liliales and Ranunculales), coastal dunes (Apiales, Asparagales, Asterales, Brassicales, Caryophyllales, Gentianales and Poales), ruderals (Solanales), scrubland (Asparagales, Caryophyllales, Fabales, Liliales and Myrtales), tropical woodlands (Solanales and Malpighiales) and woodlands (Asparagales and Dioscoreales).

From an ecogeographical point of view, there is a clear pattern that can be mainly attributed to climatic conditions. It is noteworthy that PISG is absent from both humid tropical and cold areas, whereas regions with seasonal and especially arid climates host the majority of photoinhibited taxa (Fig. 4). However, a bias in the distribution may be due to the low number of studies conducted outside Eurasia. We speculate that PISG became more frequent mainly in mid-latitude seasonal climates and in coincidence of palaeoclimatic events related to the Neogenic orogenesis, leading to the expansion of open habitats and the establishment of modern deserts (Patterson and Givnish, 2002). However, ancestral state reconstructions based on a worldwide phylogenetic comparative study should be encouraged to elucidate the patterns behind PISG evolution.

Presumed mechanisms

A rigorous discussion of the molecular and photomorphogenetic mechanisms that modulate PISG is beyond the scope of this review. Nevertheless, it must be noted that phytochrome has been routinely implicated in PISG although the involvement (coaction) of another photoreceptor cannot be excluded entirely (Casal and Sánchez, 1998). PISG can be described graphically by photoinhibition curves (final germination *vs* log fluence rate), which are usually linear (Thanos, 1993). Furthermore, PISG certainly belongs to the HIR class of responses as it requires long durations of irradiation (white, red, far red or blue) and depends on both fluence rate and wavelength. On the other hand, it does not show a red/far red reversibility, nor does it obey the reciprocity law. It should be stressed that, in striking contrast to other HIR, PISG inhibits – rather than promotes – a photomorphogenetic response. A possible mechanism proposed by Thanos *et al.* (1991) attributes this response to phytochrome intermediates that are trapped during seed desiccation in a form that upon seed imbibition can slowly revert to Pfr (active phytochrome) and thus eventually promote dark germination. Furthermore, a sufficiently intense, long irradiation is required to inhibit seed germination by continuously recycling phytochrome between its active and inactive forms and thus obstructing it from acting. A modern approach would probably implicate phytochrome A (light-labile, type I phytochrome) or even phytochrome C, but no relevant experimental investigation has been recently attempted.

Outlook

Although currently the survival value of PISG cannot be measured, the present study offers useful hints to understand its ecological significance. That is, PISG is a physiological adaptation to avoid germination on the soil surface, where conditions may not be suitable for seedling establishment, especially in habitats susceptible to drought (Koller, 1956; Thanos *et al.*, 1991; Bell *et al.*, 1993; Thanos *et al.*, 2005). Nevertheless, these conclusions should be treated with caution, since we have considered only the effects of light; other factors, such as temperature, may modify the responses to light considerably and should be investigated in future studies. In contrast to the strong association of PISG to aridity, certain species growing in wet habitats and temperate climates also show PISG, apparently without a clear ecological benefit. A possible explanation is that although phylogeny itself cannot be the single predictor of PISG, this dark germination might have been conserved among related species, despite the fact that it confers no obvious advantage in such habitats (phylogenetic inertia). It is suggested that evolutionary patterns, like PISG, should be further investigated, especially among monocots.

Overall, PISG is probably much more widespread in seed plants than previously thought and special attention should be paid in designing germination experiments under both dark and light conditions and, if possible, using sunlight-type, prolonged illuminations with different levels of irradiance.

Acknowledgements

We are grateful to Jerry Baskin and Hugh W. Pritchard for their valuable comments.

Financial support

The European Native Seed Conservation Network (ENSCONET) Consortium is acknowledged for financial support.

Conflicts of interest

None.

Supplementary material

To view supplementary material for this article, please visit https://doi.org/10.1017/S0960258517000137

References

Note: numbers following references in square brackets refer to Table 1.

Adair, J.A., Higgins, T.R. and Brandon, D.L. (1990) Effects of fruit burial depth and wrack on the germination and emergence of the strandline species *Cakile edentula* (Brassicaceae). *Bulletin of the Torrey Botanical Club* **117**, 138–142. [1]

Antonidaki-Giatromanolaki, A., Dragassaki, M., Papadimitriou, M. and Vlahos, I. (2008) Effects of stratification, temperature and light on seed germination of *Colchicum macrophyllum* B. L. Burtt. *Propagation of Ornamental Plants* **8**, 105–107. [2]

APG IV (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* **181**, 1–20.

Arditti, J., Michaud, J.D. and Oliva, A.P. (1981) Seed germination of North American orchids. I. Native California and related species of *Calypso*, *Epipactis*, *Goodyera*, *Piperia* and *Platanthera*. *Botanical Gazette* **142**, 442–453. [3]

Balestri, E. and Cinelli, F. (2004) Germination and early-seedling establishment capacity of *Pancratium maritimum* L. (Amaryllidaceae) on coastal dunes in the north-western Mediterranean. *Journal of Coastal Research* **20**, 761–770. [4]

Bansal, R.P. and Sen, D.N. (1978) Contribution to the ecology and seed germination of *Cucumis callosus*. *Folia Geobotanica et Phytotaxonomica* **13**, 225–233. [5]

Barbour, M.G. (1968) Germination requirements of the desert shrub *Larrea divaricata*. *Ecology* **49**, 915–923. [6]

Barbour, M.G. (1970) Germination and early growth of the strand plant *Cakile maritima*. *Bulletin of the Torrey Botanical Club* **97**, 13–22. [7]

Barrero, J.M., Jacobsen, J.V., Talbot, M.J., White, R.G., Swain, S.M., Garvin, D.F. and Gubler, F. (2012) Grain dormancy and light quality effects on germination in the model grass *Brachypodium distachyon*. *New Phytologist* **193**, 376–386. [8]

Baskin, C.C. and Baskin, J.M. (1988) Germination ecophysiology of herbaceous plant species in a temperate region. *American Journal of Botany* **75**, 286–305. [9]

Baskin, C.C. and Baskin, J.M. (1994) Deep complex morphophysiological dormancy in seeds of the mesic woodland herb *Delphinium tricorne* (Ranunculaceae). *International Journal of Plant Sciences* **155**, 738–743. [10]

Baskin, C.C. and Baskin, J.M. (2014) *Seeds: Ecology, Biogeography and Evolution of Dormancy and Germination* (2nd edition). San Diego: Elsevier/Academic Press.

Baskin, J.M. and Baskin, C.C. (1974) Some aspects of the autecology of *Bupleurum rotundifolium* in Tennessee cedar glades. *Journal of the Tennessee Academy of Science* **49**, 21–24. [11]

Baskin, J.M. and Baskin, C.C. (1979) The ecological life cycle of *Nothoscordum bivalve* in Tennessee cedar glades. *Castanea* **44**, 193–202. [12]

Baskin, J.M. and Baskin C.C. (1992) Seed germination biology of the weedy biennial *Alliaria petiolata*. *Natural Areas Journal* **12**, 191–197. [13]

Baskin, J.M. and Baskin, C.C. (2004) A classification system for seed dormancy. *Seed Science Research* **14**, 1–16.

Batanouny, K.H. and Ziegler, H. (1971) Eco-physiological studies on desert plants II. Germination of *Zygophyllum coccineum* L. seeds under different conditions. *Oecologia* **8**, 52–63. [14]

Bell, D.T. and Bellairs, S.M. (1992) Effects of temperature on the germination of selected Australian native species used in the rehabilitation of bauxite mining disturbance in Western Australia. *Seed Science and Technology* **20**, 47–55. [15]

Bell, D.T., Plummer, J.A. and Taylor, S.K. (1993) Seed germination ecology in Southwestern Western Australia. *The Botanical Review* **59**, 24–73. [16]

Bell, D.T., Rokich, D.P., McChesney, C.J. and Plummer, J.A. (1995) Effects of temperature, light and gibberellic acid on the germination of seeds of 43 species native to Western Australia. *Journal of Vegetation Science* **6**, 797–806. [17]

Bell, D.T., King, L.A. and Plummer, J.A. (1999) Ecophysiological effects of light quality and nitrate on seed germination in species from Western Australia. *Australian Journal of Ecology* **24**, 2–10. [18]

Benvenuti, S., Simonelli, G. and Macchia, M. (2001) Elevated temperature and darkness improve germination in *Passiflora incarnata* L. seed. *Seed Science and Technology* **29**, 533–541. [19]

Bewley, J.D. and Black, M. (1982) *Physiology and Biochemistry of Seeds*. Berlin: Springer-Verlag. [20]

Bond, W.J., Honig, M. and Maze, K.E. (1999) Seed size and seedling emergence: an allometric relationship and some ecological implications. *Oecologia* **120**, 132–136.

Bullowa, S., Negbi, M. and Ozeri, Y. (1975) Role of temperature, light and growth regulators in germination in *Anemone coronaria* L. *Functional Plant Biology* **2**, 91–100. [21]

Burrows, C.J. (1996) Germination behaviour of seeds of the New Zealand woody species *Melicope simplex*, *Myoporum laetum*, *Myrsine divaricata* and *Urtica ferox*. *New Zealand Journal of Botany* **34**, 205–213. [22]

Bürün, B. and Sahin, O. (2009) In vitro and in vivo germination of *Cyclamen alpinum* seeds. *Turkish Journal of Botany* **33**, 277–283. [23]

Bussmann, R.W. and Lange, S. (2000) Germination of important East African mountain forest trees. *Journal of East African Natural History* **89**, 101–111.

Cain, S.A. (1950) Life forms and phytoclimate. *The Botanical Review* **16**, 1–32.

Carpenter, W.J. and Boucher, J.F. (1992) Germination and storage of *Vinca* seed is influenced by light, temperature, and relative humidity. *HortScience* **27**, 993–996. [24]

Carta, A., Probert, R., Moretti, M., Peruzzi, L. and Bedini, G. (2014) Seed dormancy and germination in three *Crocus* ser. *Verni* species (Iridaceae): implications for evolution of dormancy within the genus. *Plant Biology* **16**, 1065–1074. [25]

Casal, J.J. and Sánchez, R.A. (1998) Phytochromes and seed germination. *Seed Science Research* **8**, 317–329.

Chen, S.S.C. (1968) Germination of light-inhibited seed of *Nemophila insignis*. *American Journal of Botany* **55**, 1177–1183. [26]

Chen, S.S.C. and Thimann, K.V. (1966) Nature of seed dormancy in *Phacelia tanacetifolia*. *Science* **153**, 1537–1539. [27]

Chen, Z.H. and Zhang, D.M. (1999) Seed germination and seedling growth of 24 tree species in lower subtropical forest. *Journal of Tropical and Subtropical Botany* **7**, 37–46. [28]

Christenhusz, M.J.M. and Byng, J.W. (2016) The number of known plants species in the world and its annual increase. *Phytotaxa* **261**, 201–217.

Cirak, C., Kevseroğlu, K. and Sağlam, B. (2004) Physical and physiological dormancy in black henbane (*Hyoscyamus niger* L.) seeds. *Journal of Plant Biology* **47**, 391–395. [29]

Clark, D.C. and Bass, L.N. (1970) Germination experiments with seeds of Indian ricegrass, *Oryzopsis hymenoides* (Roem. and Schult.) Ricker. *Proceedings of the Association of Official Seed Analysts of North America* **60**, 226–239. [30]

Clarke, P.J., Davison, E.A. and Fulloon, L. (2000) Germination and dormancy of grassy woodland and forest species: effects of smoke, heat, darkness and cold. *Australian Journal of Botany* **48**, 687–699. [31]

Conner, A.J. and Conner, L.N. (1988) Germination and dormancy of *Arthropodium cirratum* seeds. *New Zealand Natural Sciences* **15**, 3–10. [32]

Copete, E., Herranz, J.M., Copete, M.A., Baskin, J.M. and Baskin, C.C. (2011) Non-deep complex morphophysiological dormancy in seeds of the Iberian Peninsula endemic geophyte *Merendera montana* (Colchicaceae). *Seed Science Research* **21**, 267–281. [33]

Copete, E., Herranz, J.M., Copete, M.Á. and Ferrandis, P. (2014) Interpopulation variability on embryo growth, seed dormancy break, and germination in the endangered Iberian daffodil *Narcissus eugeniae* (Amaryllidaceae). *Plant Species Biology* **29**, 72–84. [34]

Corbineau, F., and Côme, D. (1982) Effect of the intensity and duration of light at various temperatures on the germination of *Oldenlandia corymbosa* L. seeds. *Plant Physiology* **70**, 1518–1520.

Corner, E.J.H. (1976) *The Seeds of Dicotyledons*, vol. 2. Cambridge: Cambridge University Press.

CRETAPLANT (2007) CRETAPLANT: A Pilot Network of Plant Micro-Reserves in Western Crete. Action D.2: Ex situ conservation. [35]

Cruden, R.W. (1974) The adaptive nature of seed germination in *Nemophila menziesii* Aggr. *Ecology* **55**, 1295–1305. [36]

Dalling, K.J. and Van Staden, J. (1999) Germination requirements of *Combretum bracteosum* seeds. *South African Journal of Botany* **65**, 83–85. [37]

Daskalakou, E.N. and Thanos, C.A. (1995) Mechanisms of seed germination in *Consolida ajacis*. Abstracts of Poster Presentations, Fifth International Workshop on Seeds, Reading, UK. [38]

Datta, S.C. and Sinha-Roy, S.P. (1975) Germination-regulating mechanisms in aquatic angiosperms. II. *Aeschynomene aspera* L. *Broteria* **44**, 81–91. [39]

Daws, M.I., Gamene, C.S., Glidewel, S.M. and Pritchard, H. W. (2004) Seed mass variation potentially masks a single critical water content in recalcitrant seeds. *Seed Science Research* **14**, 185–195.

Daws, M.I., Crabtree, L.M., Dalling, J.W., Mullins, C.E. and Burslem, D.F.R.P. (2008) Germination responses to water potential in neotropical pioneers suggest large-seeded species take more risks. *Annals of Botany* **102**, 945–951.

de Villiers, M.A.J., van Rooyen, M.W. and Theron, G.K. (2002a) Germination strategies of Strandveld Succulent Karoo plant species for revegetation purposes: I. Temperature and light requirements. *Seed Science and Technology* **30**, 17–33. [40]

de Villiers, M.A.J., van Rooyen, M.W. and Theron, G.K. (2002b) Germination strategies of Strandveld Succulent Karoo plant species for revegetation purposes: II. Dormancy-breaking treatments. *Seed Science and Technology* **30**, 35–49. [41]

De Vitis, M., Seal, C.E., Ulian, T., Pritchard, H.W., Magrini, S., Fabrini, G. and Mattana, E. (2014) Rapid adaptation of seed germination requirements of the threatened Mediterranean species *Malcolmia littorea* (Brassicaceae) and implications for its reintroduction. *South African Journal of Botany* **94**, 46–50. [42]

Debeaujon, I., Leon-Kloosterziel, K.M. and Koornneef, M. (2000) Influence of the testa on seed dormancy, germination, and longevity in *Arabidopsis*. *Plant Physiology* **122**, 403–413.

Del Vecchio, S., Mattana, E., Acosta, A.T. and Bacchetta, G. (2012) Seed germination responses to varying environmental conditions and provenances in *Crucianella maritima* L., a threatened coastal species. *Comptes Rendus Biologies* **335**, 26–31. [43]

Delipetrou, P. (1996) Ecophysiology of seed germination in maritime plants with emphasis on the action of light. PhD thesis, University of Athens, Greece [in Greek]. [44]

Dias, L.A.S., Kagheyama, P.Y. and Issiki, K. (1992) Qualidade de luz e germinacao de sementes de especies arboreas tropicais. *Acta Amazonica* **22**, 79–84. [45]

Doğan, Y., Başlar, S. and Mert, H.H. (2002) A study on *Reseda lutea* L. distributed naturally in West Anatolia in Turkey. *Acta Botanica Croatica* **61**, 35–43. [46]

Doussi, M.A. and Thanos, C.A. (2002) Ecophysiology of seed germination in Mediterranean geophytes. *1. Muscari* spp. *Seed Science Research* **12**, 193–201. [47]

Dreesen, D.R. and Harrington, J.T. (1997) Propagation of native plants for restoration projects in the southwestern U.S. – preliminary investigations, pp. 77–88 *in* Landis, T. D. and Thompson, J.R. (eds), *National Proceedings, Forest and Conservation Nursery Associations*. Portland: Pacific Northwest Research Station. [48]

Dumbroff, E.B. and Webb, D.P. (1970) Factors influencing the stratification process in seeds of *Acer ginnala*. *Canadian Journal of Botany* **48**, 2009–2015. [49]

Dutra, D., Johnson, T.R., Kauth, P.J., Stewart, S.L., Kane, M. E. and Richardson, L. (2008) Asymbiotic seed germination, in vitro seedling development, and greenhouse acclimatization of the threatened terrestrial orchid *Bletia purpurea*. *Plant Cell, Tissue and Organ Culture* **94**, 11–21.

Dutra, D., Kane, M.E. and Richardson, L. (2009) Asymbiotic seed germination and in vitro seedling development of *Cyrtopodium punctatum*: a propagation protocol for an endangered Florida native orchid. *Plant Cell, Tissue and Organ Culture* **96**, 235–243. [50]

Edwards, D.G.W. and El-Kassaby, Y.A. (1996) The effect of stratification and artificial light on the germination of mountain hemlock seeds. *Seed Science and Technology* **24**, 225–236.

Ellis, R.H., Hong, T.D. and Roberts, E.H. (1986) The response of seeds of *Bromus sterilis* L. and *Bromus mollis* L. to white light of varying photon flux density and photoperiod. *New Phytologist* **104**, 485–496. [51]

Estrelles, E., Ferrando, I. and Ibars, A.M. (2004) *Galanthus nivalis* L.: germination requirements for a west Mediterranean population. Fourth European Conference on the Conservation of Wild Plants. A workshop on the implementation of the global strategy for plant conservation in Europe. Valencia, Spain, 17–20 September 2004. [52]

Felippe, G. M. and Polo, M. (1983) Germinação de ervas invasoras: efeito de luz e escarificação. *Revista Brasileira de Botânica* **6**, 55–60. [53]

Fenner, M. and Thompson, K. (2005) *The Ecology of Seeds*. Cambridge: Cambridge University Press.

Ferreira, A.G., Cassol, B., Rosa, S.G.T.D., Silveira, T.S.D., Stival, A.L. and Silva, A.A. (2001) Germination of seeds of Asteraceae natives of Rio Grande do Sul, Brazil. *Acta Botanica Brasilica* **15**, 231–242. [54]

Flora of China Editorial Committee (1994+) Flora of China. http://www.efloras.org

Flora of North America Editorial Committee (1993+). Flora of North America. http://www.efloras.org

Forbis, T.A. (2010) Germination phenology of some Great Basin native annual forb species. *Plant Species Biology* **25**, 221–230. [55]

Fournaraki, C. (2010) Conservation of threatened plants of Crete: seed ecology, operation and management of a gene bank. PhD thesis, University of Athens, Greece [in Greek]. [56]

French, R.C. and Sherman, L.J. (1976) Factors affecting dormancy, germination, and seedling development of *Aeginetia indica* L. (Orobanchaceae). *American Journal of Botany* **63**, 558–570. [57]

Fulbright, T.E., Redente, E.F. and Wilson, A.M. (1983) Germination requirements of green needlegrass (*Stipa viridula* Trin.). *Journal of Range Management* **36**, 390–394. [58]

Garcia, Q.S. (1999) Germination ecology of *Jacquinia brasiliensis*, an endemic species of the Brazilian 'restinga', in relation to salinity. *Tropical Ecology* **40**, 207–212. [59]

Garcia, Q.S. and Lucas, N.M.C. (1994) Germinative behaviour of *Jacquinia brasiliensis* seeds. *Revista Brasileira de Botânica* **17**, 13–18. [60]

Georghiou, K., Thanos, C.A., Tafas, T.P. and Mitrakos, K. (1982) Tomato seed germination. Osmotic pretreatment and far red inhibition. *Journal of Experimental Botany* **33**, 1068–1075. [61]

Goldthwaite, J.J., Bristol, J.C., Gentile, A.C. and Klein, R.M. (1971) Light-suppressed germination of California poppy seed. *Canadian Journal of Botany* **49**, 1655–1659. [62]

Górski, T. and Górska, K. (1979) Inhibitory effects of full daylight on the germination of *Lactuca sativa* L. *Planta* **144**, 121–124. [63]

Greipsson, S. and Davy, A.J. (1994) Germination of *Leymus arenarius* and its significance for land reclamation in Iceland. *Annals of Botany* **73**, 393–401. [64]

Greipsson, S. and Davy, A.J. (1996) Aspects of seed germination in the dune-building grass *Leymus arenarius*. *Buvisindi* **10**, 209–217. [65]

Grime, J.P., Mason, G., Curtis, A.A., Rodman, J., Band, S.R., Mowforth, M.A.G., Neal, A.M. and Shaw, S. (1981) A comparative study of germination characteristics in a local flora. *Journal of Ecology* **69**, 1017–1059.

Gutterman, Y. (1996) Effect of day length during plant development and caryopsis maturation on flowering and germination, in addition to temperature during dry storage and light during wetting, of *Schismus arabicus* (Poaceae) in the Negev Desert, Israel. *Journal of Arid Environments* **33**, 439–448. [66]

Gutterman, Y. (2006) Deserts and arid lands, pp. 122–127 *in* Black, M., Bewley, J.D. and Halmer, P. (eds), *The Encyclopedia of Seeds: Science, Technology and Uses*. Wallingford: CAB International.

Gutterman, Y., Kamenetsky, R. and Van Rooyen, M. (1995) A comparative study of seed germination of two *Allium* species from different habitats in the Negev Desert highlands. *Journal of Arid Environments* **29**, 305–315. [67]

Hammouda, M.A. and Bakr, Z.Y. (1969) Some aspects of germination of desert seeds. *Phyton* (*Austria*) **13**, 183–201. [68]

Hamze, S.I. and Jolls, C.L. (2000) Germination ecology of a federally threatened endemic thistle, *Cirsium pitcheri*, of the Great Lakes. *The American Midland Naturalist* **143**, 141–153. [69]

Harty, R.L. and McDonald, T.J. (1972) Germination behaviour in beach spinifex (*Spinifex hirsutus* Labill.). *Australian Journal of Botany* **20**, 241–251. [70]

Harvais, G. and Hadley, G. (1967) The development of *Orchis purpurella* in asymbiotic and inoculated cultures. *New Phytologist* **66**, 217–230. [71]

Hawkins, T.S., Walck, J.L. and Hidayati, S.N. (2011) Seed ecology of *Lindera melissifolia* (Lauraceae) as it relates to rarity of the species 1. *The Journal of the Torrey Botanical Society* **138**, 298–307. [72]

Heinricher, E. (1903) Notwendigkeit des Lichtes und befordernde Wirkung desselben bei der Samenkeimung. *Beihefte zum Botanischen Centralblatt* **13**, 164–172.

Herranz, J.M., Ferrandis, P. and Martínez-Duro, E. (2010) Seed germination ecology of the threatened endemic Iberian *Delphinium fissum* subsp. *sordidum* (Ranunculaceae). *Plant Ecology* **211**, 89–106. [73]

Herranz, J.M., Copete, M.A. and Ferrandis, P. (2013) Environmental regulation of embryo growth, dormancy breaking and germination in *Narcissus alcaracensis* (Amaryllidaceae), a threatened endemic Iberian daffodil. *The American Midland Naturalist* **169**, 147–167. [74]

Herranz, J.M., Copete, E. and Ferrandis, P. (2013) Non-deep complex morphophysiological dormancy in *Narcissus longispathus* (Amaryllidaceae): implications for evolution of dormancy levels within section *Pseudonarcissi*. *Seed Science Research* **23**, 141–155. [75]

Herrranz Sanz, J.M.H., Carreño, E.C., Carreño, M.Á.C. and Gotor, P.F. (2015) Germination ecology of the endemic Iberian daffodil *Narcissus radinganorum* (Amaryllidaceae). Dormancy induction by cold stratification or desiccation in late stages of embryo growth. *Forest Systems* **24**, e-013. [76]

Hilton, J.R. (1982) An unusual effect of the far-red absorbing form of phytochrome: Photoinhibition of seed germination in *Bromus sterilis* L. *Planta* **155**, 524–528. [77]

Huber, H. (1969) Die Samenmerkmale und Verwandtschaftsverhaltnisse der Liliifloren. *Mitteilungen der Botanischen Staatssammlung München* **8**, 219–538.

Jankowska-Blaszczuk, M. and Daws, M.I. (2007) Impact of red:far red ratios on germination of temperate forest herbs in relation to shade tolerance, seed mass and persistence in the soil. *Functional Ecology* **21**, 1055–1062.

Johnston, B., Olivares, E., Henríquez, C. and Fernandez, H. (1997) Factores abióticos en la germinación de terófitas de interés forrajero. *Phyton* (*Buenos Aires*) **60**, 63–71. [78]

Joly, C.A. and Felippe, G.M. (1979) Germinação e fenologia de *Zeyhera digitalis* (Vell.) Hoehne. *Hoehnea* **8**, 35–40. [79]

Jones, M.B. and Bailey, L.F. (1956) Light effects on the germination of seeds of henbit (*Lamium amplexicaule* L.). *Plant Physiology* **31**, 347–349. [80]

Jurado, E. and Flores, J. (2005) Is seed dormancy under environmental control or bound to plant traits? *Journal of Vegetation Science* **16**, 559–564.

Kadis, C.C. (1995) Reproductive biology of the strictly protected plants of Cyprus. PhD thesis, University of Athens, Greece [in Greek]. [81]

Kadis, C.C. and Georghiou, K. (1992) The germination physiology of the endangered plants of Cyprus, *Alyssum akamasicum* and *Origanum cordifolium*. p. 461 *in* Côme, D. and Corbineau, F. (eds), Book of abstracts from the 4th International Workshop on Seeds. Angers, France. [82]

Kamenetsky, R. and Gutterman, Y. (2000) Germination strategies of some *Allium* species of the subgenus *Melanocrommyum* from arid zone of Central Asia. *Journal of Arid Environments* **45**, 61–71. [83]

Keeley, J.E. and Bond, W.J. (1997) Convergent seed germination in South African fynbos and Californian chaparral. *Plant Ecology* **133**, 153–167. [84]

Keith, D.A. (1997) Combined effects of heat shock, smoke and darkness on germination of *Epacris stuartii* Stapf., an endangered fire-prone Australian shrub. *Oecologia* **112**, 340–344. [85]

Kendrick, R.E. and Frankland, B. (1969) Photocontrol of germination in *Amaranthus caudatus*. *Planta* **85**, 326–339. [86]

Khan, M.A. and Ungar, I.A. (1997) Effects of light, salinity, and thermoperiod on the seed germination of halophytes. *Canadian Journal of Botany* **75**, 835–841. [87]

Kier, G., Mutke, J., Dinerstein, E., Ricketts, T.H., Küper, W., Kreft, H. and Barthlott, W. (2005) Global patterns of plant diversity and floristic knowledge. *Journal of Biogeography* **32**, 1107–1116.

Kinzel, W. (1913–1926) *Frost und Licht als beeinflussende Kräfte bei der Samenkeimung*. 1st edition 1913, 2nd edition 1915, 3rd edition 1920, 4th edition 1926. Stuttgart: Ulmer.

Koller, D. (1955) Germination regulating mechanisms in some desert seeds. II. *Zygophyllum dumosum* Boiss. *Bulletin of the Research Council of Israel* **4**, 381–387. [88]

Koller, D. (1956) Germination regulating mechanisms in some desert seeds. III. *Calligonum comosum* L'Her. *Ecology* **37**, 430–433. [89]

Koller, D. (1957) Germination-regulating mechanisms in some desert seeds. IV. *Atriplex dimorphostegia* Kar. et Kir. *Ecology* **38**, 2–13. [90]

Koller, D., Poljakoff-Mayber, A., Berg, A. and Diskin, T. (1963) Germination-regulating mechanisms in *Citrullus colocynthis*. *American Journal of Botany* **50**, 597–603. [91]

Koller, D., Sachs, M. and Negbi, M. (1964) Spectral sensitivity of seed germination in *Artemisia monosperma*. *Plant and Cell Physiology* **5**, 79–84.

Kondo, T., Mikubo, M., Yamada, K., Walck, J.L. and Hidayati, S.N. (2011) Seed dormancy in *Trillium camschatcense* (Melanthiaceae) and the possible roles of light and temperature requirements for seed germination in forests. *American Journal of Botany* **98**, 215–226. [92]

Kondo, T., Narita, M., Phartyal, S.S., Hidayati, S.N., Walck, J.L., Baskin, J.M. and Baskin, C.C. (2015) Morphophysiological dormancy in seeds of *Convallaria keiskei* and a proposal to recognize two types of double dormancy in seed dormancy classification. *Seed Science Research* **25**, 210–220. [93]

Kosiński, I. (2008) Long-term variability in seed size and seedling establishment of *Maianthemum bifolium*. *Plant Ecology* **194**, 149–156. [94]

Kulkarni, M.G., Sparg, S.G., Van Staden, J. and Berjak, P. (2005) Seed germination of valuable high-altitude medicinal plants of southern Africa. *South African Journal of Botany* **71**, 173–178. [95]

Kulkarni, M.G., Sparg, S.G. and Van Staden, J. (2006) Dark conditioning, cold stratification and a smoke-derived compound enhance the germination of *Eucomis autumnalis* subsp. *autumnalis* seeds. *South African Journal of Botany* **72**, 157–162. [96]

Kullmann, W.H. (1982) *Seed Germination Records of Western Australian Plants*. West Perth: Kings Park and Botanic Garden. [97]

Kumar, L.S.S. and Solomon, S. (1940) The influence of light on the germination of species of *Striga*. *Current Science* **9**, 541. [98]

Lai, L., Chen, L., Jiang, L., Zhou, J., Zheng, Y. and Shimizu, H. (2016) Seed germination of seven desert plants and implications for vegetation restoration. *AoB Plants* **8**, plw031. [99]

Leishman, M.R., Wright, I.J., Moles, A.T. and Westoby, M. (2000) The evolutionary ecology of seed size, pp. 31–57 *in* Fenner, M. (ed), *Seeds: the Ecology of Regeneration in Plant Communities*. Wallingford: CAB International.

Lesica, P. (1992) Autecology of the endangered plant *Howellia aquatilis*; implications for management and reserve design. *Ecological Applications* **2**, 411–421. [100]

Li, X.J., Burton, P.J., and Leadem, C.L. (1994) Interactive effects of light and stratification on the germination of some British Columbia conifers. *Canadian Journal of Botany* **72**, 1635–1646.

Lopez, J., Devesa, J.A., Ruiz, T. and Ortega-Olivencia, A. (1999) Seed germination in *Genisteae* (Fabaceae) from south-west Spain. *Phyton* (*Austria*) **39**, 107–129. [101]

Lorenzi, H. (1998) *Arvores Brasileiras: Manual de Identificacao e Cultivo de Plantas Arboreas Nativas do Brasil*, vol. 1. Instituto Plantarum de Estudos da Flora, Nova Odessa, Sao Paulo. [102]

Malik, N. and Vanden Born, W.H. (1987) Germination response of *Galium spurium* L. to light. *Weed Research* **27**, 251–258. [103]

Mamut, J., Tan, D.Y., Baskin, C.C. and Baskin, J.M. (2014) Intermediate complex morphophysiological dormancy in seeds of the cold desert sand dune geophyte *Eremurus anisopterus* (Xanthorrhoeaceae; Liliaceae s.l.). *Annals of Botany* **114**, 991–999. [104]

Marques, I. and Draper, D. (2012) Seed germination and longevity of autumn-flowering and autumn-seed producing Mediterranean geophytes. *Seed Science Research* **22**, 299–309. [105]

Mattana, E., Daws, M.I. and Bacchetta, G. (2010) Comparative germination ecology of the endemic *Centranthus amazonum* (Valerianaceae) and its widespread congener *Centranthus ruber*. *Plant Species Biology* **25**, 165–172. [106]

Maun, M.A. and Payne, A.M. (1989) Fruit and seed polymorphism and its relation to seedling growth in the genus *Cakile*. *Canadian Journal of Botany* **67**, 2743–2750. [107]

Maun, M.A., Boyd, R.S. and Olson, L. (1990) The biological flora of coastal dunes and wetlands. 1. *Cakile edentula* (Bigel.) Hook. *Journal of Coastal Research* **6**, 137–156. [108]

Maze, K.M. and Whalley, R.D.B. (1992) Germination, seedling occurrence and seedling survival of *Spinifex sericeus* R. Br. (Poaceae). *Australian Journal of Ecology* **17**, 189–194. [109]

McDonough, W.T. (1967) Dormant and non-dormant seeds: similar germination responses when osmotically inhibited. *Nature* **214**, 1147–1148. [110]

Medeiros Filho, S., França, E.A.D. and Innecco, R. (2002) Seeds germination of *Operculina macrocarpa* (L.) Farwel and *Operculina alata* (Ham.) Urban. *Revista Brasileira de Sementes* **24**, 102–107. [111]

Milberg, P. (1994) Germination ecology of the endangered grassland biennial *Gentianella campestris*. *Biological Conservation* **70**, 287–290. [112]

Milberg, P., Andersson, L. and Thompson, K. (2000) Large-seeded spices are less dependent on light for germination than small-seeded ones. *Seed Science Research* **10**, 99–104. [113]

Mitchell, E. (1926) Germination of seeds of plants native to Dutchess County, New York. *Botanical Gazette* **81**, 108–112. [114]

Mollard, F.P.O. and Naeth, M.A. (2014) Photoinhibition of germination in grass seed – implications for prairie revegetation. *Journal of Environmental Management* **142**, 1–9. [115]

Moyo, M., Kulkarni, M.G., Finnie, J.F. and Van Staden, J. (2009) After-ripening, light conditions, and cold stratification influence germination of marula [*Sclerocarya birrea* (A. Rich.) Hochst. subsp. *caffra* (Sond.) Kokwaro] seeds. *HortScience* **44**, 119–124. [116]

Nakamura, S., Okasako, Y. and Yamada, E. (1955) Effect of light on the germination of vegetable seeds. *Engei References Gakkai Zasshi* **24**, 17–28 [in Japanese]. [117]

Navarro, L. and Guitian, J. (2003) Seed germination and seedling survival of two threatened endemic species of the northwest Iberian Peninsula. *Biological Conservation* **109**, 313–320. [118]

Neveur, N., Corbineau, F. and Côme, D. (1986) Some characteristics of *Cyclamen persicum* L. seed germination. *Journal of Horticultural Science* **61**, 379–387. [119]

Newton, R.J., Hay, F.R. and Ellis, R.H. (2015) Ecophysiology of seed dormancy and the control of germination in early spring-flowering *Galanthus nivalis* and *Narcissus pseudonarcissus* (Amaryllidaceae). *Botanical Journal of the Linnean Society* **177**, 246–262. [120]

Noronha, A., Vicente, M. and Felippe, G.M. (1978) Photocontrol of germination of *Cucumis anguria* L. *Biologia Plantarum* **20**, 281–286. [121]

Ochuodho, J.O. and Modi, A.T. (2007) Light-induced transient dormancy in *Cleome gynandra* L. seeds. *African Journal of Agricultural Research* **2**, 587–591. [122]

Okagami, N. and Kawai, M. (1982) Dormancy in *Dioscorea*: differences of temperature responses in seed germination among six Japanese species. *Botanical Magazine Tokyo* **95**, 155–166. [123]

Okusanya, O.T. (1979) An experimental investigation into the ecology of some maritime cliff species: II. Germination studies. *Journal of Ecology* **67**, 293–304. [124]

Oliva, A.P., and Arditti, J. (1984) Seed germination of North American orchids. II. Native California and related species of *Aplectrum*, *Cypripedium*, and *Spiranthes. Botanical Gazette* **145**, 495–501.

Oliver, L.R., Harrison, S.A. and McClelland, M. (1983) Germination of Texas gourd (*Cucurbita texana*) and its control in soybeans (*Glycine max*). *Weed Science* **31**, 700–706. [125]

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. and Kassem, K.R. (2001) Terrestrial ecoregions of the world: a new map of life on Earth. *Bioscience* **51**, 933–938.

Pamukov, K. and Schneider, M.J. (1978) Light inhibition of *Nigella* germination: the dependence of a high irradiance reaction on 720-nm irradiance. *Botanical Gazette* **139**, 56–59. [126]

Patterson, T.B. and Givnish, T.J. (2002) Phylogeny, concerted convergence, and phylogenetic niche conservatism in the core Liliales: insights from rbcL and ndhF sequence data. *Evolution* **56**, 233–252.

Pearson, T.R.H., Burslem, D.F.R.P., Mullins, C.E. and Dalling, J.W. (2002) Germination ecology of Neotropical Pioneers: interacting effects of environmental conditions and seed size. *Ecology* **83**, 2798–2807.

Pimenta, M.R., Fernandes, L.S., Pereira, U.J., Garcia, L.S., Leal, S.R., Leitão, S.G., Salimena, F.R.G., Viccini, L.F. and Peixoto, P.H.P. (2007) Floração, germinação e estaquia em espécies de *Lippia* L. (Verbenaceae). *Brazilian Journal of Botany* **30**, 211–220. [127]

Pirovano, L., Morgutti, S., Espen, L. and Cocucci, S.M. (1996) Differences in transcription products and in translation and enzymatic activities during the early stages of imbibition of *Phacelia tanacetifolia* seeds with germination inhibited by light. *Physiologia Plantarum* **96**, 714–721. [128]

Pirovano, L., Morgutti, S., Espen, L. and Cocucci, S.M. (1997) Differences in the reactivation process in thermosensitive seeds of *Phacelia tanacetifolia* with germination inhibited by high temperature (30°C). *Physiologia Plantarum* **99**, 211–220. [129]

Pons, T.L. (2000) Seed responses to light, pp. 237–260 *in* Fenner, M. (ed), *Seeds: the Ecology of Regeneration in Plant Communities* (2nd edition). Wallingford: CAB International.

Pritchard, H.W. and Manger, K.R. (1990) Quantal response of fruit and seed germination rate in *Quercus robur* L. and *Castanea sativa* Mill, to constant temperatures and photon dose. *Journal of Experimental Botany* **41**, 1549–1557. [185]

Pritchard, H.W., Wood, J.A. and Manger, K.R. (1993) Influence of temperature on seed germination and the nutritional requirements for embryo growth in *Arum maculatum* L. *New Phytologist* **123**, 801–809. [130]

Pritchard, H.W., Daws, M.I., Fletcher, B.J., Gamene, C.S., Msanga, H.P. and Omondi, W. (2004) Ecological correlates of seed desiccation tolerance in tropical African dryland trees. *American Journal of Botany* **91**, 863–870. [131]

Pujol, B., Gigot, G., Laurent, G., Pinheiro-Kluppel, M., Elias, M., Hossaert-McKey, M. and McKey, D. (2002) Germination ecology of cassava (*Manihot esculenta* Crantz, Euphorbiaceae) in traditional agroecosystems: seed and seedling biology of a vegetatively propagated domesticated plant. *Economic Botany* **56**, 366–379. [132]

R Development Core Team. (2015) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.R project.org/

Rangaswamy, N.S. and Rangan, T.S. (1966) Effects of seed germination-stimulants on the witch-weed *Striga euphrasioides* (Vahl) Benth. *Nature* **210**, 440–441. [133]

Remer, W. (1904) Der Einfluss des Lichtes auf die Keimung bei *Phacelia tanacetifolia* Benth. *Berichte der Deutschen Botanischen Gesellschaft* **22**, 328–339.

Rivera, R.L. and Freeman, C.E. (1979) The effects of some alternating temperatures on germination of creosote bush (*Larrea tridentata* [D.C.] Cov.: Zygophyllaceae). *The Southwestern Naturalist* **24**, 683–714. [134]

Rollin, M.P. (1958) Action qualitative de la lumiere sur la germination des graines de *Phacelia tanacetifolia*. *Comptes rendus de l'Académie des Sciences* **247**, 1484–1487. [135]

Rollin, P. and Maignan, G. (1967) Phytochrome and the photoinhibition of germination. *Nature* **214**, 741–742. [136]

Ronnenberg, K., Wesche, K., Pietsch, M. and Hensen, I. (2007) Seed germination of five mountain steppe species of Central Asia. *Journal of Arid Environments* **71**, 404–410. [137]

Rosa, S.G.T. and Ferreira, A.G. (1997) Germination of medicinal plant: *Smilax campestris* Griseb. (Salsaparrilha). *Acta Horticulturae* **502**, 105–112. [138]

Roy, M., Gonneau, C., Rocheteau, A., Berveiller, D., Thomas, J.-C., Damesin, C. and Selosse, M.-A. (2013) Why do mixotrophic plants stay green? A comparison between green and achlorophyllous orchid individuals in situ. *Ecological Monographs* **83**, 95–117.

Royal Botanic Gardens Kew (2016) Seed Information Database (SID). Version 7.1. Available from: http://data.kew.org/sid/ (accessed April 2016).

Sacheti, U. (1998) Germination responses of some coastal dune plants of SE Australia. *Journal of Tropical Ecology* **39**, 243–253. [139]

Santo, A., Mattana, E., Frigau, L. and Bacchetta, G. (2014) Light, temperature, dry after-ripening and salt stress effects on seed germination of *Phleum sardoum* (Hackel) Hackel. *Plant Species Biology* **29**, 300–305. [140]

Santo, A., Mattana, E., and Bacchetta, G. (2015) Inter- and intra-specific variability in seed dormancy loss and germination requirements in the *Lavatera triloba* aggregate (Malvaceae). *Plant Ecology and Evolution* **148**, 100–110. [141]

Santos, C.M.R., Ferreira, A.G. and Aquilla, M.E.A. (2004) Caracteristicas de frutos e germinacao de sementes de seis especies de Myrtaceae nativas do Rio Grande do Sul. *Ciência Florestal* **14**, 13–20. [142]

Schütz, W. and Rave, G. (1999) The effect of cold stratification and light on the seed germination of temperate sedges (*Carex*) from various habitats and implications for regenerative strategies. *Plant Ecology* **144**, 215–230. [143]

Schütz, W., Milberg, P. and Lamont, B.B. (2002) Seed dormancy, after-ripening and light requirements of four annual Asteraceae in south-western Australia. *Annals of Botany* **90**, 707–714. [144]

Schwienbacher, E., Navarro-Cano, J.A., Neuner, G. and Erschbamer, B. (2011) Seed dormancy in alpine species. *Flora* **206**, 845–856. [145]

Semclimed (2006) *Prácticas de germinación en los bancos de semillas de la red GENMEDOC*. Electronic publication by the network Semclimed: www.reteribes.it/scaricatore.asp?c=x6bg4twnvd8pkgtz86asquvz7 [146]

Sen, D.N. (1968) Ecology of desert plants and observations on their seedlings. II. Germination behaviour of seeds in Asclepiadaceae. *Plant Systematics and Evolution* **115**, 18–27. [147]

Sheikh, K.H. and Mahmood, K. (1986) Some studies on field distribution and seed germination of *Suaeda fruticosa* and *Sporobolus arabicus* with reference to salinity and sodicity of the medium. *Plant and Soil* **94**, 333–340. [148]

Shimono, Y. and Kudo, G. (2005) Comparisons of germination traits of alpine plants between fellfield and snowbed habitats. *Ecological Research* **20**, 189–197. [149]

Shtein, I., Noy-Porat, T. and Eshel, A. (2014) Effects of light, temperature and nitrogen on *Scilla hyacinthoides* germination and seedling development. *Seed Science and Technology* **42**, 113–125. [150]

Silva, A.D. and Aguiar, I.D. (1998) Germinação de sementes de canela-preta (*Ocotea catharinensis* Mez-Lauraceae) sob diferentes condições de luz e temperatura. *Revista do Instituto Florestal* **10**, 17–22. [151]

Skourti, E. and Thanos, C.A. (2015) Seed afterripening and germination photoinhibition in the genus *Crocus* (Iridaceae). *Seed Science Research* **25**, 306–320. [152]

Skourti, E., Delipetrou, P. and Georgiou, K. (2009) Contribution to the study of the role of light in the germination of the seeds of endemic or threatened maritime plants, p. 153 *in* Doussi, M. and Thanos, C.A. (eds), Book of Abstracts from the 11th Panhellenic Scientific Conference of the Hellenic Botanical Society. Athens, University of Athens. [153]

Slade, E.A. and Causton, D.R. (1979) The germination of some woodland herbaceous species under laboratory conditions: a multifactorial study. *New Phytologist* **83**, 549–557. [154]

Smith, A.L. (1972) Factors influencing germination of *Scolochloa festucacea* caryopses. *Canadian Journal of Botany* **50**, 2085–2092. [155]

Spessard, L.L. (1988) Seed-germination studies of *Psoralea esculenta* Pursh (Indian turnip) and *Psoralea argophylla* Pursh (silver scurfpea). *Transactions of the Nebraska Academy of Sciences* **16**, 123–126. [156]

Stahnke, A., Hayes, M., Meyer, K., Witt, K., Weideman, J., Fernando, A.P., Burrows, R. and Reese, R.N. (2008) Prairie turnip *Pediomelum esculentum* (Pursh) Rydb., historical and modern use, propagation, and management of a new crop. *Native Plants Journal* **9**, 47–58. [157]

Stefanello, R., Garcia, D.C., Menezes, N.D., Muniz, M.F.B. and Wrasse, C.F. (2006) Efeito da luz, temperatura e estresse hídrico no potencial fisiológico de sementes de funcho. *Revista Brasileira de Sementes* **28**, 135–141. [158]

Stevens, P.F. (2001 onwards) Angiosperm Phylogeny Website. Version 12, July 2012 [and more or less continuously updated since].

Suñé, A.D. and Franke, L.B. (2006) Superação de dormência e metodologias para testes de germinação em sementes de *Trifolium riograndense* Burkart e *Desmanthus depressus* Humb. *Revista Brasileira de Sementes* **28**, 29–36. [159]

Takagi, K., Okazawa, A., Wada, Y., Mongkolchaiyaphruek, A., Fukusaki, E., Yoneyama, K., Takeuchi, Y. and Kobayashi, A. (2009) Unique phytochrome responses of the holoparasitic plant *Orobanche minor*. *New Phytologist* **182**, 965–974. [160]

Takhtajan, A. (1986) *Floristic Regions of the World*. Berkeley: University of California Press.

Taylorson, R.B. (1991) Inhibition of the germination in *Amaranthus albus* seeds by prolonged irradiation: a physiological basis. *Seed Science Research* **1**, 51–56. [161]

Tester, M. and Morris, C. (1987) The penetration of light through soil. *Plant, Cell and Environment* **10**, 281–286.

Thanos, C.A. (1993) Germination and the high irradiance reaction, pp. 187–190 *in* Hendry, G.A.F. and Grime, J.P. (eds), *Methods in Comparative Plant Ecology. A Laboratory Manual*. London: Chapman and Hall.

Thanos, C.A. and Mitrakos, K. (1992) Walermelon seed germination. 1. Effects of light, temperature and osmotica. *Seed Science Research* **2**, 155–162. [162]

Thanos, C.A., Georghiou, K. and Skarou, F. (1989) *Glaucium flavum* seed germination – an ecophysiological approach. *Annals of Botany* **63**, 121–130. [163]

Thanos, C.A., Georghiou, K., Douma, D.J. and Marangaki, C.J. (1991) Photoinhibition of seed germination in Mediterranean maritime plants. *Annals of Botany* **68**, 469–475. [164]

Thanos, C.A., Georghiou, K. and Delipetrou, P. (1994) Photoinhibition of seed germination in the maritime plant *Matthiola tricuspidata*. *Annals of Botany* **73**, 639–644. [165]

Thanos, C.A., Fournaraki, C. and Makri, N. (2005) Photoinhibition of seed germination: ecology, phylogeny and presumptive mechanisms, p. 44 *in* Book of Abstracts from the 8th International Workshop on Seeds, May 2005, Brisbane, Australia.

Thanos, C.A., Fournaraki, C., Tsiroukis, A. and Panayiotopoulos, P. (2010) Timing of seed germination and life history of trees: case studies from Greece, pp. 103–111 *in* Chien, C.T. and Chen, F.H. (eds), IUFRO Tree Seed Symposium: Recent Advances in Seed Research and ex situ Conservation. Taipei, Taiwan Forestry Research Institute. [166]

Thompson, K., Grime, J.P. and Mason, G. (1977) Seed germination in response to diurnal fluctuations of temperature. *Nature* **267**, 147–149. [167]

Tobe, K., Zhang, L. and Omasa, K. (2006) Seed germination and seedling emergence of three *Artemisia* species (Asteraceae) inhabiting desert sand dunes in China. *Seed Science Research* **16**, 61–69. [168]

Turner, S.R., Merritt, D.J., Baskin, C.C., Dixon, K.W. and Baskin, J.M. (2005) Physical dormancy in seeds of six genera of Australian Rhamnaceae. *Seed Science Research* **15**, 51–58. [169]

Tutin, T.G., Heywood, V.H., Burges, N.A., Valentine, D.H., Walters, S.M. and Webb, D.A. (1964) Flora Europaea. Cambridge University Press, Cambridge (1964–1980).

Tweddle, J.C., Dickie, J.B., Baskin, C.C. and Baskin, J.M. (2003) Ecological aspects of seed desiccation sensitivity. *Journal of Ecology* **91**, 294–304.

Válio, I.F. and Scarpa, F.M. (2001) Germination of seeds of tropical pioneer species under controlled and natural conditions. *Brazilian Journal of Botany* **24**, 79–84. [170]

Van Breemen, A.M.M. (1984) Comparative germination ecology of three short-lived monocarpic Boraginaceae. *Acta Botanica Neerlandica* **33**, 283–305. [171]

van der Kinderen, G. (1995) A method for the study of field germinated seeds of terrestrial orchids. *Lindleyana* **10**, 68–73.

Van Deynze, A.E., Beversdorf, W.D. and Pauls, K.P. (1993) Temperature effects on seed color in black-and yellow-seeded rapeseed. *Canadian Journal of Plant Science* **73**, 383–387.

Van Rooden, J., Akkermans, L.M.A. and Van Der Veen, R. (1970) A study on photoblastism in seeds of some tropical weeds. *Acta Botanica Neerlandica* **19**, 257–264. [172]

Vandelook, F., Verdú, M. and Honnay, O. (2012) The role of seed traits in determining the phylogenetic structure of temperate plant communities. *Annals of Botany* **110**, 629–636.

Vazquez-Yanes, C., Orozco-Segovia, A., Rincon, E., Sanchez-Coronado, M.D., Huante, P., Toledo, J.R. and Barradas, U.L. (1990) Light beneath the litter in a tropical forest: effect on seed germination. *Ecology* **71**, 1952–1958.

Waes, J.V. and Debergh, P.C. (1986) In vitro germination of some Western European orchids. *Physiologia Plantarum* **67**, 253–261. [173]

Walck, J.L. and Hidayati, S.N. (2004) Differences in light and temperature responses determine autumn versus spring germination for seeds of *Schoenolirion croceum*. *Canadian Journal of Botany* **82**, 1429–1437. [174]

Wang, J.H., Baskin, C.C., Cui, X.L. and Du, G.Z. (2009) Effect of phylogeny, life history and habitat correlates on seed germination of 69 arid and semi-arid zone species from northwest China. *Evolutionary Ecology* **23**, 827–846. [175]

Watanabe, H., Kusagaya, Y. and Saigusa, M. (2002) Environmental factors affecting germination of apple of Peru. *Weed Science* **50**, 152–156. [176]

Weiersbye, I.M. and Witkowski, E.T.F. (2002) Seed fate and practical germination methods for 46 perennial species that colonize gold mine tailings and acid mine drainage-polluted soils in the grassland biome, pp. 221–255 *in* Seydack, A.H.W., Vorster, T., Vermeulen, W.J. and van der Merwe, I.J. (eds), *Multiple Use Management of Natural Forests and Woodlands: Policy Refinements and Scientific Progress*. South Africa, Department of Water Affairs and Forestry. [177]

Western Australian Herbarium (1998–). FloraBase – the Western Australian Flora. Department of Parks and Wildlife. https://florabase.dpaw.wa.gov.au/

Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* **199**, 213–227.

Widell, K.O. and Vogelman, T.C. (1988) Fiber optic studies of light gradient and spectral regime within *Lactuca sativa* achenes. *Physiologia Plantarum* **72**, 706–712.

Willis, C.G., Baskin, C.C., Baskin, J.M., Auld, J.R., Venable, D.L., Cavender-Bares, J., Donohue, K. and Rubio de Casas, R. (2014) The evolution of seed dormancy: environmental cues, evolutionary hubs, and diversification of the seed plants. *New Phytologist* **203**, 300–309.

Yaniv, Z. and Mancinelli, A.L. (1968) Phytochrome and seed germination. IV. Action of light sources with different spectral energy distribution on the germination of tomato seeds. *Plant Physiology* **43**, 117–120. [178]

Zaman, A.U., Khan, M.A. (1992) The role of buried viable seeds in saline desert plant community. *Bangladesh Journal of Botany* **21**, 1–10. [180]

Zeng, Y.-J., Wang, Y.-R., Zhang, B.-L. and Li, B.-E. (2000) Eco-adaptability studies of seed germination in species of *Reaumuria soongorica* and *Oxytropis aciphylla*. *Acta Prataculturae Sinica* **9**, 36–42. [179]

Zettler, L.W., and McInnis, T.M. Jr (1994) The effect of white light on the symbiotic seed germination of an endangered orchid, *Platanthera integrilabia*. *Association of Southeastern Biologists Bulletin* **41**, 129.

Zhang, L.-X., Lan, Q.-Y., Li, H.-T., Tan Y.-H., Guan, Y.-H. and Li, X.-L. (2011) Developmental changes in relation to desiccation tolerance and storage characteristics of *Aquilaria sinensis* (Thymelaeaceae) seeds. *Plant Diversity* **33**, 458–464. [181]

Zhang, R., Wang, Y.R., Baskin, J.M., Baskin, C.C., Luo, K. and Hu, X.W. (2016) Germination and persistence in soil of the dimorphic diaspores of *Atriplex centralasiatica*. *Seed Science Research* **26**, 273–283. [182]

Zheng, Y., Gao, Y., An, P., Shimizu, H. and Rimmington, G.M. (2004) Germination characteristics of *Agriophyllum squarrosum*. *Canadian journal of Botany* **82**, 1662–1670. [183]

Zucareli, V., Henrique, L.A.V. and Ono, E.O. (2015) Influence of light and temperature on the germination of *Passiflora incarnata* L. seeds. *Journal of Seed Science* **37**, 162–167. [184]