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Inhibition of seed germination by far red radiation transmitted through leaf canopies

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Abstract. Perception of light by phytochrome is one of the mechanisms that enable seeds to optimize the place and time of germination. In an effort to determine how widespread in nature is the inhibition of seed germination by light transmitted by competing plants, the seeds of various species were exposed for germination beneath leaf canopies. A high ratio of far red (FR) to red (R) light under the canopies inhibited to various extent the germination in most of samples. Only 91 species (out of 487 tested) did not indicate any FR-inhibition and might be determined as truly light-insensitive. Although particular seed samples of the same species often differ in response to white light (photoblastism), the responses to the FR irradiation seem to be much more stable. The ability to the FR-dormancy may be treated as a species-specific feature. After several-day exposure under leaf canopy, the seeds become extremely sensitive to the white light, but this sensitivity diminishes slowly in the course of treatment. Every seed cohort may be diversified in germination by the irregular and variable structure of leaf canopy. The acquired state of photosensitivity may persist during several years and may impact on seed longevity. The seeds needing winter prechilling (stratification) for a substantial germination, often become more indifferent to the white light, but always show a FR-sensitivity. The relations between taxonomic position and FR-sensitivity are weak. No difference in the FR-sensitivity was observed among life-forms. Distinct relations were stated between seed size and FR-sensitivity; seeds of FR-insensitive species are in average much larger. A relationship was found between the dynamics of germination and the photoresponses. Positively photoblastic and FR-sensitive seeds usually need much more time to full germination. These relationships may explain the fact that often the seeds of cultivated plants are photoblastically indifferent and FR-insensitive; they have been selected for fast and uniform germination. Full daylight exerted usually an inhibitory effect on germination of seeds of almost all tested species. The concept of positive photoblastism ought be treated with caution, because it proves true only in weak light.

Keywords: far red irradiation, leaf canopy, seed germination, seed longevity, seed photosensitivity

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INTRODUCTION

The germination of seeds of many plant species is influenced by light and this has been known since at least the second half of the 19th century (Caspary, 1860). Knowledge of photobiological pathways leading to seed germination (or dormancy) has been developed considerably in the last six decades. Especially important was the discovery of phytochrome by the „Beltsville Group" (Borthwick et al., 1952; Hendricks et al., 1959).

Phytochrome system, controlling many aspects of plant development, consists of two interconvertible forms, with absorption maxima at approx. 660 nm and 730 nm. Although the concepts of the mechanisms of action and of the molecular structure of phytochrome (or phytochromes) has evolved considerably since then (Smith, 2000), there was no doubt as regards its basic role in plant photomorphogenesis (Rollin, 1972; Heschel et al., 2008). The understanding of the ecological significance of the observed photoresponses has been increasing steadily, and seems to be a fascinating intellectual adventure.

Seed photoresponses may be treated as an effect of adaptation to the varying environment. Generally speaking, these responses enable the seeds to optimize the choice of time and place of germination in relation to species survival. Information on the environmental conditions are transferred by three features of light: photoperiod (relative length of day and night), intensity, and spectral composition. All three signals are received by the phytochrome which opens appropriate metabolic pathways. To detect

competition from other plants, the most important factor for seeds is the spectral composition of the light. Since red radiation is almost fully absorbed by green tissues of plants, and far red is largely transmitted (Holmes and Smith, 1977), the preponderance of the far red (FR, about 730 nm) irradiation over the red (R, about 660 nm) means the presence of competing plants (Franklin and Whitelam, 2005). Using some anthropomorphisation, one may say that the phytochrome is the eye of the plant.

The spectral sensitivity of seeds or spores was studied (Kommerell, 1927; Listowski, 1927; Flint and McAllister, 1935) in laboratory experiments well before the concept of phytochrome had emerged. The inhibiting effect of far red light transmitted through living leaves was firstly described by Meischke (1936). Probably the results of Meischke remained unknown for a long time; the next such reports appeared much later (Taylorson and Borthwick, 1969; Van der Veen, 1970; Stoutjesdijk, 1972; Górski, 1975; King, 1975; Massantini, 1978; Valio and Joly, 1979; Fenner, 1980; Silvertown, 1980). Since then, many researchers have performed experiments with seeds exposed for germination in the shadow of plants or even in the light reflected from plants (Batlla et al., 2000).

The aim of this report is to present the results of experiments with impact of the natural FR on seed germination, performed by us over many years starting in 1974. Some of these results have been published earlier in various forms (Górski, 1975; Górski et al., 1977, 1978; Górska and Pięta, 1981), but the new version gives a more complete information.

We cannot exclude – and we hope – that the empirical data accumulated here will be useful in the interpretations performed by other authors too.

MATERIALS

Three main groups of seed collections were used in the germination tests. The majority of seeds were collected by ourselves and coworkers (229 species), or by the staff of the Wrocław Botanical Garden (23 species) from wild plants growing under natural conditions. The second group of seeds came from plants growing in the Wrocław Botanical Garden (129 species). The third group, from cultivated plants (106 species) was obtained mainly commercially. Appropriate information on seed origin is presented (Table 1).

After collection, the seeds in paper bags were dried at laboratory temperature for several days and then stored in a refrigerator (about 5°C) until used. Only in a few cases seeds were tested shortly after harvesting (seed age signed as "0"). These were sown as fresh or partly dried in an ambient temperature, without cold storage. One can assume that the commercially obtained seeds underwent normal standard procedures until stored in our refrigerator.

The life forms of maternal plants (Table 1) were defined according to Szafer et al. (1976) and – in the case of foreign species – after Hegi (various issues). The term "seed" will be used throughout this paper for any germinating structure, independently of its proper botanical definition.

METHODS

Germination test

As a rule, 30 seeds were sown in each 9 cm Petri dish on at least two layers of white flannel and a Whatman filter, moistened with distilled water. The water was supplied – if necessary – when the seeds were inspected.

In the initial experiments the seeds were tested for their sensitivity to white light (photoblastism). The dishes were exposed to the diffuse natural light in a room near a north-facing window, or were enclosed inside light-tight boxes. The temperature in the room was partly controlled and maintained at 19±2°C. Each experiment consisted of at least three replicates. The difference in germination (protrusion of radicle through seed coat) between treatments made it possible to categorise the seeds as positively or negatively photoblastic. When the difference was not statistically significant, the seeds were defined as photoblastically indifferent (I). Because in several additional experiments, performed outdoors, the interactions between light and temperature were observed, in the Table 1 only the class of photoblastism is presented, but not the percentage germination, which might not be fully reliable for natural conditions, under which the main experiments were done.

The main experiments were performed from 1974. Until 1978 they consisted of two treatments: leaf canopy (F), and diffuse white light control (L). In 1979 the third treatment, darkness (D) was added and since then the percentage dark germination was presented. Up to 1976, the standard for the first treatment was a dense rhubarb canopy. Subsequently, a special framework shelter (2 x 3 x 1.8 m) was constructed and covered by shoots of Virginia creeper (*Parthenocissus quinquefolia* (L.) Planch). The dishes with seeds were placed on the ground beneath the canopies. Because under direct solar irradiation all seeds can be inhibited in their germination (Doroszewski, 1989), the white light control dishes were located in big wooden framework chests, permitting no spots of sunlight, together with dark control dishes packed in small light-tight boxes. The global solar irradiation (300–3000 nm, measured by Moll-Gorczyński solarimeters) inside the chests was maintained (by regulation of openings in the walls) at the approximate level measured under leaf canopy; it constituted normally 10–15% of global irradiation at an open site.

The spectral distribution of light beneath leaf canopies, as measured by an OBRTS spectroradiometer, did not differ significantly from the general patterns described by many authors (Stoutjesdijk, 1972; Holmes and Smith,

1977; Sattin et al., 1994). The FR/R ratio under rhubarb leaves attained 10, whilst under Virginia creeper shelter it was in the range of 5–10, depending on the season, solar angle and cloud cover.

The experiments started normally about 20 May, when the creeper leaves were well developed, and finished at the end of September, before the leaves turned red. The ambient temperature in these periods changed significantly also between years; the mean temperature of the period between 20 May and 20 September varied in the range of 15 –18°C, and the mean temperature of the warmest month of the year between 17 and 20°C. Daily extremes of temperature in the chests and beneath the plant canopies differed by 1–3°C in both directions.

To examine the photoresponses at a full natural variability of temperature, the particular experiments (usually without replicates) were repeated in various periods. At least three experiments were performed with each lot of seeds; when a marked variability appeared between particular tests, the number of repetitions increased, even up to 8.

Counting of the germinated seeds was usually performed 4, 8, 12, 18, 24, 30, 36, 45 and 60 days after sowing. Dark-treated dishes were transferred to a dark room and inspected in dim green "safelight". The germination was defined as final if subsequent counting showed no further germination in the control (white light for positively photoblastic and indifferent seeds, or darkness for negatively photoblastic seeds). If in any of the treatments the germination reached at least 10%, the results of experiments are presented (Table 1), as percent germination for each treatment.

The seeds of many wild species did not germinate in any treatment, or have very low germination. Since the prechilling requirement is a well-known phenomenon among many species (Kinzel, 1920; Grzesiuk, 1967), we attempted to break the observed primary dormancy by stratification (layering), exposing the seeds to wintering outdoors under conditions possibly similar to the natural ones.

Apart from the stratification we did not use any other method to break the seed dormancy.

Prechilling of seeds

Thin layers of seeds were packed in filter paper bags and placed on the ground under framework covers. The exposure was from late November to early April (about 130 days). Because the imbibition is the necessary condition for cold-requiring seeds for the start of after-ripening processes (Roberts, 1972; Lewak and Rudnicki, 1977), the bags were wetted several times, and the seeds were moist throughout the winter, as expected in nature. In several batches, a part of seeds germinated during stratification. These were rejected before drying at laboratory temperature (about 19°C). All the stratified seeds, as well as the non-stratified control seeds were kept dry in a refrigerator until used in experiments. If then the control seeds – treated along with stratified ones – germinated to some extent, the germination percents in both treatments are shown (Table 1). If these did not germinate, only the result from the stratified treatment is presented.

Testing of probable impact of gaseous inhibitors

Because effects of gases or volatile materials on germination have been reported (Barton, 1965), an attempt was done to eliminate suspicions about such effects in our experiments. The technique consists of two types of small boxes in which the dishes were placed. The boxes were either light-tight or has a glass top. All the boxes had identical (unforced) ventilation through short twisted pipes, permitting no light. The photoblastically indifferent seeds of *Lactuca sativa* L. inside light-tight boxes germinated well under all tested types of canopies, while those in boxes under glass were inhibited to the same extent as those in dishes outside the boxes.

It may be concluded that the inhibition of germination under leaf canopies observed in our experiments was caused by agents other than gaseous or volatile inhibitors.

Comparison of the effects of natural and artificial sources of far red radiation

Additional evidence for the radiative nature of inhibition of seed germination under leaf canopies came from special experiments with artificial sources of FR and R. Light from a 200 W incandescent bulb was filtered through a 2 cm layer of water and combinations of Schott glass filters: RG8 (2 mm) + BG17 (6 mm), (FR source) and RG2 (2 mm) + BG17 (12 mm), (R source). At seed level, the FR source gave 0.7 mW cm^{-2} in the 700–740 nm band and only 0,065 mW cm^{-2} in the 640–680 nm band. The ratio FR/R was close to the ratio measured under leaf canopies. Irradiation from the R source was 0.51 mW cm^{-2} in the 640–680 nm band and 0.33 mW cm^{-2} in the 700–740 nm band. This ratio resembles that in natural white light on cloudy days (on sunny days the ratio FR/R is nearer to 1). As natural analogues for the filters, fresh rhubarb leaves (for FR) and diffuse natural light (for R) were used.

The experiments summarized in Table 2 show clearly that effects of the artificial FR irradiation mimic the effects of light transmitted through the leaves. The red/far-red reversion, which is the most important criterion for the phytochrome involvement, can be simply obtained by using natural light and a leaf.

Table 2 illustrates partly seed classification used throughout the report. *Arabis hirsuta* represents positively photoblastic and FR-dormant seeds (class PP-A), *Lactuca serriola* is photoblastically indifferent and FR-dormant (class I-A), while *Dianthus barbatus* is truly light-indifferent (I-Z).

RESULTS AND DISCUSSION

Table 1 presents averaged results of all experiments giving at least 10% germination in any of the treatments. The families and species within families are listed in alphabetical order.

The extent of germination inhibition under leaf canopy was categorized in classes (A, B, C, Z) according to the

Table 1. Results of seed testing as to their photoblastism and sensitivity to light transmitted through leaf canopy.

Family and Species	Lf	Col	Age	FG	Germination [%]				Class	
					D	L	F	F/L		
1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	
ACERACEAE										
Acer negundo L.	t	wgV	1 S	24	99	86	43	50	N	B
AIZOACEAE										
Mesembryanthemum cristallinum L.	a, b	cp	1	4		99	98	99	I	Z
AMARANTHACEAE										
Amaranthus ascendens Lois.	a	wgV	4	60	3	73	0	0	PP	A
Amaranthus caudatus L.	a	bg	2	30		26	0	0	N	A
Amaranthus retroflexus L.	a	wgV	5	18	90	0	0		NN	Y
Amaranthus retroflexus L.			5 S	18	91	23	0	0	N	A
Celosia cristata L.	a	cp	2	8		98	97	99	I	Z
APIACEAE										
Anethum graveolens L.	a	wgV	2	36	66	59	60	101	I	Z
Daucus carota L. *var. carota*	b	cp	2	18		80	85	106	I	Z
Daucus carota L.	b	wgV	5	24	14	28	4	14	P	A
Daucus carota L.			5 S	24	22	42	18	43	P	B
Eryngium planum L.	p	wgV	2	30		31	0	0	P	A
Heracleum sibiricum L.	b, p	wgV	2 S	30	19	17	16	94	I	Z
Pastinaca sativa L.	b	cp	3	30	77	68	60	88	I	C
Petroselinum sativum Hoffm. cv. Berlińska	b	cp	2	24		52	47	90	I	Z
Torilis japonica (Houtt.) DC.	a, b	wgV	3	24	7	18	0	0	P	A
Torilis japonica (Houtt.) DC.			3 S	24	18	21	3	14	I	A
ASCLEPIADACEAE										
Vincetoxicum officinale Mnch.	p	wgV	3	45		41	12	29	I	B
ASTERACEAE										
Achillea ageratifolia (S.S.) Boiss.	p	bg	2	18		62	66	106	I	Z
Achillea compacta Willd.	p	bg	2	8		85	22	26	P	B
Achillea millefolium L.	p	wgV	1	8		90	32	36	I	B
Achillea ptarmica L.	p	bg	2	18		73	0	0	P	A
Achillea salicifolia Bess.	p	bgM	1	12		82	33	40	P	B
Adenostyles alliariae (Gouan) Kern.	p	wgQ	3	45		24	1	4	I	A
Ageratum houstonianum Mill.	a	cp	1	18		65	65	100	I	Z
Ammobium alatum R.Br. cv. *grandiflora*	a	bg	2	12	89	96	34	35	I	B
Anthemis arvensis L.	a	wgO	4 S	24	15	12	6	50	I	B
Arctium lappa L.	b	wgV	1	45		72	2	3	PP	A
Arctium minus (Hill.) Bernh.	b	wgV	1	24		20	0	0	PP	A
Artemisia absinthium L.	p	wgV	1	18	12	25	4	16	P	A
Artemisia absinthium L.			1 S	18	32	94	24	26	P	B
Artemisia arborescens L.	hs	bg	2	12		95	61	64	P	B
Artemisia campestris L.	p	wgV	2	36	14	65	15	23	P	B
Artemisia campestris L.			2 S	36	32	90	37	41	P	B
Artemisia vulgaris L.	p	wgV	1	18		30	0	0	PP	A
Aster alpinus L.	p	bg	2	18		83	73	86	I	Z
Bellis perennis L.	p	wgV	2	12		92	87	94	I	C
Bellis perennis L. cv. Pomponette	p	cp	2	12		93	87	93	I	C
Bidens cernuus L.	a	wgO	2	45		25	7	28	PP	B
Bidens melanocarpus Wiegand	a	wgV	2 S	18	1	90	2	2	PP	A
Bidens tripartitus L.	a	wgV	1 S	30	0	79	0	0	PP	A

Table 1 continuation

1	2	3	4	5	6	7	8	9	10	
Calendula officinalis L.	a	cp	1	8		84	70	83	I	C
Callistephus chinensis Nees.	a	cp	2	24		45	39	87	I	C
Carduus crispus L.	b	wgV	3	24	16	66	16	24	P	B
Centaurea cyanus L.	a, b	wgO	2	12		70	6	9	I	A
Centaurea jacea L.	p	wgV	1	18		67	12	18	P	A
Centaurea Kotschyana Heuff.	p	bgK	3	30		42	19	45	I	B
Centaurea macrocephala Puschk.	p	bg	3	8		95	86	91	I	Z
Centaurea montana L.	p	bg	2	30	46	48	12	25	I	B
Centaurea moschata L.	p	cp	2	8		34	39	115	I	Z
Centaurea oxylepis (Wimm.et Gr.) Hay.	p	bg	2	12		93	7	8	I	A
Centaurea rhenana Bor.	b, p	bgM	2	8		88	38	43	I	B
Centaurea scabiosa L.	p	wgM	1	18		32	23	72	I	C
Chrysanthemum argenteum Wild.	p	bg	2	18	15	13	8	62	I	B
Chrysanthemum balsamita L.	p	bg	2	12	30	28	12	43	I	B
Chrysanthemum carinatum Schousb.	a	cp	1	18		44	10	23	I	B
Chrysanthemum parthenium (L.) Bernh.	p	cp	1	12		95	82	86	I	C
Cichorium endivia L.	a, b	cp	1	12		74	0	0	I	A
Cichorium intybus L.	p	cp	1	12		95	76	80	I	C
Cineraria maritima L.	hs	cp	2	12		34	40	118	I	Z
Cirsium arvense (L.) Scop.	p	wgV	2	18		24	0	0	P	A
Cirsium oleraceum (L.) Scop.	p	bgQ	2	12		67	0	0	PP	A
Cirsium palustre (L.) Scop.	b	bgM	2	18		75	0	0	P	A
Cirsium rivulare (Jacq.) All.	p	bg	1	12		43	0	0	P	A
Coreopsis grandiflora Hogg.	p	cp	1	12		82	82	100	I	Z
Coreopsis lanceolata L.	p	bg	2	30	50	70	16	23	P	B
Crepis biennis L.	b	wgV	1	8	84	79	21	27	I	B
Crepis capillaris (L.) Wallr.	a, b	wgV	2	12	84	89	11	12	I	A
Cynara cardunculus L.	p	cp	1	30		65	22	34	I	B
Dimorphoteca aurantiaca DC.	a	cp	2	12		37	27	73	I	C
Doronicum caucasicum M.B.	p	cp	2	30		27	27	100	I	Z
Erigeron acer L.	b, p	wgM	3	12		72	46	63	I	B
Erigeron alpinus L.	p	bg	2	12		90	10	11	I	A
Erigeron canadensis L.	a, b	wgO	2	12		45	43	96	I	Z
Erigeron hybridus hort.	p	bg	2	12		82	20	24	P	B
Erigeron ramosus (Walt.) B.S.P.	b, p	wgV	1	24		57	0	0	PP	A
Galinsoga parviflora Cav.	a	wgO	1	24		66	3	5	PP	A
Galinsoga quadriradiata Ruiz et Pav.	a	wgV	2	36		87	0	0	PP	A
Gazania rigens R. Br.	a	cp	2	18		47	33	70	I	C
Helianthus annuus L.	a	cp	1	8	97	97	91	94	I	C
Helichrysum bracteatum (Vent.) Willd.	p	cp	2	8		96	93	97	I	Z
Hieracium umbellatum L.	p	wgV	1 S	8		85	52	61	P	B
Homogyne alpina (L.) Cass.	p	bg	1	45		23	12	52	I	B
Hypochoeris radicata L.	p	wgV	1	12		82	6	7	P	A
Inula ensifolia L.	p	wgV	2	24	51	71	42	59	P	B
Iva xanthiifolia Nutt.	a	wgV	1	24		21	14	67	P	B
Lactuca sativa L. cv. Cud Vorburgu	b	cp	1	8		97	14	14	I	A
Lactuca serriola Torner (*L. scariola* L.)	b	wgV	1	8		100	10	10	I	A
Lapsana communis L.	a	wgV	1	30		58	0	0	I	A
Leontodon autumnalis L.	p	wgV	1	18		80	28	35	I	B
Leontodon hispidus L.	p	wgQ	1	30		70	35	50	P	B
Ligularia clivorum Maxim.	p	wgV	3	30		49	9	18	P	A
Linosyris vulgaris Cass.	p	wgV	1	12		57	57	100	I	Z
Matricaria chamomilla L.	a	wgV	1	18	0	53	0	0	PP	A
Matricaria discoidea DC.	a	wgV	2	24	24	88	80	91	P	C
Matricaria inodora L.	a, p	wgO	1	18		50	14	28	P	B

Table 1 continuation

1	2	3	4	5	6	7	8	9	10	
Mycelis muralis (L.) Dum.	p	wgV	2	24	52	83	72	87	P	C
Onopordon acanthium L.	b	wgV	4	30	37	57	10	18	P	A
Petasites albus (L.) Gaertn.	p	wgQ	1	24		18	21	117	I	Z
Petasites officinalis Mch.	p	wgQ	0	4		96	14	15	I	A
Prenanthes purpurea L.	p	bgQ	1	24		45	4	9	PP	A
Rudbeckia laciniata L.	p	cp	2	24		81	30	37	I	B
Senecio cruentus DC.	p, hs	cp	2	12		74	83	112	N	Z
Senecio Fuchsii Gmel.	p	bgQ	1	24		56	6	11	PP	A
Senecio nemorensis L.	p	bgQ	3	30		73	0	0	PP	A
Senecio vernalis W.K.	a, b	wgV	2	18	77	82	9	11	I	A
Senecio viscosus L.	a	wgV	1 S	8	12	58	0	0	P	A
Senecio vulgaris L.	a, b	wgV	1	12		60	0	0	P	A
Solidago canadensis L.	p	bg	2	30		39	24	62	I	B
Solidago serotina Ait.	p	bg	2	24		29	23	79	I	C
Solidago virga-aurea L.	p	wgV	2	12		91	74	81	I	C
Solidago virga-aurea L. ssp. *alpestris*	p	bgQ	2	30		60	67	112	I	Z
Sonchus arvensis L.	p	wgO	4	18	3	34	0	0	PP	A
Sonchus arvensis L.			4 S	12	42	43	1	2	I	A
Sonchus asper (L.) Hill.	a	wgV	2 S	12		80	40	50	I	B
Sonchus oleraceus L.	a	wgV	1	30		33	0	0	PP	A
Tagetes erectus L.	a	cp	2	12		87	2	2	PP	A
Tanacetum vulgare L.	p	bgU	2	18		75	19	25	P	B
Taraxacum officinale Web.	p	wgV	0	12		87	2	2	P	A
Tragopogon maior Jacq.	b	wgO	1	8		92	2	2	N	A
Tragopogon orientalis L.	b	bgU	2	18		90	0	0	I	A
Tussilago farfara L.	p	wgQ	0	4		92	0	0	I	A
BALSAMINACEAE										
Impatiens balsamina L.	a	cp	2	4		90	93	103	I	Z
Impatiens parviflora DC.	a	wgV	2	18	39	14	9		N	Y
BERBERIDACEAE										
Berberis sibirica Pall.	s	wgM	1 S	18		90	46	51	P	B
Berberis vulgaris L.	s	wgV	1 S	60		37	3	8	P	A
BETULACEAE										
Alnus glutinosa (L.) Gaertn.	t	wgV	2	12		82	37	45	PP	B
Betula verrucosa Ehrh.			1	18	3	30	0	0	PP	A
Betula verrucosa Ehrh.	t	wgV	1 S	18	6	49	2	4	PP	A
BORAGINACEAE										
Cerinthe minor L.	b, p	wgV	1 S	18		18	5	28	I	B
Echium vulgare L.	b	wgM	2	18		10	12		I	Z
Lappula myosotis Mnch.	a, b	wgV	2	8		94	0	0	I	A
Myosotis arvensis (L.) Hill.	a, b	wgV	1	18		82	10	12	PP	A
Myosotis silvatica Hoff. *alpestris* hort.	p	cp	0	18		70	50	71	I	C
BRASSICACEAE										
Alyssum maritimum Lam.	p	cp	2	4		96	96	100	I	Z
Alyssum saxatile L.	p	bg	2	24	70	94	79	84	P	C
Arabidopsis Thaliana (L.) Heynh.	a, b	wgQ	0	30		45	2	4	PP	A
Arabis albida Stev.	p	bg	2	8		93	80	86	I	C
Arabis allioni DC.	p	bg	4	24	0	21	5	24	PP	B
Arabis allioni DC.			4 S	24		86	5	6	PP	A
Arabis alpina L.	p	bg	2	8		90	62	69	P	B
Arabis aubrietioides Boiss.	p	bg	2	45		70	40	57	P	B
Arabis bellidifolia Jacq.	p	bg	1	30		65	13	20	I	B
Arabis hirsuta Scop.	b, p	bg	2	8		98	10	10	PP	A
Arabis jacquini Beck	p	bg	2	30		30	14	47	I	B
Arabis pieninica Wol.	p	bg	1	12		94	70	74	I	C

Table 1 continuation

1	2	3	4	5	6	7	8	9	10	
Arabis procurrens Waldst. et Kit.	p	bg	2	30		70	32	46	P	B
Arabis pumila Jacq.	p	bg	2	12		97	7	7	PP	A
Arabis vochinensis Spreng.	p	bg	2	24		72	8	11	I	A
Berteroa incana (L.) DC.	a	wgV	1	18		43	4	9	I	A
Brassica oleracea L. convar. *acephala* DC.	a, b	cp	1	12		96	88	92	I	C
Brassica oleracea L. var. *gemmifera* DC.	a, b	cp	2	8		99	88	89	I	C
Brassica oleracea L. var. *gongyloides* L.	a, b	cp	2	12		96	88	92	I	C
Brassica pekinensis Rupr.	a	cp	2	18		74	58	78	I	C
Bunias orientalis L.	b	wgV	3	45	30	0	0		NN	Y
Camelina microcarpa Andrz.	a, b	wgV	1	8		35	20	57	I	B
Camelina microcarpa Andrz.			1 S	8	87	83	63	76	I	C
Capsella bursa-pastoris (L.) Med.	a, b	wgV	3 S	12	28	20	14	70	N	C
Cheiranthus cheiri L.	p	cp	1	8		96	92	96	I	Z
Descurainia sophia (L.) Webb.	a, b	wgV	2	12		17	0	0	P	A
Descurainia sophia (L.) Webb.			2 S	12		67	0	0	P	A
Erysimum cheiranthoides L.	b	wgQ	3 S	18		34	2	6	P	A
Iberis amara L.	a	cp	1	8		84	90	107	I	Z
Lepidium densiflorum Schrad.	a, b	wgV	2	45	9	27	10	37	P	B
Lepidium densiflorum Schrad.			2 S	45	25	52	32	62	P	B
Lepidium ruderale L.	a	wgM	3	30		64	0	0	P	A
Lepidium sativum L.	a	cp	1	8		94	96	102	I	Z
Lunaria annua L.	a, b	wgV	2	36		14	6	43	N	B
Matthiola bicornis DC.	a	cp	1	8		78	50	64	P	B
Matthiola incana L.	a	cp	2	8		88	78	89	I	Z
Raphanus raphanistrum L.	a	wgO	4 S	12	19	3	2		NN	Y
Raphanus sativus L.	a, b	cp	1	8		93	79	85	I	C
Sinapis alba L.	a	cp	1	8		98	98	100	I	Z
Sinapis arvensis L.	a	wgO	1	8		62	37	59	I	B
Sisymbrium Loeselii L.	b	wgV	2	30		77	31	40	P	B
Sisymbrium officinale (L.) Scop	a, b	wgV	2 S	8		25	2	8	P	A
Thlaspi arvense L.	a, b	wgO	8 S	8	23	2	2		NN	Y
BROMELIACEAE										
Pitcairnia flammea Ldl.	p	bg	2	45	0	78	64	82	PP	C
CAMPANULACEAE										
Campanula alliariaefolia Willd.	p	bg	1	12		94	80	85	P	C
Campanula carpatica Jacq.	p	bg	1	18		41	29	71	P	C
Campanula carpatica Jacq. var. *turbinata*	p	bg	1	24		70	27	39	P	B
Campanula cochleariifolia Lam.	p	bg	1	24		77	7	9	P	A
Campanula glomerata L. var. *superba*	p	bg	1	12		80	80	100	I	Z
Campanula lactiflora Bieb.	p	bg	1	12		81	8	10	PP	A
Campanula latifolia L.	p	bg	1	12		90	24	27	P	B
Campanula latiloba A.DC.	p	bg	1	30		67	0	0	PP	A
Campanula linifolia Scop.	p	bg	3	24	10	51	9	17	P	A
Campanula linifolia Scop.			3 S	24	10	90	15	16	P	A
Campanula medium L.	a, b	cp	1	18		88	88	100	I	Z
Campanula patula L.	b, p	bgQ	2	24		77	7	9	PP	A
Campanula persicifolia L.	p	bg	2	24		80	48	60	P	B
Campanula punctata Lam.	p	bg	2	12		96	73	76	I	C
Campanula rapunculoides L.	p	bg	1	12		96	54	56	I	B
Campanula rotundifolia L.	p	bgU	2	24		100	3	3	PP	A
Campanula sarmatica Ker-Gawl.	p	bg	1	12		98	66	68	P	B
Jasione jankae Neilr.	p	bg	2	12		97	91	93	I	C
Jasione montana L.	b	wgV	2	12	80	87	95	109	I	Z
Jasione perennis Lam.	p	bg	2	12	96	98	86	87	I	C
Phyteuma orbiculare L.	p	bg	2	18		97	0	0	PP	A
Phyteuma scheuchzerii All.	p	bg	2	24		83	62	75	P	C

Table 1 continuation

1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	
Platycodon grandiflorus A.DC.	p	bg	2	24		87	63	72	P	C
Specularia speculum-Veneris (L.) DC.	a	bg	2	18	79	98	69	70	P	C
CAPRIFOLIACEAE										
Lonicera xylosteum L.	p	wgV	1 S	45		58	13	22	P	B
CARYOPHYLLACEAE										
Agrostemma githago L.	a	wgO	1	18		73	61	84	I	C
Arenaria grandiflora L.	p	bg	1	12		97	40	41	I	B
Cerastium arvense L.	p	wgQ	1	18		92	13	14	PP	A
Cerastium vulgatum L.	a, p	wgQ	1	12		98	3	3	PP	A
Dianthus barbatus L.	p	cp	2	12		96	95	99	I	Z
Dianthus carthusianorum L.	p	bg	1	8		88	78	89	I	Z
Dianthus caryophyllus L.	p	cp	2	12		84	84	100	I	Z
Dianthus compactus Kit.	p	bgK	1	24		86	63	73	P	C
Dianthus deltoides L.	p	bg	1	8		96	83	86	I	C
Dianthus gratianopolitanus Vill.	p	bg	1	4		97	98	101	I	Z
Dianthus kitaibelli Janka	p	bg	1	12		83	32	39	PP	B
Dianthus petraeus Waldst. et Kit.	p	bg	1	8		84	68	81	I	C
Dianthus plumarius L.	p	bg	1	8		90	97	108	I	Z
Dianthus silvestris Wulf.	p	bg	1	8		92	80	87	I	C
Dianthus sinensis L.	a, b	cp	1	8		98	93	95	I	C
Dianthus spiculifolius Schur	p	bg	1	8		99	87	88	I	C
Dianthus sternbergii Sibth.	p	bg	1	8		92	87	95	I	Z
Dianthus strictus Sibth. et Sm.	p	bg	1	8		95	79	83	I	C
Gypsophila elegans Bieb.	a, p	cp	1	12	87	86	80	92	I	Z
Heliosperma quadrifidum Rchb.	p	bg	2	18	29	94	38	40	P	B
Lychnis coronaria Desv.	p	bg	2	8	99	99	12	12	I	A
Melandrium album (Mill.) Garcke	a, p	bgU	1	30		36	7	19	I	A
Melandrium rubrum (Weig.) Garcke	a, b	bgQ	2	30	21	60	0	0	P	A
Melandrium rubrum (Weig.) Garcke			2 S	30	59	63	0	0	I	A
Melandrium rubrum var. *zetlandicum* Com.	a, b	bg	2	24		47	4	8	PP	A
Saponaria officinalis L.	p	wgV	2 S	12	70	33	0	0	N	A
Scleranthus annuus L.	a, b	wgV	3	60	17	10	1	10	N	A
Silene armeria L.	a, b	bg	2	8	97	99	24	24	I	B
Silene coeli-rosa A.Br.	a	bg	1	8		96	38	39	I	B
Silene hayekiana Hand.-Mazz. et Janchen	p	bg	1	12		90	47	52	P	B
Silene inflata (Salisb.) Sm.	p	wgQ	1	18		73	3	4	I	A
Silene saxifraga L.	p	bg	1	18		95	10	11	I	A
Silene viridiflora L.	p	bg	1	8		97	33	34	I	B
Spergula arvensis L.	a	wgO	1	18		50	32	64	I	B
Stellaria media Vill.	a, b	wgV	2	12	8	5	0			
Stellaria media Vill.			2 S	12	50	47	3	6	I	A
Stellaria nemorum L.	p	wgV	2 S	30	23	88	0	0	P	A
Viscaria vulgaris Rohl.	p	bg	2	18	98	86	73	85	N	C
CHENOPODIACEAE										
Atriplex hastatum L.	a	wgV	1	12	46	70	14	20	P	B
Atriplex hortense L. (black seeds)	a	wgV	2	24	0	4	2			
Atriplex hortense L. (black seeds)			2 S	12	4	61	4	7	PP	A
Atriplex hortense L. (yellow seeds)			2	18	24	68	62	91	P	C
Atriplex hortense L. (yellow seeds)			2 S	18	56	63	64	102	I	Z
Atriplex nitens Schkuhr (black seeds)	a	wgV	1	24	1	6	0	0		
Atriplex nitens Schkuhr (yellow seeds)				24	74	100	96	96	P	C
Atriplex patulum L.	a	wgV	4	60	0	10	1	10	PP	A
Atriplex patulum L.			4 S	60	19	46	8	17	P	A
Beta vulgaris L. ssp. *cicla* L.	b	cp	1	12		82	85	102	I	Z
Beta vulgaris L. ssp. *esculenta* Salisb.	b	cp	1	12		83	85	102	I	Z

Table 1 continuation

1	2	3	4	5	6	7	8	9	10	
Chenopodium album L.	a	wgV	1	18		47	28	60	P	B
Chenopodium glaucum L.	a	wgV	1	18	20	87	2	2	P	A
Chenopodium polyspermum L.	a	wgV	2	24	0	39	2	5	PP	A
Chenopodium polyspermum L.			2 S	18	10	77	7	9	P	A
Chenopodium rubrum L.	a	wgV	1 S	12	45	86	0	0	P	A
Corispermum hyssopifolium L.	a	wgV	1 S	12	83	0	7		NN	Y
Kochia scoparia (L.) Schrad.	a	cp	1	24		43	40	93	N	Z
Salsola kali L.	a	wgV	1 S	12	27	23	19	83	I	C
CONVOLVULACEAE										
Ipomoea hederacea Jacq.	a	bg	1	4		97	97	100	I	Z
Ipomoea purpurea Roth.	a	bg	1	4		98	91	93	I	Z
Ipomoea rubro-coerulea (L.) Mnch.	a	bg	1	8		71	82	115	I	Z
Quamoclit coccinea (L.) Mnch.	a	bg	1	8		83	90	108	I	Z
CRASSULACEAE										
Sedum acre L.	p	wgV	3	60	0	42	6	14	PP	A
Sedum maximum Sut.	p	wgV	1	18	14	76	46	60	PP	B
CUCURBITACEAE										
Cucumis sativus L.	a	cp	1	12		98	20	20	I	B
Cucurbita pepo L.	a	cp	2	18		72	12	17	N	A
CUPRESSACEAE										
Biota orientalis (L.) Endl.	s, t	wgV	0	30		61	54	88	I	C
Thuia occidentalis L.	t	wgV	1	12	52	65	65	100	I	Z
CUSCUTACEAE										
Cuscuta europea L.	a	wgV	1	18		26	22	85	I	Z
CYPERACEAE										
Carex silvatica Huds.	p	wgV	1	45	1	70	0	0	PP	A
DIPSACACEAE										
Dipsacus silvester Huds.	b	wgV	2	45	0	95	13	14	PP	A
Scabiosa atropurpurea L.	a	cp	2	18		42	32	74	I	C
Scabiosa ochroleuca L.	b, p	wgU	2	24		77	10	13	PP	A
Succisa pratensis Mnch.	p	bgU	2 S	36		34	16	47	I	B
ELEAGNACEAE										
Eleagnus angustifolia L.	s	wgV	1 S	60	20	43	27	63	P	B
Hippophae rhamnoides L.	s	wgV	1	30		78	60	77	I	C
ERICACEAE										
Rhododendron L. sp.	s	wgV	1	45		82	18	22	PP	B
EUPHORBIACEAE										
Euphorbia helioscopia L.	a	wgV	3	24		26	23	88	I	Z
FABACEAE										
Caragana arborescens Lam.	s	wgM	3	30		74	58	78	P	C
Colutea arborescens L.	s	wgV	1	18		18	18	100	I	Z
Hedysarum multijugum Maxim.	a, p	bg	2	12	56	60	64	107	I	Z
Laburnum alpinum Bertcht. et Presl	s	bg	2	45	29	33	31	94	I	Z
Laburnum anagyroides Med.	s	bg	2	45	43	45	45	100	I	Z
Lotus uliginosus Schk.	p	wgM	2	30		69	69	100	I	Z
Lupinus luteus L.	a	wgV	3	60	70	57	53	93	N	Z
Lupinus polyphyllus Ldl.	p	bgQ	2	45		37	22	59	I	B
Medicago falcata L.	p	wgV	2	45		10	11	110	I	Z
Medicago sativa L.	p	cp	2	30		73	80	109	I	Z
Melilotus albus Med.	b	bgK	2	12		57	50	88	I	Z
Phaseolus vulgaris L. cv. Złota Saxa	a	cp	2	8		99	89	90	I	C
Pisum sativum L.	a	cp	2	12		81	50	61	I	B
Robinia pseudoacacia L.	t	wgM	3 S	36	20	24	10	42	I	B
Sarothamnus scoparius (L.) Wimm.	p	wgM	2	45		33	22	67	I	B
Trifolium pratense L.	p	cp	2	18		99	99	100	I	Z

Table 1 continuation

1	2	3	4	5	6	7	8	9	10	
Vicia angustifolia L.	a	wgQ	4 S	18		33	33	100	I	Z
Vicia faba L. var. *maior* L.	a	cp	1	18		93	15	16	N	A
Vicia hirsuta (L.) S.F.Gray	a	wgO		18		33	28	85	I	Z
Vicia villosa Roth	a, b	bg	2	45	74	69	72	104	I	Z
GERANIACEAE										
Erodium cicutarium (L.) L' Herit.	a, b	wgV	3 S	36		86	67	78	I	C
Geranium pratense L.	p	wgV	1	60	13	34	23	68	P	B
Geranium pussillum L.	a, b	wgV	3	24		66	69	105	I	Z
GESNERIACEAE										
Synninga hybrida hort.	a	cp	1	24		65	10	15	PP	A
HYDROPHYLLACEAE										
Phacelia tanacetifolia Benth.	a	cp	1	12	87	28	29	104	N	Z
HYPERICACEAE										
Hypericum perforatum L.	p	wgQ	2	24		100	7	7	PP	A
JUNCACEAE										
Juncus articulatus L.	p	bgM	3	30	0	33	1	3	PP	A
Juncus articulatus L.			3 S	30	0	69	0	0	PP	A
Juncus bufonius L.	a	bgQ	1	24		53	0	0	PP	A
Juncus conglomeratus L.	p	wgQ	3 S	18		28	0	0	PP	A
Juncus inflexus L.	p	wgM	4 S	30	3	48	0	0	PP	A
Juncus squarrosus L.	p	bgQ	2	30		90	3	3	PP	A
Luzula nemorosa (Poll.) E. Mey.	p	wgQ	2	12		100	10	10	PP	A
LAMIACEAE										
Calamintha vulgaris (L.) Druce	p	wgV	1	24		36	0	0	P	A
Elsholtzia Patrini (Lepechin) Garcke	a	wgV	2	12		98	2	2	PP	A
Galeopsis bifida Boenn.	a	wgV	3	24		10	6	60	I	B
Galeopsis tetrahit L.	a	wgO	3 S	30		12	12	100	I	Z
Leonurus cardiaca L.	p	wgV	2	45	18	21	0	0	I	A
Lycopus europaeus L.	p	wgV	2 S	12		30	0	0	I	A
Nepeta cataria L.	p	wgV	2	36		11	0	0	P	A
Origanum vulgare L.	p	wgV	1	30		63	1	2	P	A
Prunella vulgaris L.	p	wgV	1	36		75	13	17	PP	A
Salvia aethiopis L.	b	bg	1	8		68	27	40	I	B
Salvia horminum L.	a, b	bg	1	12		93	0	0	I	A
Salvia jurisicii Kosanin	p	bg	1	12		80	27	34	I	B
Salvia officinalis L.	hs	bg	1	12		89	77	87	I	C
Salvia pratense L.	p	bg	1	18		47	14	30	I	B
Salvia sclarea L.	b	bg	1	8		88	90	102	I	Z
Salvia splendens L.	hs	cp	1	30		29	25	86	I	Z
Salvia verticillata L.	p	bg	1	24		60	8	13	I	A
Stachys grandiflora Benth.	p	bg	2	45	12	27	7	26	P	B
Stachys lanata Jacq.	p	bg	2	18	95	69	9	13	N	A
Stachys silvatica L.	p	wgV	3	45	3	17	1	6	PP	A
Thymus serpyllum L.	hs	bg	2	12	93	94	93	99	I	Z
LILIACEAE										
Allium cepa L. cv. Czerniakowska	p	cp	1	8		95	95	100	I	Z
Allium farreri Stearn.	p	bg	1	18		94	87	93	I	Z
Allium fistulosum L.	p	bg	1	30		72	70	97	I	Z
Allium flavum L.	p	bg	1	30		83	87	105	I	Z
Allium montanum Schmidt var. *petroeum*	p	bg	1	12		85	81	95	I	Z
Allium porum L.	b, p	cp	1	24		37	34	92	I	Z
Allium pulchellum Don.	p	bg	2	45	79	87	56	64	I	B
Allium schenoprasum L.	p	cp	1	24		36	34	95	N	Z
Asparagus officinalis L.	p	cp	1	24		62	38	61	N	B
LINACEAE										
Linum usitatissimum L.	a	cp	1	4	100	100	100	100	I	Z

Table 1 continuation

1	2	3	4	5	6	7	8	9	10	
LOBELIACEAE										
Lobelia erinus L.	a	cp	1	12		92	72	78	I	C
LYTHRACEAE										
Lythrum salicaria L.	p	wgV	2	24	0	41	2	5	PP	A
MALVACEAE										
Althea rosea (L.) Cav.	p	cp	1	12		84	83	99	I	Z
Malva pusilla Sm. et Sow.	a, p	wgV	4	60	31	53	42	79	P	C
MORACEAE										
Morus alba L.			2	30		33	0	0	P	A
Morus alba L.	t	wgV	2 S	30		68	8	12	P	A
OLEACEAE										
Fraxinus oxycarpa Willd.	t	wgV	1 S	60	63	57	0	0	I	A
Ligustrum vulgare L.	s	wgV	1	30		17	0	0	P	A
Syringa vulgaris L.	s, t	wgV	1	36	17	77	6	8	P	A
ONAGRACEAE										
Chamaenerion angustifolium (L.) Scop.	p	bg	2	30	18	18	12	67	I	B
Epilobium montanum L.	p	bgQ	2	12	3	94	0	0	PP	A
Oenothera biennis L.	b	wgV	3	12	4	20	0	0	PP	A
Oenothera biennis L.				12	39	45	2	4	I	A
Oenothera muricata L.	b	wgV	6	30	0	24	0	0	PP	A
Oenothera muricata L.			6 S	30	57	72	7	10	P	A
Oenothera rubricaulis Kleb.	b	wgV	2	12	27	40	0	0	P	A
Oenothera rubricaulis Kleb.			2 S	12	58	57	1	2	I	A
PAPAVERACEAE										
Chelidonium maius L.	p	wgV	0	30		80	1	1	N	A
Eschscholtzia californica Cham.	a, p	cp	1	24		28	14	50	N	B
Papaver argemone L.	a, b	wgV	3	18	80	3	3		NN	Y
Papaver dubium L.			2	12	19	8	2		N	
Papaver dubium L.	a	wgV	2 S	12	96	24	12	50	N	B
Papaver nudicaule L.	p	cp	1	18		84	60	72	I	C
Papaver orientale L.	p	cp	2	8		96	74	77	I	C
PINACEAE										
Larix decidua Mill.			3	24	14	28	13	49	P	B
Larix decidua Mill.	t	wgM	3 S	18	22	38	20	52	P	B
Picea excelsa (Lam.)Lk.	t	wgM	3 S	12		94	83	86	I	C
Pinus mughus Scop.	s	wgQ	1	12		70	5	7	I	A
Pinus silvestris L.	t, s	wgV	1	12		99	78	79	I	C
Pseudotsuga douglasii Carr.	t	wgV	2	30	25	38	14	36	P	B
PLANTAGINACEAE										
Plantago lanceolata L.	p	wgV	1	18		70	72	103	I	Z
Plantago maior L.	p, a	wgV	1	24		68	2	3	PP	A
Plantago media L.	p	wgV	1	24		30	1	3	PP	A
Plantago pauciflora Gilib.	p, a	wgV	4	12		86	0	0	PP	A
Plantago ramosa (Gilib.) Aschers.	a	bg	2	30		88	13	15	I	A
POACEAE										
Agropyron repens (L.) P.B.	p	wgO	1	24		90	4	4	I	A
Agrostis alba L.	p	wgO	2	12		79	27	34	I	B
Alopecurus pratensis L.	p	cp	2	24		38	37	97	I	Z
Apera spica-venti (L.) P.B.	a	wgO	1	18		83	12	14	P	A
Arrhenatherum elatius (L.) P.B.	p	wgV	1	30		45	31	69	P	B
Avena fatua L.	a	wgO	2	18		72	26	36	I	B
Avena sativa L. cv. Romulus	a	cp	1	8		97	95	98	I	Z
Bromus inermis Leyss.	p	wgV	1	8	86	56	65	116	N	X
Bromus mollis L.	b	wgV	1	6	97	69	78	113	N	X
Bromus secalinus L.	b	wgO	2	8		88	65	74	I	C

Table 1 continuation

1	2	3	4	5	6	7	8	9	10	
Bromus sterilis L.	b	wgV	1	8	95	72	78	108	N	X
Bromus tectorum L.	b	wgV	1	4	96	43	83	193	N	X
Calamagrostis epigeios (L.) Roth	p	bg	2	30		12	0	0	P	A
Dactylis glomerata L.	p	wgO	1	24		91	20	22	P	B
Deschampsia caespitosa (L.) P.B.	p	wgV	2	30	43	97	52	53	P	B
Deschampsia flexuosa (L.) Trin.	p	wgV	2	24	21	33	27	82	P	C
Festuca duriuscula L.	p	bg	2	12		95	92	97	I	Z
Festuca pallens Host.	p	bg	2	30		38	28	74	I	C
Festuca pratensis Huds.	p	cp	2	12		83	33	40	P	B
Festuca rubra L.	p	cp	1	24		81	70	86	P	C
Festuca sulcata (Hack.) Nym.	p	bg	2	30		26	15	58	I	B
Festuca varia Haenke	p	bg	2	30		32	25	78	I	C
Holcus lanatus L.	p	wgV	1	12	16	43	3	8	P	A
Hordeum jubatum L.	a	bg	1	8		93	88	95	I	Z
Hordeum murinum L.	b	wgV	1	12	97	97	68	70	I	C
Hordeum vulgare L. cv. Damazy	a, b	cp	1	4	97	98	98	100	I	Z
Lolium multiflorum Lam.	p	cp	2	8		93	70	75	I	C
Lolium perenne L.	p	cp	2	8		84	82	98	I	Z
Molinia cerulea (L.) Moench.	p	wgM	2 S	45	12	56	27	48	P	B
Panicum capillare L.	a	bg	6	30	2	88	20	23	PP	B
Panicum crus-galli (L.) P.B.	a	wgO	2	12		90	82	91	I	C
Phalaris arundinacea L.	p	wgV	1	24		82	20	24	N	B
Phleum pratense L.	p	cp	2	12		90	35	39	I	B
Poa alpina L.	p	bg	2	18		40	42	105	I	Z
Poa alpina L. var. *vivipara* L.	p	bg	2	8		95	84	88	I	C
Poa annua L.	a, b	wgV	1	30	45	63	6	10	P	A
Poa nemoralis L.	p	wgV	4	18		50	3	6	P	A
Poa palustris L.	p	cp	2	30		35	20	57	N	B
Poa pratensis L.	p	wgV	1	24		44	5	11	PP	A
Poa trivialis L.	p	wgV	2	30		80	0	0	PP	A
Secale cereale L. cv. DSV	a, b	cp	1	8		98	98	100	I	Z
Secale silvestre Host	a	wgH	1	8		80	77	96	I	Z
Setaria glauca (L.) P.B.	a	wgV	1	18		85	83	98	I	Z
Setaria viridis (L.) P.B.	a	cp	1	8		94	86	91	I	C
Triticum vulgare Vill. cv. Grana	a, b	cp	1	8		96	94	98	I	Z
Zea mays L. hybrid S54*S72	a	cp	1	8		90	93	103	I	Z
POLYGONACEAE										
Fagopyrum sagittatum Gilib. cv. Hruszowska	a	cp	1	12		90	90	100	I	Z
Polygonum aviculare L.	a, b	wgV	3 S	4		60	40	67	I	B
Polygonum convolvulus L.	a	cp	1	4		78	66	85	I	C
Polygonum molle D.Don.	a	bg	1	12		32	8	25	I	B
Polygonum nodosum Pers.	a	wgO	1	18		50	49	98	I	Z
Polygonum persicaria L.	a	wgV	1	12		42	14	33	P	B
Polygonum tomentosum Schrk.	a	bgR	1	18		50	7	14	P	A
Rheum rhaponticum L.	p	cp	1	12		93	17	18	I	A
Rumex acetosa L.	p	wgV	1	8		93	78	84	I	C
Rumex acetosa L. cv. Large de Belleville	p	cp	1	8		99	92	93	I	C
Rumex acetosella L.	p	wgO	3	45	6	17	5	29	P	B
Rumex acetosella L.			3 S	45	11	27	1	4	P	A
Rumex alpinus L.	p	bgK	1	12		80	3	4	I	A
Rumex confertus Willd.	p	wgV	2	18	58	96	0	0	P	A
Rumex conglomeratus Murr.	p	wgQ	3	12		96	0	0	PP	A
Rumex crispus L.	p	wgV	1	12		87	0	0	PP	A
Rumex hydrolapathum Huds.	p	wgM	2	12		93	0	0	PP	A
Rumex obtusifolius L.	p	wgV	1	12		93	0	0	PP	A

Table 1 continuation

1	2	3	4	5	6	7	8	9	10	
PRIMULACEAE										
Lysymachia vulgaris L.			2	45	0	44	0	0	PP	A
Lysymachia vulgaris L.	p	wgM	2 S	45	0	65	0	0	PP	A
RANUNCULACEAE										
Aquilegia vulgaris L.	p	cp	1	24		45	20	44	I	B
Delphinium consolida L.	a	cp	1	60		80	51	64	N	B
Nigella damascena L.	a	cp	1	18		60	37	62	N	B
Ranunculus acris L.	p	bg	2	30		43	0	0	PP	A
Ranunculus gramineus L.	p	bg	2	45		62	31	50	I	B
RESEDACEAE										
Reseda odorata L.	a, b	cp	1	24		66	56	85	I	C
ROSACEAE										
Alchemilla pastoralis Bus.	p	wgQ	3	30		10	0	0	P	A
Filipendula ulmaria (L.) Maxim.	p	wgM	1	24	4	17	0	0	P	A
Filipendula ulmaria (L.) Maxim.			1 S	18	31	47	2	4	P	A
Fragaria vesca L.	p	cp	1	36		54	0	0	P	A
Geum urbanum L.	p	wgV	3	36		42	0	0	PP	A
Malus domestica Borb. cv. Jonathan	t	cp	1 S	8	91	88	61	69	I	B
Potentilla argentea L.	p	wgQ	3	12		86	0	0	PP	A
Sanguisorba officinalis L.	p	wgV	1	12	0	43	2	5	PP	A
Sanguisorba officinalis L.			1 S	12	30	72	11	15	P	A
RUBIACEAE										
Galium mollugo L.	p	wgV	1	18		89	39	43	I	B
Galium Schultesii Vest	p	wgV	2	24		70	37	53	P	B
Galium verum L. ssp. *Wirtgenii* (Schultz)	p	wgV	1	24		61	13	21	I	B
SALICACEAE										
Populus alba L.	t	wgV	0	8		100	100	100	I	Z
Populus nigra L.	t	wgV	0	12		57	43	75	I	C
SAXIFRAGACEAE										
Hydrangea hortensis Sm.	s	wgM	1	24		81	0	0	PP	A
Philadelphus coronarius L.	s	wgV	2	30	3	53	3	6	PP	A
Philadelphus coronarius L.			2 S	24	25	67	20	30	P	B
Saxifraga crustata Vest	p	bg	2 S	24	2	36	16	44	PP	B
Saxifraga decipiens Ehrh.	p	bg	1	18		95	43	45	P	B
Saxifraga rotundifolia L.	p	bg	2	30		72	10	14	PP	A
Saxifraga umbrosa L.	p	bg	2	45		40	0	0	PP	A
Saxifraga umbrosa L. var. *primuloides*	p	bg	2	45		57	0	0	PP	A
SCROPHULARIACEAE										
Antirrhinum maius L.	p	cp	1	12		96	40	42	I	B
Digitalis purpurea L.	p	wgV	1	8		98	97	99	I	Z
Nemesia strumosa Benth.	a	cp	2	18		82	66	80	N	C
Scrophularia nodosa L.	p	wgM	2	12		98	0	0	PP	A
Tetranema mexicanum Benth.	p	bg	2	45		90	0	0	PP	A
Verbascum lychnitis L.	b	wgV	2	12		91	3	3	PP	A
Verbascum phlomoides L.	b	wgV	3	12	10	87	5	6	PP	A
Verbascum phlomoides L.			3 S	12	30	92	2	2	P	A
Veronica austriaca L.	p	bg	2	18		90	28	31	I	B
Veronica caucasica Bieb.	p	bg	2	12		87	17	19	I	A
Veronica fruticans Jacq.	hs	bg	2	18		57	13	23	PP	B
Veronica fruticulosa L.	p	bg	6 S	18	87	93	67	73	I	C
Veronica gentianoides Vahl.	p	bg	2	18		92	65	71	P	C
Veronica incana L.	p	bg	2	8		75	70	93	I	Z
Veronica longifolia L.	p	bg	2	12		78	23	29	I	B
Veronica peduncularis Bieb.	p	bg	2	30		68	29	43	P	B
Veronica persica Poir.	a	wgV	5	18	88	43	0	0	N	A
Veronica spicata L.	p	bg	2	8		93	20	22	P	B
Veronica spuria L.	p	bg	2	18		89	50	56	P	B

Table 1 continuation

1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	
Veronica teucrium L.	p	bg	2	18		90	28	31	I	B
Veronica triphyllos L.	a	wgO	2	12		84	7	8	I	A
SIMARUBACEAE										
Ailanthus glandulosa Desf.	t	wgV	1	24		46	0	0	PP	A
SOLANACEAE										
Atropa belladonna L.	p	bg	2	45		30	1	3	PP	A
Capsicum annuum L. subsp. *macrocarpum*	a	cp	1	36	93	93	72	77	I	C
Datura stramonium L.	a	wgV	3	12	35	55	2	4	P	A
Hyoscyamus niger L.	a	wgV	6 S	18	38	11	0	0	N	A
Lycopersicon esculentum Mill.	a	cp	1	24		48	6	12	N	A
Nicotiana rustica L. cv. Pomorski	b	cp	1	12		79	61	77	I	C
Nicotiana tabacum L. cv. Kentucky 10	a	cp	1	12		98	45	46	PP	B
Petunia hybrida hort.	a	cp	1	12		70	39	56	I	B
Schizanthus pinnatus Ruiz et Pavon	a	cp	1	8		98	97	99	I	Z
Solanum dulcamara L.	hs	wgV	1	24	3	21	0	0	PP	A
Solanum dulcamara L.			1 S	36	4	34	0	0	PP	A
Solanum melongena L.	a	cp	2	24		65	1	2	N	A
Solanum nigrum L.	a	wgV	1 S	24	3	74	0	0	PP	A
Solanum tuberosum L.	p	wgV	3	24		92	3	3	P	A
TROPAEOLACEAE										
Tropaeolum maius L.	a	cp	2	12		50	46	92	P	C
Tropaeolum minus L.	a	cp	2	12		86	10	11	I	A
URTICACEAE										
Parietaria officinalis L.	p	wgV	3	60		81	54	67	P	B
Urtica dioica L.	p	wgV	1	30		47	0	0	PP	A
Urtica urens L.	a	wgV	6 S	18	67	0	0		NN	Y
VALERIANACEAE										
Valeriana angustifolia Tausch.	p	bg	2	24	57	55	27	49	I	B
Valerianella dentata (L.) Poll.	a	bg	2	18	10	25	20	80	P	C
Valerianella locusta (L.) Betcke	a	cp	1	24		88	72	82	I	C
VERBENACEAE										
Verbena hybrida hort.	p, hs, s	cp	1	18		43	41	95	I	Z
VIOLACEAE										
Viola silvestris Rchb.	p	bg	2	45	10	23	14	61	P	B
Viola Vittrockiana Gams	p	cp	1	24	90	93	82	88	I	C
VITACEAE										
Parthenocissus quinquefolia (L.) Planch.	s	wgV	1 S	45	8	23	10	43	P	B

Abbreviations used in Table

Lf – life form: a – annual; b – biennal; p – perennial; t – tree; s – shrub; hs – half-shrub

Col – seed collection: cp – cultivated plants (often commercially obtained), bg– plants growing in the Wrocław Botanical Garden; the third letter (if any) indicates the region outside Wrocław in which seeds were collected by the Botanical Garden staff, wg – own seed collection from wild-grown plants

Place of collection (third letter)

V – the vicinity of Puławy (up to 30 km); U – Lower Silesia, O – North-eastern Poland (mainly Olsztyn Province); R – Northern Poland
M – Central Poland (mainly Piotrków Province); Q – Sudetes Mountains, K – Carpathian Mountains; H – Hungary, near Kecskemet

Age – seed age; year of collection is signed „0"
the prechilled seeds are signed by „S" following number

FG – final germination; number of days after which the germination ended in the control (diffuse white light for positively photoblastic and indifferent seeds, dark for negatively photoblastic seeds)

Treatments: D – dark outdoors; lack of a number means that photoblastism was determined at room temperature, L – diffuse white light outdoors; F – under leaf canopy

Class – type of photoresponse

PP – strong positive photoblastism; ratio D/L less than 0.2
P – moderately positive photoblastism; ratio D/L 0.2 or more, but significantly less than 1
NN – strong negative photoblastism; ratio L/D less than 0.2
N – moderately negative photoblastism; ratio L/D 0.2 or more, but significantly less than 1
I – photoblastically indifferent seeds; difference L - D statistically insignificant
A – strong inhibition by FR; ratio F/L less than 0.2
B – moderate inhibition by FR; ratio F/L 0.2 or more, but significantly less than 0.7
C – weak inhibition by FR; ratio F/L 0.7 or more, but significantly less than 1
Z – no inhibition by FR; difference L – F statistically insignificant
Y – inhibition by FR could not be determined; similar inhibition was imposed by L treatment
X – FR accelerates germination relative to L treatment

Table 2. Germination [%] of seeds of three species differing in the photoblastism.

Treatment	*Arabis hirsuta*	*Lactuca serriola*	*Dianthus barbatus*
4 h D + 10 min. R + 92 h D	97	98	94
4 h D + 10 min. R + 10 min. FR + 92 h D	4	97	93
4 h D + 10 min. L + 92 h D	92	97	92
4 h D + 10 min. L + 10 min. F + 92 h D	6	97	94
96 h D	6	96	92
96 h L	97	99	93
96 h F	7	8	93
96 h F + 10 min. L + 48 h D	97	94	95
96 h F + 10 min. L + 10 min. F + 48 h D	12	11	96
96 h L + 48 h D	98	99	95

L, D, F – see Table 1; R – red light; FR – far red light

percentage relation of seeds germinating under canopy to those germinating in white diffuse light (F/L). In some rare cases, concerning negatively photoblastic seeds, both treatments gave near zero germination. In such cases the germination ratio F/L could not be determined. However, the example of *Amaranthus retroflexus* (Table 1) seems to indicate that in the better germinating lots of seeds (as it was after prechilling) the FR inhibition becomes distinct. Therefore we assign those seeds to the special class "Y" instead of "Z" which marks the lack of inhibition. Only five cases were found, when the F/L ratio in negatively photoblastic seeds might be determined as statistically not different from 1. These cases are marked "Z". A strange photoresponse was found in four out of five tested species of *Bromus*; they germinated faster under leaf canopy than in the white light; a similar response was found in *Bromus sterilis* by Hilton (1982). We introduced for them a special class "X". It is assumed that classes Y and X may concern only negatively photoblastic seeds

A considerable number of seed lots (119 species apart from 487 species mentioned in Table 1) did not germinate at all, or showed less than 10% germination even after prechilling.

Intraspecific variability of FR-inhibition

After examination of particular lots of seeds, the question arises to which extent the results are representative for species as a whole? It may be inferred from many studies (Froud-Williams et al., 1984; Anderson and Milberg, 1998) that a great variability exists between samples of seeds in their responses to light. Any categorization of species on the basis of light responses can be misleading (Vidaver, 1977). However, some species exhibit unequivocal responses irrespective of germination circumstances. For example, all known tests of germination of *Phacelia tanacetifolia* (Schulz and Klein, 1965) indicated a negative photoblastism, while solely positive photoblastic responses are known in the genus *Juncus* (Grime et al., 1981). It is easy to observe that different lots of seeds of the same species may differ in their responses to white light. The responses may be affected by internal, as well as external factors. The first group embraces genetic differences among populations (Lewak and Rudnicki, 1977), endogenous cycle of dormancy (Froud-Williams et al., 1984; Baskin and Baskin, 1985; Anderson and Milberg, 1998), and growth conditions of the parent plants and post-harvest treatment (Vidaver, 1977; Fenner, 1991). Among external factors controlling light responses especially important seems to be temperature (Baskin and Baskin, 1977; Frankland and Taylorson, 1983; Bażańska and Lewak, 1986) interacting with seed hydration (Bochenek et al., 2007). In our experiments the importance of light conditions often diminished after winter chilling (stratification) of seeds. Nevertheless, the particular lots of seeds of the same species exhibit usually similar features as to the responses to light, although exceptions to this rule may be observed. For example, some authors classify the seeds of *Amaranthus retroflexus* as positively photoblastic (Baskin and Baskin, 1977), but five different Polish collections, tested in our experiments, exhibited only negative photoblastism.

The responses to light filtered through leaf canopies are termed "far red dormancy" (FR-dormancy) after Blaauw-Jansen and Blaauw (1976). This inhibition may be treated as a type of secondary dormancy; applying classification after Roberts (1972) it might be named *induced dormancy*. A newer classification (Baskin and Baskin, 2004) regards seeds with only a light requirement for germination as *non-dormant*.

To assess the representativeness of our results, the comparisons with results obtained elsewhere seem to be useful. Among species tested by Jankowska-Błaszczuk and Daws (2007) there are 7 species examined and qualified by us as strongly FR-dormant (*Epilobium montanum, Hypericum perforatum, Lapsana communis, Poa nemoralis, Scrophularia nodosa, Stellaria nemorum, Urtica dioica*); the results from both studies agree very well.

Among 27 herbaceous species listed by Silvertown (1980), there are 12 species tested also by us. Only in 2 cases a small discrepancy appeared. *Centaurea scabiosa* classified after our experiments as I-C (weak FR-dormancy) did not show any leaf-canopy induced dormancy. *Plantago lanceolata* classified by us as I-Z (no FR-dormancy), after Silvertown exhibited a weak dormancy. The rest: *Achillea millefolium, Arabis hirsuta, Daucus carota, Galium verum, Hypericum perforatum, Leontodon hispidus, Origanum vulgare, Plantago media, Prunella vulgaris and Rumex acetosa* responded to the leaf canopy similarly in both places.

Table 3. Germination [%] of various samples of seeds of *Taraxacum officinale* Web. Tests were performed simultaneously in the year following harvest.

Collection			T	Days after sowing			
Place	m a.s.l.	month		6	8	12	18
Puławy	140	May	F	0	0	0	0
			L	0	0	50	76
		September	F	0	0	0	0
			L	27	66	83	83
Sudetes	320	June	F	0	3	3	4
Mountains			L	53	84	87	88
	450	June	F	0	0	0	0
			L	0	0	24	36
	850	June	F	0	0	0	0
			L	0	0	6	49
	1200	June	F	0	0	3	3
			L	10	36	46	61
	1200	September	F	0	0	0	0
			L	0	31	36	41
West Virginia	450	May	F	0	4	4	4
USA			L	31	58	72	72

T – treatments; m a.s.l. – meter above sea level
F, L – see Table 1

Comparison of seeds harvested in different locations and seasons indicated usually that the FR-dormancy does not vary or does so only scarcely. For example, Table 3 presents the FR-dormancy of seeds of *Taraxacum officinale* collected in various habitats. As may be seen, the course and extent of germination in white light often differed among samples, but the FR-dormancy did not.

Table 4 presents the results of testing of two different lots of *Stellaria media*. When fresh, the seeds of *Stellaria media* germinated scarcely, with a tendency to a negative photoblastism. After a long storage, the germination improved a little; after double (over two winters) stratification the seeds germinated almost fully, equally well in white light and in darkness. However, the seeds were always inhibited by light transmitted through leaf canopy (class N-A, or I-A) independently of the former treatment or age (at least up to 7 years).

Table 4. Germination [%] of two seed lots of *Stellaria media* Vill.

Collection place	Age [years]	Stratification	FG	D	L	F	F/L	Class
Olsztyn	1	none	4	5	2	0	0	-
	3	none	4	8	5	0	0	N-A
	3	once	8	10	7	0	0	N-A
	3	twice	8	43	45	2	4	I-A
Puławy	1	none	8	1	0	0	0	-
	2	none	12	8	5	0	0	N-A
	2	once	12	50	47	3	6	I-A
	2	twice	12	88	85	5	6	I-A
	7	none	8	29	26	0	0	I-A
	7	once	8	83	77	0	0	I-A

FG, D, L, F – see Table 1

In some cases we observed a slight change of the grade of FR-dormancy, especially after winter chilling. There is impossible to exclude that under some circumstances the FR-dormancy can even qualitatively differ among seed batches, although such an event was never observed in our experiments. It seems that the appearance of FR-dormancy (or lack of it) may be treated as a species specific feature.

Time course of seed germination inhibition and dormancy

In the classical works of Borthwick et al. (1952) and in many other experiments with germination, the positively photoblastic seeds of lettuce cvar. „Grand Rapids", were often used. It was easy to observe that seed responses may revert after very short times (minutes, or even seconds) of exposure to far red (FR) or red (R) radiation. The seeds which germinated (after R) or did not germinate (after FR) depended on the last signal. However, „Grand Rapids" is rather an exception in lettuce; among 12 other lettuce cultivars tested by us, none could be inhibited by a short FR, and all germinated well in darkness.

In our experiments the responses to the short FR were found only in photoblastic seeds, such as *Arabis hirsuta* or *Elsholtzia Patrini*. The seeds which germinated equally well in darkness and in white light (photoblastically indifferent) could not be inhibited by short (up to several hours) FR. However, as shown long ago by Hendricks et al. (1959) prolonged FR irradiation can inhibit germination in some seeds which are insensitive to short irradiation. Such results were easily confirmed in the present study with many of such „indifferent" seeds (among these were 12 lettuce cultivars), but many others did not respond to any light treatment. We concluded that among photoblastically indifferent seeds there are truly insensitive (signed I-Z) as e.g. common cereals, or apparently insensitive but able to be sensitized by prolonged FR (signed „I-A", „I-B" or „I-C"), as lettuce or many wild plants. It ought to be added here that there are known seeds determined as trully insensitive, which may show a grade of photosensitivity under some special circumstances (Thanos and Mitrakos, 1979). The seeds sensitized by prolonged FR treatment often did not differ in their photoresponses from positively photoblastic ones. However, the degree of photosensitivity depends at least on two factors: duration of FR-treatment and time of storing in the inhib-

Table 5. Germination [%] of seeds of three species differing in the photoblastism, as scored immediately after treatment.

Pretreatment	Treatment	*Lactuca sativa* (I-A)	*Rumex crispus* (PP-A)	*Amaranthus retroflexus* (N-A)
-	7 d L	96	77	0
-	7 d D	91	0	0
-	12 d L	98	85	0
-	12 d D	93	1	68
3 d F	4 d D	39	0	0
3 d F	1 s E + 4 d D	95	3	0
3 d F	10 m L + 4 d D	90	61	2
3 d F	4 d L	92	73	0
8 d F	4 d D	20	0	17
8 d F	1 s E + 4 d D	37	4	30
8 d F	10 m L + 4 d D	71	45	34
8 d F	4 d L	78	48	8
18 d F	4 d D	15	0	22
18 d F	10 m L + 4 d D	20	39	28
18 d F	4 d L	59	42	5
18 d F	10 d L	92	75	7

L, D, F – see Table 1; E – direct sunlight; s, m, d – second, minute, day

ited state. The „I-A" seeds of lettuce cv. Cud Vorburgu after 3 days under leaf canopy are strongly inhibited, but a weak 10 minutes R or white irradiation, or a half-second flash of direct sunlight promote full germination. After 18 days under leaf canopy, 10 minutes of white irradiation produced very little effect, and 10 days of white light were necessary for full germination (Table 5). The acquired state of photosensitivity (i.e. state of phytochrome) may persist also in dried seeds (Vidaver and Hsiao, 1972; Hartmann et al., 2005), although the aged seeds become gradually less sensitive to light. In our experiments it took 3 years before the inhibited dry seeds of *Lactuca sativa* cv. Cud Vorburgu indicated some signs of loss of photosensitivity, and after 5 years they germinated equally well in the dark as in white light. Probably the rate of such changes can differ depending on conditions of storage.

It seems that three main stages in the course of FR-dormancy of normally "insensitive" seeds could be distinguished. The first stage begins after several hours of FR treatment when a short exposure to R or white light becomes necessary for germination. In our experiments this stage was fully developed usually after 3–4 days under leaf canopy. At this stage the photoresponses resemble those observed without any pretreatment in positively photoblastic seeds. After further FR exposure, or during dark storage, the FR-dormancy becomes gradually deeper and the seeds need at least several days of white light to begin germination. In *Lactuca sativa* this stage was observed in seeds which had been stored moist as well as in those which had been stored dry; it lasted several years. In the third stage – just before loss of viability – the seeds need less and less light to germinate and finally germinate after moistening also in the dark, as before the FR-inhibition.

Photoblastism

Considering photoblastism, we ought to stress once more that it was determined under diffuse natural white light conditions, where the seeds received between 5 and 15% of normal daylight. In full daylight all the seeds are usually inhibited (Doroszewski, 1989) and therefore they might be defined as negatively photoblastic. On the other hand, a short period of irradiation may promote germination even in those seeds which are classified as negatively photoblastic (see *Amaranthus retroflexus* in the Table 5), when moderately weak but long-lasting light inhibits germination relative to a dark control (Frankland and Taylorson, 1983). Whenever photoblastism is tested, the irradiance conditions must be carefully considered.

In our experiments the majority of tested species (250 of 487) germinated equally well in diffuse white light and in the dark, and were classified as photoblastically indifferent (Table 6). Another 196 species were defined as positively photoblastic, and among these 84 species showed very strong responses. Only 41 tested species showed negative responses to light, and among these 7 were strongly inhibited.

Although phytochrome governs both photoresponses – photoblastism and ability to FR-inhibition, they do not always appear jointly. The main body of exceptions is described above: apparently „insensitive" seeds which can be inhibited by prolonged FR. The positively photoblastic seeds usually show strong FR inhibition (Table 6). In the extremely photoblastic group (class PP), seeds of 74 species out of 84 were greatly inhibited (class A). Also among negatively photoblastic seeds, the most frequently represented is class A. Almost all the FR-insensitive seeds were also photoblastically indifferent, but only about 36% of indifferent species were also FR-insensitive (class I-Z). Only about 19% of tested species (91 out of 487) did not demonstrate any phytochrome-mediated responses in germination: neither photoblastism, nor FR-inhibition.

Table 6. Number of species in particular classes of photoblastism (PP, P, I, N, NN) and of FR-dormancy (A-X).

Photo-response	A	B	C	Z	Y	X	Total
PP	74	9	1	0	0	0	84
P	47	49	16	0	0	0	112
I	39	58	62	91	0	0	250
N	13	8	3	5	1	4	34
NN	0	0	0	0	7	0	7
Total	173	124	82	96	8	4	487

PP, P, I, N, NN, A, B, C, Z, Y, X – see Table 1.

Prechilling

Many lots of seeds, even after several years of dry-cold storage in the refrigerator, showed a deep dormancy which could not be alleviated by summer sowing. A considerable part of these seeds germinated, however, after one-winter of outdoor moist prechilling (stratification).

Stratification was applied in the case of seeds that did not germinate in the autumn, or germinated in a very low proportion. After this treatment seeds were tested along with control seeds which spent the winter dry in a refrigerator.

The seeds of 191 species underwent stratification and among these the seeds of 119 species maintained their dormancy and did not germinate in summer, or germinated less than in 10%. In the case of 72 species, the seeds germinated significantly better after stratification.

Table 7 presents typical examples of response to FR in stratified seeds in comparison with unstratified ones. Particularly spectacular in this respect are the seeds of *Amaranthus retroflexus*, which did not germinate at all without stratification, whereas after stratification germination was 99%. This is not a case of after-ripening, observed in numerous species, because seeds stored in a dry state, both at room temperature and in a refrigerator, failed to germinate. It should be noted here that not all batches of seeds of *A. retroflexus* displayed such rigorous requirements as shown in the Table 7; the 5-year old seeds germinated also without stratification, although only in the dark.

If weakly germinating seeds showed positive or negative photoblastism prior to stratification, the character displayed tends to continue also after stratification. Often, however, the response of seeds become more indifferent (e.g. *Oenothera muricata, Sonchus arvensis*). Among 30 cases in which the photoblastism could be directly compared, seeds of 17 species did not change the class of photoblastism, but in 6 cases the seeds shifted from PP to P class, in 4 cases from P to I, in 2 cases from PP to I, and in 1 case from NN to N class. A contrary effect, with stronger photoblastism after stratification, was never observed.

Among 72 stratified lots of seeds, 69 showed an inhibition of germination under leaf canopy, which was mostly very strong (Table 8). The exceptions regard seeds of *Vicia angustifolia*, where the effects of wintering may be simply ascribed to the softening of the „hard" seed cover (Grzesiuk, 1967), and may be named scarification rather than stratification. In two other cases (*Galeopsis tetrahit* and *Heracleum sibiricum*) germination was very low and formal testing of differences may be unreliable.

These results are intriguing, as among the seeds not requiring stratification there is a considerable percentage (about 22%) of species that do not display any FR-inhibition. Table 8 presents the appropriate comparisons between species which do or do not require stratification for germination. The thesis that the differences observed in the two samples were incidental, would have, after statistical testing, a probability of virtually zero. Seeds requiring stratification are usually under stronger phytochrome control than seeds easily germinating without stratification. Since almost all the stratified species displayed phytochrome control of germination, and many of them changed their type of response to white light, it may be inferred that the effect

Table 7. Germination [%] of seeds before and after winter chilling.

Species	Before winter			After wintering under natural conditions			After wintering under laboratory conditions; 4°C; dry seeds		
	L	D	F	L	D	F	L	D	F
Amaranthus retroflexus	0	0	0	17	99	0	0	0	0
Arabis allioni	18	0	4	86	0	5	21	0	5
Bidens melanocarpus	1	0	0	90	1	2	1	0	0
Melandrium rubrum	37	0	0	63	54	0	60	21	0
Oenothera muricata	23	3	0	72	57	7	25	3	0
Saponaria officinalis	0	3	0	33	70	0	0	0	0
Sonchus arvensis	12	0	0	43	42	1	34	3	0

L, D, F – see Table 1

Table 8. Photoresponses of seeds with chilling requirements (stratified) and of easy germinating seeds (non-stratified). Number of species in particular classes.

Seeds	PP	P	I	N	NN	A	B	C	Z	Y+X	Total
Stratified	12	28	22	6	4	37	22	6	3	4	72
Non-stratified	72	84	228	28	3	136	102	76	93	8	415
Total	84	112	250	34	7	173	124	82	96	12	487

PP, P, I, N, NN, A, B, C, Z, Y, X – see Table 1

of stratification is somehow related to the phytochrome mechanism. Of course, such an „induction by enumeration" does not constitute sufficient evidence.

Since the time of Kinzel (1920), however, there has been a lot of data, confirming various types of interaction between light and chilling effects (Taylorson and Hendricks, 1969; Li et al., 1994), or even between the effects of chilling and the state of phytochrome (Van der Woude and Toole, 1980). Without going into molecular mechanisms, it is still possible to state that seeds requiring stratification show also phytochrome control of germination. Both the mechanisms of adaptation (thermic towards winter and radiative towards competition) are therefore not mutually exclusive, but occur jointly.

Systematic position

The relations between taxonomic position and FR-inhibition seems to be rather weak. A great diversity of responses may be observed between species belonging to the same family. Table 9 includes families represented in our experiments by at least 4 species. There are species of various classes of FR-inhibition in almost all families; moreover, we observed great differences also within genera.

However, some regularities may be found. All 6 tested species of *Juncaceae* family and 6 out of 7 *Rosaceae* species showed a strong FR-inhibition. On the other hand, all 4 tested *Convolvulaceae* species did not respond to FR at all, similarly as 7 out of 9 *Liliaceae* and 13 out of 20 *Fabaceae* species.

Taking into account only these families which are represented by at least 10 species, one can arrange the following series from the most to the least sensitive to FR: *Solanaceae* (77% of species in the classes A+B), *Lamiaceae* (76%), *Scrophulariaceae* (75%), *Asteraceae* (72%), *Polygonaceae* (71%), *Caryophyllaceae* (56%), *Chenopodiaceae* (54%), *Campanulaceae* (52%), *Brassicaceae* (51%), *Poaceae* (43%) and *Fabaceae* (25%). The differences between five top and two last families are statistically significant at 0.01 confidence level (chi square test). Perhaps, formal testing may be not justified here, because the choice of species not always was done at random (e.g. we attempted to test all available *Dianthus* species, to determine the variability within genera), and therefore further examples of such testing will be not shown. However, the conclusion that the mentioned differences between families are true, seems to be reasonable.

Table 9. Photoresponses within families. Table values are number of species.

Family	Photoblastism					FR-dormancy					Total	Ch	N.g.
	PP	P	I	N	NN	A	B	C	Z	Y+X			
AMARANTHACEAE	1	0	1	2	0	3	0	0	1	0	4	1	0
APIACEAE	0	2	6	0	0	2	1	1	4	0	8	3	11
ASTERACEAE	16	27	56	2	0	41	32	14	14	0	101	9	7
BORAGINACEAE	1	0	4	0	0	2	1	1	1	0	5	0	0
BRASSICACEAE	4	11	19	2	3	10	10	10	6	3	39	9	1
CAMPANULACEAE	5	11	7	0	0	7	5	8	3	0	23	1	2
CARYOPHYLLACEAE	4	4	25	3	0	12	8	9	7	0	36	4	2
CHENOPODIACEAE	1	7	3	1	1	5	2	2	3	1	13	7	1
CONVOLVULACEAE	0	0	4	0	0	0	0	0	4	0	4	0	2
DIPSACACEAE	2	0	2	0	0	2	1	1	0	0	4	1	0
FABACEAE	0	1	17	2	0	1	4	2	13	0	20	3	6
JUNCACEAE	6	0	0	0	0	6	0	0	0	0	6	4	2
LAMIACEAE	3	4	13	1	0	11	5	1	4	0	21	2	7
LILIACEAE	0	0	7	2	0	0	2	0	7	0	9	0	5
ONAGRACEAE	1	1	3	0	0	4	1	0	0	0	5	3	1
PAPAVERACEAE	0	0	2	3	1	1	2	2	0	1	6	2	3
PINACEAE	0	2	3	0	0	1	2	2	0	0	5	1	0
PLANTAGINACEAE	3	0	2	0	0	4	0	0	1	0	5	0	0
POACEAE	3	12	25	6	0	8	12	10	12	4	46	2	7
POLYGONACEAE	4	4	9	0	0	9	3	3	2	0	17	0	2
RANUNCULACEAE	1	0	2	2	0	1	4	0	0	0	5	0	9
ROSACEAE	2	4	1	0	0	6	1	0	0	0	7	3	12
SAXIFRAGACEAE	5	2	0	0	0	4	3	0	0	0	7	2	0
SCROPHULARIACEAE	4	5	9	2	0	7	8	3	2	0	20	3	4
SOLANACEAE	4	2	4	3	0	8	2	2	1	0	13	3	1

PP, P, I, N, NN, A, B, C, Z, Y, X – see Table 1; Ch – species requiring winter chilling to germinate; N.g. – species not germinating in any test used.

Table 10. Photoresponses within life-forms. Table values are number of species.

Life-form	Photoblastism					FR-dormancy					Total	Ch	N.g.
	PP	P	I	N	NN	A	B	C	Z	Y+X			
a	16	19	61	15	4	36	24	20	30	5	115	19	17
a, b	3	5	27	3	2	17	4	9	8	2	40	12	2
a, p	1	2	3	1	0	2	2	1	2	0	7	0	0
b	4	8	17	4	1	15	5	4	6	4	34	5	14
b, p	4	0	4	0	0	4	3	0	1	0	8	2	5
p	47	66	119	10	0	87	73	41	40	1	242	21	48
p, a	2	0	0	0	0	2	0	0	0	0	2	0	0
p, hs, s	0	0	1	0	0	0	0	0	1	0	1	0	0
hs	2	1	4	0	0	1	2	1	3	0	7	1	0
s	2	7	5	0	0	4	5	2	3	0	14	5	18
s, t	0	1	2	0	0	1	0	2	0	0	3	0	7
t	3	3	7	1	0	4	6	2	2	0	14	7	8
Total	84	112	250	34	7	173	124	82	96	12	487	72	119

PP, P, I, N, NN, A, B, C, Z, Y, X, a, b, p, s, hs, t – see Table 1.
Ch – species requiring winter chilling to germinate; N.g. – species not germinating in any test used.

Considering the Table 9, one can distinguish *Juncaceae, Rosaceae, Saxifragaceae* and *Onagraceae* as the most FR-sensitive families. *Convolvulaceae* and *Fabaceae* may be mentioned as the least sensitive. Relatively great proportion of insensitive species has been found also in *Poaceae and Brassicaceae* families.

Seeds of all tested species of *Juncus, Cirsium* and *Solanum* were strongly inhibited by FR. Also *Senecio, Chenopodium, Plantago, Rumex* and *Saxifraga* species were mostly FR-sensitive.

Life-form

It might be expected that plants differing in life-form also differ somewhat in the seed photoresponses. However, no confirmation of this assumption was found in our experiments. Table 10 presents responses of plants belonging to various life-forms, as classified after Szafer et al. (1976) or Hegi (different issues). The distribution of FR-dormancy in particular classes seems to be similar within all life-forms. Class A (strong inhibition) is the most numerous in annuals, as well as in biennals and perennials, and the percent of species in class Z (lack of inhibition) is everywhere similar. As concerns shrubs and trees, the small number of species does not allow any firm conclusion. The only difference may be found between annuals and perennials in the percentage of species with negatively photoblastic seeds; in annuals this percent is significantly greater (test "t").

Seed size

Many authors found a distinct relation between seed size and photoblastism (Grime et al., 1981; Pons, 1992; Thompson et al., 1993; Jankowska-Błaszczuk et al., 1998; Milberg et al., 2000); large-seeded species are more independent on light than small-seeded ones. Small seeds usually are positively photoblastic, while large seeds are often indifferent or (more rarely) negatively photoblastic.

An attempt was performed to determine relations between seed size and FR-dormancy among wild-grown plants (252 species). The dimension of seeds were quoted after Kulpa (1974) or, if lacking there, after Brouwer and Stählin (1955). As may be seen in Table 11, our results support strongly the relation between seed size and photoblastism, described earlier by others. Average volume of negatively photoblastic seeds are more than three times greater than that of positively photoblastic ones. The indifferent seeds occupy a middle position. Similar differences exhibit seeds belonging to various classes of FR-dormancy. The most FR-sensitive seeds (class A) are exceptionally tiny. The differences of average volume between other classes

Table 11. Arithmetic means of seed size and photoresponses in 252 wild species.

Class	J	W	T	Vol	F/L
P+PP	2.4	1.2	0.8	2.3	18
I	2.8	1.5	1.0	4.2	55
N+NN	4.2	1.8	1.1	8.3	52
A	2.3	1.1	0.7	1.8	4
B+C	3.1	1.6	1.1	5.5	55
Z	2.7	2.0	1.2	6.5	99

J, W, T – seed length, width, thickness [mm]; Vol – JWT product;
F/L percent germination under leaf canopy relative to the diffuse light control.

(B, C, Z) are moderate. However, between classes B+C and Z, a significant difference of shape appears. The seeds absolutely insensitive to the FR (class Z), are more rounded; all three dimensions (especially length and width) are relatively close to each other. Perhaps, this feature of seeds may be of importance for germination and reproduction, but any speculation needs more sophisticated study.

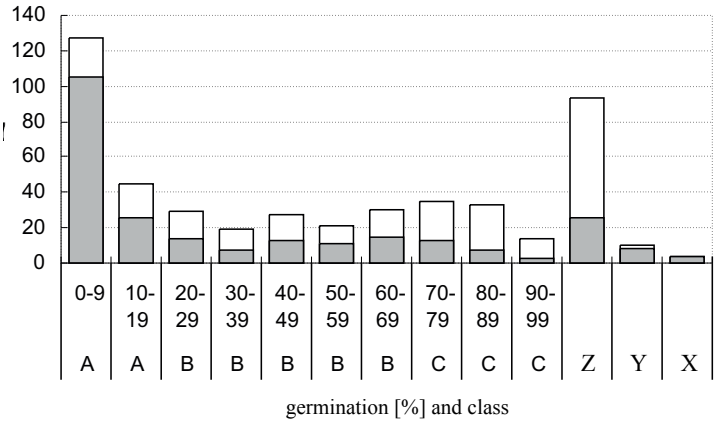
Germination rate

An excellent relationship was found between the dynamics of germination and the photoresponses of seeds. Among 86 species that germinated finally within 8 days (fast germinators), 72 species (84%) were photoblastically indifferent, while among species requiring 9–18 days for final germination this percentage dropped to 54%, and among those requiring more than 18 days (slow germinators) to 34% (Table 12).

Similarly, the FR-dormancy is much more frequent and stronger among slow germinators; only 11% of them are insensitive to the FR, and 44% are strongly FR-dormant; among fast germinators these values are 41% and 12%, respectively.

Wild versus cultivated plants

Our experiments gave also a strong evidence that the FR-dormancy is much more frequent among wild grown plants than among cultivated ones (Table 13, Figure 1).



A, B, C, Z, Y, X – see Table 1

Figure 1. Number of species in particular classes of FR-dormancy. Grey bars indicate wild-grown plants.

A great majority (79%) of cultivated species were photoblastically indifferent, and 42% of them did not indicate any FR-dormancy. Among wild plants these respective values were 36% and 10%. The botanical garden subsample occupies an intermediate position, which might be expected to occur in this miscellaneous collection.

It seems that the evident difference between cultivated and wild plants may be explained (at least in a considerable part) by selection against slow germination in cultivated plants. E. Salisbury (1961) wrote: "*…during the many centuries that man has cultivated cereals and saved their seed he has tended to select those strains which gave an immediate germination"*. This conclusion seems to be true also in relation to other cultivated plants.

Table 12. Seed photoresponses as related to the time of final germination (FG, days). Table values are number of species.

FG	Photoblastism					FR-dormancy					Total
	PP	P	I	N	NN	A	B	C	Z	Y+X	
< 9	1	7	72	5	1	10	15	21	35	5	86
9–18	31	45	112	14	5	78	48	37	39	5	207
>18	52	60	66	15	1	85	61	24	22	2	194
Total	84	112	250	34	7	173	124	82	96	12	487

FG, PP, P, I, N, NN, A, B, C, Z, Y, X – see Table 1

Table 13. Seed photoresponses within collections (Coll) of cultivated plants (cp), plants from botanical garden (bg), and wild-grown plants (wg). Table values are number of species.

Coll	Photoblastism					FR-dormancy					Total
	PP	P	I	N	NN	A	B	C	Z	Y+X	
cp	3	5	84	14	0	11	18	33	44	0	106
bg	18	32	76	3	0	30	48	25	26	0	129
wg	63	75	90	17	7	132	58	24	26	12	252
Total	84	112	250	34	7	173	124	82	96	12	487

PP, P, I, N, NN, A, B, C, Z, Y, X – see Table 1

SPECIAL CASE STUDIES

In the experiments with germination of seeds under leaf canopy, sometimes unexpected features of seed behaviour were observed. When – in our opinion – the processes underlying these features had a more general importance, additional tests were performed to elucidate the observed phenomena. In the following paragraphs five of such cases are described.

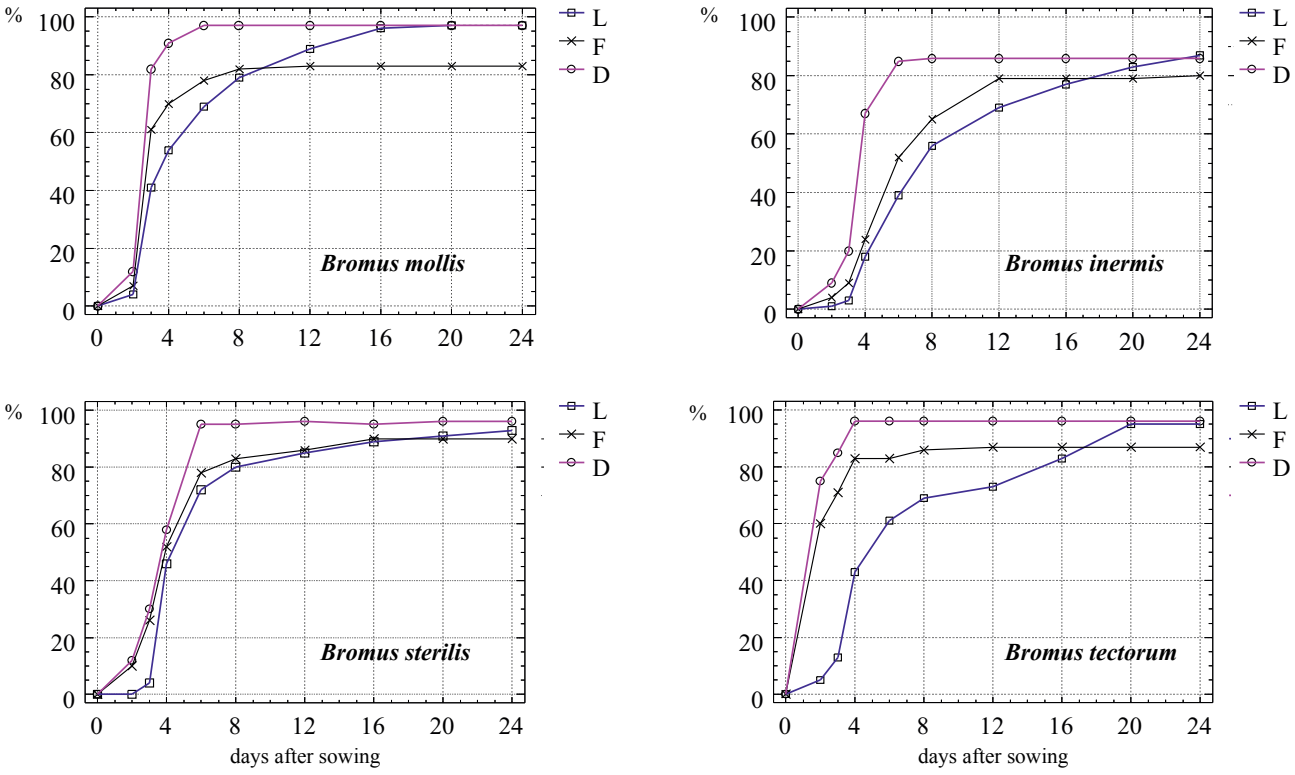
Unusual photoresponses in the genus *Bromus*

In early experiments in 1975 we also tested the seeds of 4 *Bromus* species: *Bromus inermis, B. secalinus, B. sterilis* and *B. tectorum*. Only *B. secalinus* (a rare weed of rye fields, nowadays almost extinguished) showed a weak inhibition under the leaf canopy. The other 3 species – particularly *B. tectorum* – germinated better under the canopy than in the white light control. The results were so astonishing that we decided to postpone publication until these effects would be additionally verified and observed in detail.

Hilton in 1982 and later in 1987 described – as an unusual effect – the photoinhibition by red light in *Bromus sterilis*. These publications gave us evidence that the strange behaviour of *B. sterilis* seeds is typical of the species and not only of particular provenance or lots that we have had in tests. We might suppose *per analogiam* that this is true also for other *Bromus* species.

We added to the experiments the seeds of *Bromus mollis* and conducted carefully special tests in 6 replications lasting 36 days. The results are presented in Figure 2. All 4 species showed a pronounced negative photoblastism; the germination in darkness was always faster than in the light control and than in the FR treatment. It may be speculated that the far red irradiation transmitted through a leaf canopy is perceived by seeds of *Bromus sp.* similarly as the darkness, and – furthermore – that the inhibiting effect of white light is exerted by another spectral band. Interpretation of such effects do not necessarily need the hypothesis about the specificity of *Bromus* phytochrome; they might be caused by unusual spectral features of seed coat transmittance. The role in photosensitivity of the structures surrounding the embryo of *B. rubens* seeds was described by Corbineau et al. (1992).

It must be stressed that the better germination in FR is transient; after 2 or 3 weeks under natural conditions germination in white light control prevailed (Figure 2). It seems that a proportion of the seeds (about 5–15%) undergoes the far red inhibition as other species do; in our experiments the seeds of *B. mollis* germinated finally under leaf canopy in 83%, while these in darkness and in dif-



L, F, D, – see Table 1

Figure. 2. Time course of *Bromus* seed germination [%] under various light conditions.

fuse white light germinated up to 97%. The pronounced variability of seed photoreactions within populations of *B. sterilis* and *B. mollis* was reported by Ellis et al. (1986). This may be evidence of a mixed strategy of reproduction.

Polymorphic seeds in the genus *Atriplex*

Seed dimorphism has been reported for a number of *Atriplex* ssp. (Imbert 2002). Among these in our experiments, *Atriplex nitens, A. patulum* and *A. hastatum* have dimorphic, and *A. hortense* even trimorphic seeds; nomenclature and description is after Kulpa (1974). The seeds differ in morphology, and also in colouring. The ripe seeds of *A. nitens* and *A. patulum* are black and yellow, *A. hastatum* black and brown, and *A. hortense* has two forms of black („vertical" and „horizontal"), and one kind of yellow seeds. It was easy to observe that yellow or brown seeds always germinated faster and to a greater extent than black seeds did.

After some preliminary experiments we stated that the germination of *A. hortense* seeds of both black forms did not differ in their germination and therefore in the further experiments they were treated jointly. The germination of fresh or dry-stored black seeds was erratic and very low; during 24 days germinated 6% (*A. nitens*) or 4% (*A. hortense*). They showed a kind of positive photoblastism, but it hardly could be formally tested because of the low germination rate (Table 14). The yellow seeds germinated easily up to 100% (*A. nitens*) and 68% (*A. hortense*). The dark germination was considerably smaller in both species. Under leaf canopies the yellow seeds germinated almost as well as in white light control. The diversity of *A. hastatum* seeds seems to be a little smaller than in the above mentioned species. The FR-dormancy of brown seeds of *A. hastatum,* although significant, is much weaker than that of black seeds.

Table. 14. Germination [%] of *Atriplex* seeds under various light conditions.

Species	Seed colour	Age, chilling	Dark	Diffuse white light	Under leaf canopy
A. hortense L.	black	2	0	4	2
A. hortense L.	black	2, ch	4	61	4
A. hortense L.	yellow	2	24	68	62
A. hortense L.	yellow	2, ch	56	63	64
A. nitens Schkuhr	black	1	1	6	0
A. nitens Schkuhr	yellow	1	74	100	96
A. hastatum L.	black	1	8	34	3
A. hastatum L.	brown	1	85	99	30
A. patulum L.	black	4	0	10	1
A. patulum L.	black	4, ch	19	46	8

Age – years after collection; Chilling (ch) outdoors over one winter

The prechilling of black seeds of *A. hortense* and *A. patulum* strongly increased the germination in white light control, but the germination in darkness and under leaf canopy remained low. The yellow seeds germinated in the control after chilling similarly as before, but improved their germination in darkness, as has often been observed in other species.

The observed phenomena may be interpreted as a further example of the mixed strategy of reproduction, advantageous in the variable environments (Venable, 1985; Haccou and Iwasa, 1995; Imbert, 2002). Another conclusion which may be derived from these tests is that the chilling requirements appear jointly with the ability to FR-dormancy even within the seeds produced by the same maternal plant. The situation resembles the correlation between these two adaptive mechanisms described for various species and supports the view that the effects of chilling are somehow related to the phytochrome.

Inhibitory effects of full daylight

Analyzing experiments with lettuce seed germination under leaf canopies (Górski, 1975), an unexpected result was found: the maximal germination occurred in a sparse maize canopy, but not in an open site. Further experiments including filtered spectral bands of natural daylight of different irradiances (Górski and Górska, 1979) gave evidence that the observed inhibition of germination outside canopy is a kind of photoresponse, known as High Irradiance Response (HIR), controlled by the phytochrome (Hartmann, 1966; Frankland and Taylorson, 1983). More recent findings (Casal et al., 1998; Shichijo et al., 2001) indicate that the main role in the HIR plays phytochrome A (phyA), whilst phytochrome B (phyB) is responsible for the Low Fluence Response (LFR) that acts under leaf canopy.

In order to determine the extent of the observed inhibition among species, a series of special experiments was performed (Table 15).

All tested species germinated almost fully in control i.e. in wooden framework boxes, permitting no sunflecks, where the global irradiance was limited to about 10% of full daylight. Out of 17 tested species, the inhibition in open stands occurred in 15 cases, except *Alyssum maritimum* and *Elsholtzia Patrini*. It seems that there is no simple relation between FR-sensitivity and responses to the strong light. The seeds that usually are strongly inhibited under leaf canopy (PP-A and I-A) were similarly inhibited also in open stands, but this is not a rule. *Taraxacum officinale* and *Arthemisia absinthium* germinated better in full daylight than under leaf canopy; *Elsholtzia Patrini* even better than in the control. The seeds determined previously as completely deprived of photoresponses (I-Z: *Cheiranthus cheiri, Secale silvestre, Setaria glauca, Sinapis alba*, common cereals) showed in open stands an inhibition of various strength. The only exception is *Alyssum maritimum.*

Table 15. Germination of seeds under full daylight conditions, presented as a percent of the control in diffuse light. The values are means of two unrelated experiments.

Species	Type of photoresponse	Germination [%] scored after	
		8 days	16 days
Alyssum maritimum Lam.	I-Z	100	105
Arabis hirsuta Scop.	PP-A	0	37
Arabis pumila Jacq.	PP-A	0	7
Arabis vochinensis Spreng.	I-A	0	0
Arthemisia absinthium L.	PP-A	33	87
Avena sativa L.	I-Z	20	59
Cheiranthus cheiri L.	I-Z	4	32
Elsholtzia Patrini Garcke	PP-A	103	103
Hordeum vulgare L.	I-Z	25	43
Lactuca sativa L.	I-A	0	7
Lactuca serriola L.	I-A	0	0
Secale silvestre Host	I-Z	28	27
Setaria glauca (L.) P.B.	I-Z	30	44
Sinapis alba L.	I-Z	80	97
Taraxacum officinale Web.	PP-A	21	79
Tussilago farfara L.	I-A	4	40
Triticum vulgare Vill.	I-Z	75	92

Photoresponses: I-Z – no photoresponses; PP-A – positively photoblastic and FR-sensitive; I-A – photoblastically indifferent and FR-sensitive.

Although dishes with seeds were carefully watered, it could not be excluded that the inhibition of seeds normally insensitive to light might be partly caused by a supraoptimal temperature or by a water stress in full sunlight. However, similar results are known from other investigations, where weak white light exerted positive, but strong light negative effects on germination (Negbi and Koller, 1964; Corbineau and Come, 1982; Doroszewski, 1989; Ellis et al., 1989). There is no doubt that the phytochrome is involved in these dual responses (Frankland and Taylorson, 1983), although the detailed mode of action is still under debate (Arana et al., 2007; Heschel et al., 2008).

Interpreting all experiments conducted under natural conditions, it become obvious that the classical concept of seed photoblastism, developed under laboratory conditions, should be profoundly modified. The same seeds may be positively photoblastic (in weak light) and negatively photoblastic (in strong light, usually absent in laboratory experiments). The function describing germination in relation to light intensity is nonmonotonic; the seeds differ in the position of maximal germination on the irradiance axis (Doroszewski, 1989). This position may vary with temperature; very often it depends on daylength. At high energy fluence rates germination is often higher in short days; therefore the conception of "short-day seeds" has been once developed (Isikawa, 1954).

The inhibition of germination show a linear dependence on the logarithm of the irradiance (Górski and Górska 1979, Frankland and Taylorson 1983, Thanos et al. 1994). Depending on spectral composition of the irradiance, the slopes of the function may vary, although remain parallel to each other. The maximum inhibition appears at 720 nm, which suits to the maximum of the HIR (Hartmann 1966, Pamukov and Schneider 1978). It suits also to the maximum absorption in the alpha band of water vapour (Górski 1976). Probably the coincidence between HIR and absorption of solar radiation by atmospheric water vapour is not accidental. One can hypothesise that the HIR have originated in the course of evolution as a mechanism signaling moisture conditions.

Far red dormancy increases lettuce seed longevity

After experiments with lettuce seeds cv. Cud Vorburgu, many dishes remained with seeds in the state of secondary dormancy imposed by FR (a six-day exposure to light filtered through a dense canopy of rhubarb leaves). After this treatment the dishes with achenes were removed and placed in the dark at room temperature; during several months of storage the seeds dried. When rewetted the seeds do not germinate unless irradiated for 10 days in diffuse white light. Control seeds, which had not been exposed to FR, germinated fully after 3 days in the dark.

In the following years an unexpected result was observed: the dormant seeds extended their longevity by 4–6 years as compared with the control seeds, which completely lost their viability in the third year (Table 16). Then the preirradiated seeds remain unaffected, but in the next year about 15% germinated after 15 days of imbibition in the dark. Beginning with the sixth year the seeds germinated after 3 days of imbibition equally well in the dark as in diffuse light.

In the seventh year a field test was performed; the plants from inhibited seeds and from uninhibited fresh seeds (harvested in the previous year) did not differ in their development and shape. In the eighth year the dormant seeds were still capable of germination, although about 10% of germinated seeds gave abnormal seedlings, the protrusion of cotyledon (but not radicle) being the first visible manifestation of germination. After further 2 years (i.e. 10 years after harvest) 72% of seeds still germinated, but the seedlings were mostly aberrant.

We may present a conclusion that seems to be of special importance: the FR-dormancy can considerably lengthen the longevity of dry-stored seeds. The mechanisms of this is not known; it could be only speculated that the dormancy decreases the use of the supply materials. Although we have no direct information on the behaviour of FR-dormant seeds which have been stored moist for many years, it seems probable that in this case the whole life span of seeds may be longer, because in moist seeds the repair processes can proceed (Villiers, 1974; Burgass and Powell, 1984).

Table 16. Germination [%] of seeds of *Lactuca sativa*, cv. Cud Vorburgu, after six days exposure under leaf canopies in the first year. The germination was scored 3 and 15 days after imbibition. In the brackets the percent of abnormal seedlings.

Seed age [years]	Under leaf canopy				Control seeds			
	Diffuse light		Dark		Diffuse light		Dark	
	3 days	15 days	3 days	15 days	3 days	15 days	3 days	15 days
1	77	96	18	20	95	96	92	95
2	0	95	0	0	86	87	85	87
3	0	97	0	3	0	0	0	0
4	0	94	0	15	0	0	0	0
5	28	92	20	83	-	-	-	-
6	93	96	90	95				
7	90	95(3)	90	94(4)				
8	87	90(10)	86	87(10)				
10	0	72(62)	-	-				
14	0	0	-	-				

It seems that in many cases the prolonged longevity of soil-buried seeds, as compared to dry storage in the laboratory (Roberts, 1972), may be related to leaf canopy imposed dormancy followed by burial (Fenner, 1980). In the experiments with seeds of 12 species buried in the soil (Górski and Rybicki, 1985), the number of plants emerging from FR-treated seeds was significantly greater than that from control seeds in 3 cases: *Amaranthus retroflexus, Apera spica-venti* and *Lactuca serriola*. In the experiments performed by Doroszewski (1997) among 6 tested species, a significant improvement of germination of the FR-treated seeds occurred in 5 species.

It is worthy of attention that the FR irradiation may affect the seed germinability (Hayes and Klein, 1974) and longevity (Contreras et al., 2009) even during seed development on maternal plant.

Inhibition of germination by air flow

Starting experiments with seed inhibition under leaf canopy we were aware of the necessity of eliminating the impact of gaseous or volatile materials excreted by plant tissues; such effects have been formerly reported (Barton, 1965). At the very beginning we used forced ventilation of dishes with seeds. Surprisingly, lettuce seeds did not germinate at all, neither under the canopy, nor in the control. We then used another technique (see paragraph Methods), but the problem of inhibition by the air flow remained. We eliminated the probable effects of moisture stress by using saturated humid air; still the seeds remained dormant. It was as though the air flow removed a seed-released substance that was necessary for seeds to germinate. Two such substances were possible candidates: CO_2 and ethylene (Barton, 1966; Negm and Smith, 1978; Grzesiuk and Kulka, 1981). The stimulatory effects of ethylene have been well known since at least the experiments of Toole et al. (1964), who showed that under some circumstances even the presence of a few apples (releasing ethylene) may cause germination.

Several special experiments were conducted under laboratory conditions with seeds of *Lactuca sativa* L.*, Lactuca serriola* L. and *Amaranthus retroflexus* L. The results were published in Polish (Górski and Jurzysta, 1989); the following are the main conclusions.

All three species indicated inhibition of germination by air flow or by chemical trapping of seed-released ethylene; the inhibition was cancelled by adding exogenous ethylene. These results seemed to give sufficient evidence of the role played by this compound when it is present in the air surrounding the seed. Similar features of seed behaviour have also been observed by Rudnicki et al. (1978) under low pressure conditions. We ventured the hypothesis that a thin layer of ethylene outside the seed cover is necessary to prevent excessive release of ethylene by the inner structures (according to Fick's law). A somewhat related explanation was given by Petruzzelli et al. (2000), that ethylene is needed for promoting further ethylene biosynthesis We did not found any interactions with light, which is in agreement with conclusions of Abeles and Lonski (1969) that phytochrome does not play any role in ethylene production.

Some publications indicate that the stimulatory action of ethylene is not common among seed species (Lalonde and Saini, 1992), although the number of known cases with positive reactions has been increasing (Kępczyński and Kępczyńska, 1997).

In our opinion, one more related question is worthy of attention: does the observed phenomenon play any ecological role under natural conditions? For example, one could speculate that air flow helps seeds lying on the soil surface to distinguish between safe and unsafe microsites; windy locations can be unsuitable because they are exposed to soil erosion and excessive evaporation. The question cannot be solved without further field experiments.

CONCLUDING REMARKS

About one half of tested species germinated equally well in darkness as in diffuse white light, but a great majority of these "insensitive" species could be inhibited by prolonged exposure under leaf canopy that transmits mainly far red light. Only a small fraction of species did not indicate any photoresponse and might be determined as truly light-insensitive.

Various lots of seeds of the same species may differ somewhat in their photoresponses in relation to white light (photoblastism). This diversity may be imposed by various factors, both internal and external; often the seeds become less dependent on light after winter chilling. As concerns the responses to the far red light (FR-dormancy), the variability among particular seed samples seems to be much smaller. The seeds from various habitats and times of collection, before and after prechilling, usually show similar type of FR-dormancy, although a slight quantitative difference may occur. We postulate that the type of response to the FR radiation may be treated as species specific.

Time course of the FR-dormancy commencement and ending may be related to the position of seed beneath the leaf canopy, as well as to the length of period in the leaf shade. These factors increase the diversity of seed behaviour; even primarily homogeneous seeds will germinate in different times.

All the seeds requiring winter chilling (stratification) showed also a sensitivity to far red light. Because both adaptive mechanisms appear jointly, and the chilling modifies responses to white light, it may be inferred that the effect of stratification is somehow related to the phytochrome mechanism.

Analysing species of different life-forms, no significant diversity in frequency of FR-dormancy could be found between these forms. The percent of negatively photoblastic seeds is slightly greater in annuals than in perennials.

There exists a significant relation between seed size and photoresponses. The positively photoblastic seeds in average are smaller than indifferent and negatively photoblastic ones. Tiny seeds are usually extremely sensitive to the FR.

The positively photoblastic and FR-sensitive species germinate more slowly than insensitive ones. Fast germinating seeds are usually photoblastically indifferent and FR-insensitive. Since the agricultural selection have preferred seeds germinating fast and uniformly, the cultivated plants are often deprived of any photoresponses.

It may be inferred from the above studies that the sensitivity of seeds to FR irradiation plays an important and diverse role in the reproductive strategy of plants. These advantages may be outlined as follows:

– FR-dormancy protect the seed from germinating under circumstances that give little chance for seedling survival.

– A great majority of seed samples indicate an endogenous diversity of photoresponses. The situation when all the seeds (100%) behave similarly are extremely rare in wild plants.

– Since the grade of FR-dormancy and the sensitivity to white light depend on time of exposure beneath irregular and variable leaf canopies, even primarily homogeneous seed cohort will be diversified and extended in time of germination. Together with the endogenous diversity (point 2), these features form a mixed strategy, advantageous in the variable and unpredictable environments (Cohen, 1968; Haccou and Iwasa, 1995).

– After extended FR-exposure, the deep dormancy may retain for a long time, even in dried seeds. The small dimensions of FR-sensitive seeds facilitate penetration into the soil. These features enable forming soil seed banks, with seeds able to germinate after uncovering and exposing to white light. Most probably the FR-dormancy is not the only mechanism forming soil seed banks (Wesson and Wareing, 1969; Pons, 1991), however it seems to be really important (Gallagher and Cardina, 1998; Jankowska-Błaszczuk et al., 1998).

There is a multitude of physiological mechanisms enabling seeds to optimize the probability of seedling survival in varying environments. Among the mechanisms, photoresponses are of especially great importance; the seeds can assess and remember the current circumstances and anticipate the future ones, by monitoring the spectral composition of light, its intensity and duration.

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Sadly, Henryk Stasiak, an eminent expert in Plant Kingdom, died in 1996, when this study was in progress. His knowledge and experience were greatly missed, but we decided to complete the project. We think that this would accord with his intention.

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