THE LIGHT PROMOTED GERMINATION OF THE SEEDS OF CHENOPODIUM ALBUM L. III. EFFECT OF THE PHOTOPERIOD DURING GROWTH AND DEVELOPMENT OF THE PLANTS ON THE DORMANCY OF THE PRODUCED SEEDS

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SUMMARY

The effects of three photoperiodical conditions during the growth of the mother-plants of *Chenopodium album* L. on the induction of dormancy in their seeds were determined: a long-day cycle of 18 hours light (LD), a short-day cycle of 8 hours light (SD) and a short-day cycle with an interruption of one hour red fluorescent light in the middle of the dark period (SDR).

The course of the germination behaviour of the seeds during dry storage at room temperature and the morphological differences between the seeds revealed the presence of two types of seed dormancy. LD and SDR can induce the first type but only during the period after full flowering of the plants. It is concluded that the level of the active form of phytochrome (Pfr) has an important regulating function during this induction. It is discussed whether it depends on an inhibitor present in the embryo-perisperm complex of the seeds.

The second type of dormancy can be induced only by LD conditions. The plants are sensitive to this effect during the complete life cycle. Its induction seems to be related to the length of main light period per cycle and so probably to the photosynthetic activity of the plants. It is correlated with a thick seed-coat and a low seed-weight, and depends on these morphological characteristics.

After about three months of dry storage only the second type is present in the seeds, the first one has been inactivated or has disappeared.

1. INTRODUCTION

For the study of the dormant state in the seeds of plants two different approaches are available. The classical approach is a study of the effects of various physical and chemical agents in breaking the dormancy of mature seeds. This method gives information concerning the pathways out of dormancy. The second approach – which has been followed only in a small number of studies – consists of an investigation of the conditions which induce the dormant state during the formation and the development of the seeds on the mother-plant.

A direct relationship between the germinability of the seeds and the temperature during the growth of the plants could be demonstrated in several species (VON ABRAMS & HAND 1956, for *Rosa*; GRANT LIPP & BALLARD 1963, for

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Anagallis arvensis; HARRINGTON & THOMPSON 1952, and KOLLER 1962, for *Lactuca sativa*).

LONA (1947) demonstrated an effect of the day length during plant growth on the induction of seed-dormancy in *Chenopodium amaranticolor*. In 6–8 hours photoperiods the plants produced a low percentage (10–40%) of dormant seeds and in 16–18 hours photoperiods a high percentage (90–100%). The same results were later on obtained by WENTLAND (1965) with *C. album*, JACQUES (1957, 1968) with *C. polyspermum*, KODOLENKO (1952) with *Atriplex hortensis* and *Axyris amaranthoides* and HESLOP-HARRISON (1959) with *Rottboellia exaltata*.

In most of these species it was observed that the seed-coat of the long-day seeds (LD-seeds)[1] is twice as thick as that of the short-day seeds (SD-seeds)[1]. It was supposed that the seed-coat functioned as a mechanical resistance to the protrusion of the radicle (LONA 1947; JACQUES 1957, 1968). The seed-weight of LD-seeds was, on the contrary, much lower than that of SD-seeds. WENTLAND (1965) found that LD-seeds had a much higher level of endogenous inhibitors than SD-seeds. One of the inhibitors was identical to the inhibitor-β complex.

It was decided to investigate in the whole of our study about the light promoted germination of *C. album* seeds, also these pre-harvest effects of photoperiod on the dormancy of the seeds. It was tried in the first place to determine whether either the photoperiodical timing or the total light energy received by the mother-plants was responsible for the observed effects. For that purpose to the LD and SD conditions a third one was added: SD with an interruption of the long-night with one hour red light (SDR). This experimental procedure resembles the classical experiments on flower induction in SD plants, reviewed by LANG (1965) and on the formation of winter resting buds, reviewed by VEGIS (1965).

The second reason to start this type of experiments was the good perspectives offered by this method for a comparative study between dormant and non-dormant, light requiring and non-light requiring seeds of one species.

2. MATERIAL AND METHODS

2.1. Growth conditions

The plants of *C. album* used in the present experiments were all derived, directly or indirectly, from seeds collected from one single freely pollinated plant in the field.

The plants were cultivated in growth-cabinets. The light source was formed by four Philips HPLR-bulbs of 400 Watt. The total light energy at plant level was 10.000–15.000 lux, the intensity between 400 and 500 nm was 450 μWatt.cm^{-2}, between 600 and 700 nm 560 μWatt.cm^{-2}. The lamps were separated from the plants by a glass window and cooled separately. The distance between the lamps

[1] These abbrevations will stand in this paper for: "seeds from plants cultivated under either long-day or short-day photoperiods".

and the tops of the plants was not varied. One red fluorescent tube (Philips TL 40 W/15) was employed for the interruption of the dark period. It was installed between the main light sources. The temperature in the cabinets was maintained at 22 °C ± 1 during the light period and at 14 °C ± 1 during the dark period in the 1967A and 1968B experiment. In the 1968a experiment it was 22 °C continuously. The relative humidity degree of the atmosphere in the cabinets was continuously 80 %.

Three photoperiodical conditions were tested: (1) 18 hours light, 6 hours darkness (LD), (2) 8 hours light, 16 hours darkness (SD), and (3) as 2, but with 1 hour red fluorescent light starting 7.5 hours after the beginning of the dark period (SDR).

The plants were breeded in a mixture of soil, leaf-mould and sand; during the first weeks in trays, afterwards planted out separately in pots. The plants were fertilized weekly with a 10 percent KNO_3 solution until flowerbud formation. No artificial pollination was necessary.

The seeds were harvested from the plants when the leaves and stems had yellowed. The flowering in the different parts of the same plant did not take place simultaneously. For that reason the seeds were only collected from the upper parts of the stem and the side branches.

2.2. Storing conditions

The seeds, enwrapped by the pericarp and perianth, were dried immediately after harvest by spreading them out on a filter paper at room temperature. After some days the seeds were stored in petri dishes or in desiccators at room temperatures, or as mentioned elsewhere.

2.3. Germination conditions

Before sowing the seeds the remaining parts of the perianth and the pericarp were removed. The seeds were sown in petri dishes on filter paper wetted with 4 ml de-ionized water. The germination took place at 23 °C either in complete darkness or in continuous light from three white fluorescent tubes (Philips, Eindhoven, TLF 40 W/33). The intensity was 300 μWatt.cm^{-2} between 400 and 500 nm, and 225 μWatt.cm^{-2} between 600 and 700 nm.

The final germination percentage was determined when the percentage had not changed for at least two days.

The removal of a part of either the outer or both seed-coat layers in the area overlying the extreme point of the radicle was done with a razorblade, while the seed was put on its side in a horizontal groove.

For the determination of the seedcoat thickness the seeds were halved with a razorblade and placed with the cut surface upwards on a layer of plasticine on a glass slide. The measurement was made with a micrometer in a microscope.

The anatomy of the seeds of *C. album* has been described in KARSSEN (1968).

3. RESULTS

The effects of the LD and SD conditions on the characteristics of the produced seeds (*table 1; fig. 1*) agree with the results obtained by LONA (1947), WENTLAND (1965), and JACQUES (1957, 1968). The SDR conditions, which have also been included in the present study, have a complicated effect. Two weeks after harvest the germination percentages of the RRR-seeds resemble those of the LLL-seeds, but after three months of dry storage of the seeds these percentages completely agree with those of the SSS-seeds. The thickness of their outer seed-coat layer is similar to that of the SSS-seeds, their seed-weight has an intermediate position.

The interruption of the long night with red light has also an effect on the flower induction of the plants. In SD flowering took place some weeks earlier than in LD and SDR.

Table 1. Influence of the different photoperiodical conditions during the complete life cycle of the mother-plants on the characteristics of the seeds. See *fig. 2* for explanation of the codes (1967A experiment).

	LLL	SSS	RRR
Germination two weeks after harvest (%) in light	10	92	24
in darkness	0	77	12
Germination four months after harvest (%) in light	24	100	100
in darkness	3	100	96
Weight of 100 seeds (mg)	66.5	118.0	88.7
Thickness outer seed-coat layer (μ)	36.8	13.8	14.7

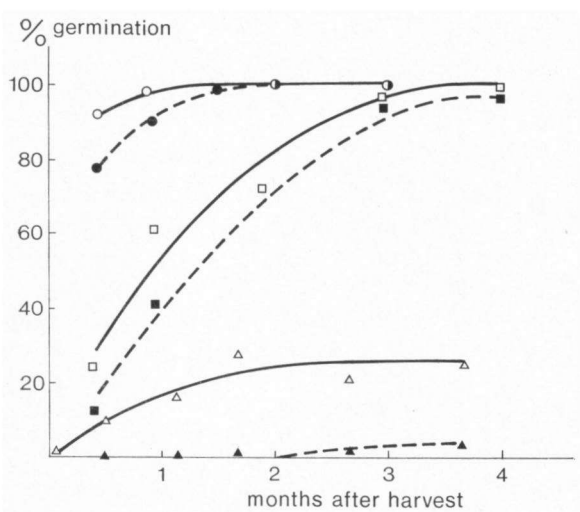

Fig. 1. The increase of the germination percentages during dry storage at room temperatures of seeds from plants grown in SSS (○), RRR (□) or LLL (△) (see *fig. 2* for explanation of the codes); open symbols: germination in continuous white fluorescent light, closed symbols: germination in darkness. (Exp. 1967A).

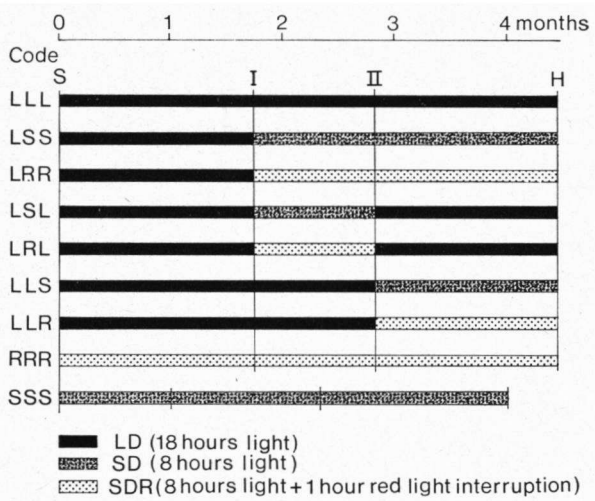

Fig. 2. Codes and transfer-moments in the experiments; S: sowing; I: flowerbud formation; II: full flowering; H: harvest of the seeds.

The vegetative development of the plants is also considerably influenced. The SD-plants are small (10 cm), with a limited number of flowers. The LD-plants reach a total length of about 1 metre and have many flowers. The SDR-plants, which have a longer period of vegetative growth than the SD-plants, nevertheless develop a habitus which is rather similar to the SD-plants: a height of 10–15 cm and a small number of flowers.

So it might be possible that the different seed properties were only a consequence of the habitus of the plants. With the purpose to distinguish between such an indirect effect and a direct effect the experiment was extented (*fig. 2*). (This experiment was carried out twice, the results of both experiments are in good agreement with each other.) To ascertain a similar development, all the plants stayed in LD till the moment of flowerbud formation. A comparison between the SSS- and RRR-seeds on the side and the LSS- and LRR- seeds on the other side shows (*figs. 3, 4* and *5*) that the effects of the SD and SDR conditions do not depend on the habitus of the plant.

The produced seeds also differ from the LLL-controls when the plants were placed in SD or SDR only between stage I and II (LSL, LRL) or after II (LLS, LLR). During the first generative period (I to II) the effect is somewhat stronger than during the second one (*fig. 3*). The data of these transfer experiments exclude, moreover, the possibility of a genetical factor being responsible for the obtained differences.

A comparison between on the one side the experiments 1967A and 1968B, with a different day- and night-temperature (22 °C and 14 °C) and on the other side experiment 1968A, with a constant temperature of 22 °C (*table 2*), reveals that these temperature changes cannot be responsible either for the obtained effects. The differences in the degree of dormancy of especially the LLL-seeds

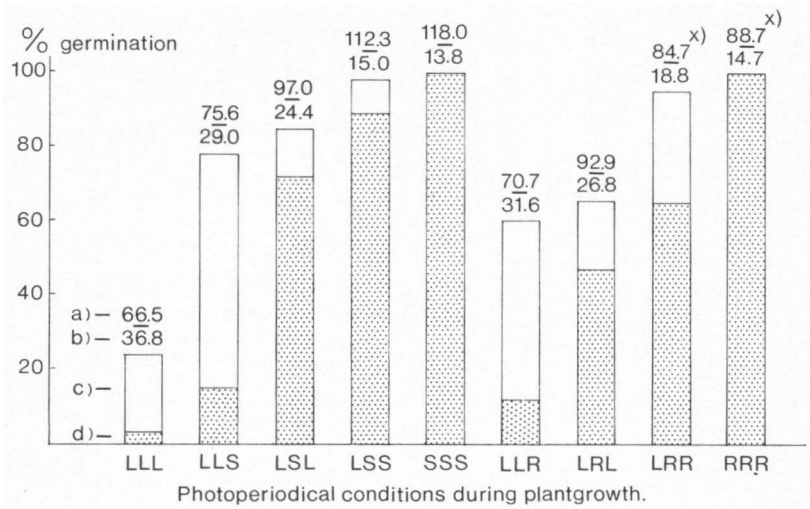

Fig. 3. The germination percentages after 3 months of dry storage at room temperature of the seeds of Exp. 1967A (see *fig. 2* for explanation of codes); a) weight of 100 seeds (mg); b) thickness of the outer seed-coat layer (μ); c) percentage germination in continuous white fluorescent light; d) percentage germination in darkness. See text for ×).

in the three experiments have evidently not been caused by the temperature conditions, but by some unknown factor, which, however, did not change the effects principally.

The seeds produced by plants, which stayed during the same developmental stage(s) in SD or SDR (compare for instance LSS with LRR) have after three months of dry storage rather similar germination percentages (*fig. 3*). They agree also with each other in having almost the same seed-coat thickness. It seems reasonable therefore to correlate the germination capacity after this post-harvest period with this morphological characteristic.

Table 2. The effects of three photoperiodical conditions, in combination either with a constant temperature or with different temperatures during the light and dark period, on the germination capacity of the seeds after three months of dry storage.

Temperature during growth of mother-plants		Experiment	Germination condition	Photoperiodical conditions		
light period	dark period			LLL	LSS	LRR
22 °C	12 °C	1967A	Light	24	100	97
			Dark	3	88	63
22 °C	12 °C	1968B	Light	90	100	100
			Dark	42	96	95
22 °C	22 °C	1968A	Light	71	85	91
			Dark	22	61	66

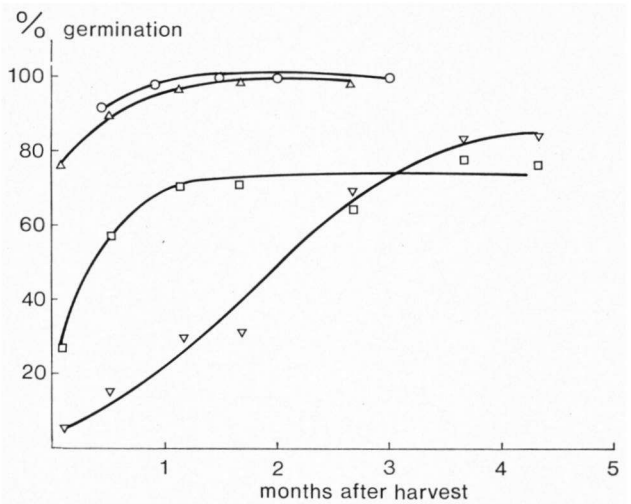

Fig. 4. The increase of the germination percentages during dry storage at room temperatures of seeds from plants grown either continuously in SD or partly in LD and partly in SD (SSS: ○, LSS △, LLS: □, LSL ▽) The germination took place in continuous white fluorescent light (Exp.1967A).

Continuous white light during the germination process antagonizes this inhibitory effect of the seed-coat (*fig. 6*). We will deal with this light effect in more detail in the next paper of this series (KARSSEN 1970).

The seed-weight, which forms an indication for the volume of the embryo-perisperm complex, is not completely identical in the SD and SDR groups. Especially the weight of the LRR- and RRR-seeds (ˣ) in *fig. 3*) differs from that of the comparable LSS- and SSS-seeds. These differences also occur in the two other experiments, although somewhat smaller (*table 3*). It is evident, however, that this factor increases more or less in proportion to the germination percentages of the seeds.

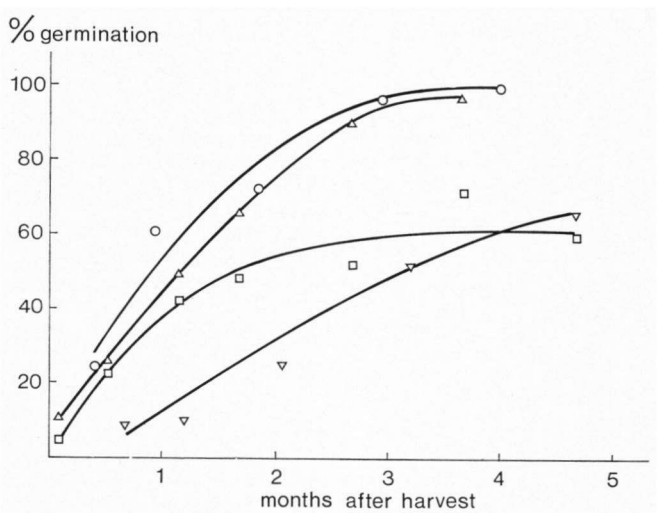

Fig. 5. As *fig. 4*, but here for SDR (RRR: ○, LRR: △. LLR: □, LRL: ▽)

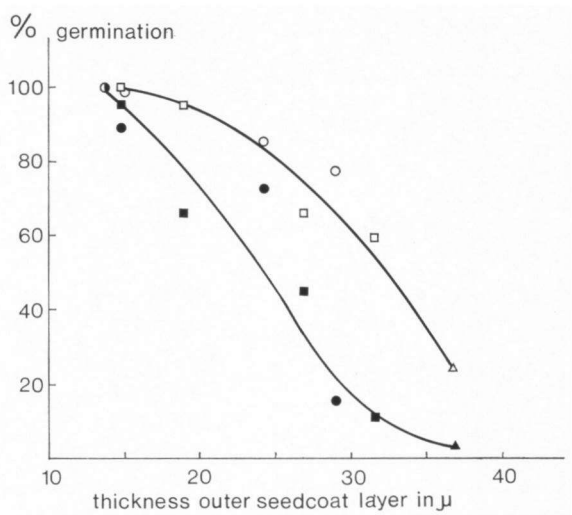

Fig. 6. The relation between the percentages germination in continuous white fluorescent ligth (open symbols) or in darkness (closed symbols) and the thickness of the outer seed-coat layer of seeds from plants grown in LD (△), or grown either continuously or partly in SD (○) or SDR (□) (Exp. 1967A).

In contrast with the situation after three months of storage, immediately after harvest there are striking differences between the SD- and SDR-groups. The germination percentages of seeds from plants, which stayed during at least the last period of their life cycle (from II to H, *fig. 2*) in SD (SSS, LSS and LLS, in *fig. 4*) rapidly increase during the dry storage period. The seeds from plants which during that period stayed in SDR or LD (LLL in *fig. 1*, LSL in *fig. 4*, RRR, LRR, LRL and LLR in *fig. 5*) lose their dormancy at a much slower rate. Moreover it can be seen that these last mentioned seeds have very low germination percentages immediately after harvest. It is evident that this dormant state at the time of harvest can not be correlated with the seed-coat thickness and the seed-weight, because it is present in seeds with great morphological differences (see *table 1* for the two extremes LLL and RRR). Nor can the rate of the loss of dormancy during dry storage be correlated with these factors. This can be concluded from the similar after-ripening rate of the RRR-, LRR- and LLR-seeds (*fig. 5*). The after-ripening rate of the LLR- and LRL-seeds is in inverse proportion to these morphological factors. It can be observed in *fig. 7* that the

Table 3. The weight of 100 seeds (in mg) raised under different photoperiodical conditions throughout the complete life cycle of the mother-plants, or after transfer from LD to SD or SDR at the first transfer moment (see *fig. 2*) in three experiments.

	1967A	1968A	1968B
LLL	66.8	65.4	56.9
SSS	118.0		122.5
RRR	88.7		112.6
LSS	112.3	89.2	109.8
LRR	84.7	85.5	99.9

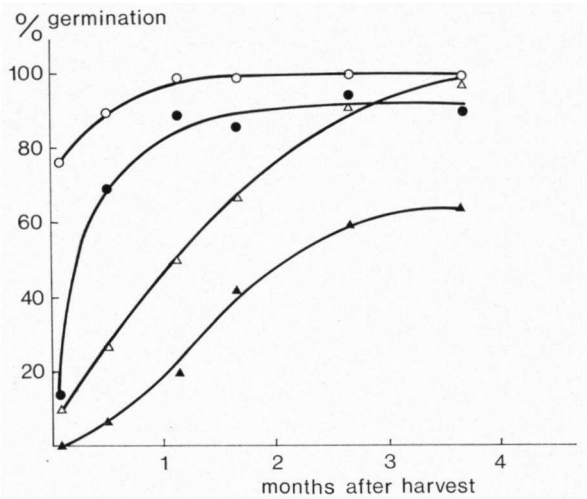

Fig. 7. The increase of the germination percentages during dry storage at room temperatures of LSS-seeds (○) and LRR-seeds (△). The germination took place either in continuous white fluorescent light (open symbols) or in darkness (closed symbols) (Exp. 1967A).

increase of the germination percentage in light has a certain lead to the increase of the percentage germination in darkness. The kinetics are, however, similar.

The influence of other storage conditions was determined with the seeds of experiment 1968a. The seeds (cultivated in LLL, LSS of LRR conditions) were transferred nine days after harvest from room temperature to one of the following conditions: dry storage at 37°C, 23°C or 4°C, or imbibed on wetted filter paper at 4°C in darkness. At several points of time samples were taken and incubated at 23°C. In *fig. 8* the post-harvest increases of the germination percentages under the different conditions are presented for the LLL-seeds. The two other seed lots showed a similar behaviour. It can be seen from these data

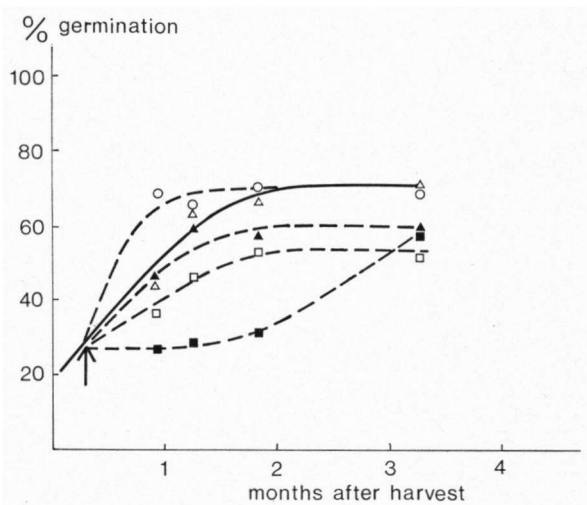

Fig. 8. The increase of the germination percentages during storage in different conditions: dry storage at 37°C (○), 23°C (▲), room temperature (△) or 4°C (□) or in imbibed state on wet filter paper at 4°C (■). The seeds were grown on plants which stayed continuously in LD. The germination took place in continuous white fluorescent light (Exp. 1968 A). The arrow indicates the moment of transfer from room temperatures to the different conditions.

Table 4. The percentages of germination in continuous white fluorescent light or in darkness of "fully operated" seeds (2×), "half operated" seeds (1×) and undamaged controls (0×) after several periods of dry storage at room temperature. The seeds were cultivated on plants grown in different photoperiodical conditions (1968A experiment).

Photoperiodical program during growth of plants	Germination conditions	Days after harvest								
		2			37			55		
		0x	1x	2x	0x	1x	2x	0x	1x	2x
LLL	Light	21	70	88	64	64	100	66	72	100
	Dark	0	9	88	6	40	100	15	46	100
LSS	Light	38	90	100				86	100	100
	Dark	5	54	90				61	100	100
LRR	Light	20	–	100				83	88	100
	Dark	1	18	100				71	96	100

that 37 °C increases the rate of the loss of dormancy, as compared with room temperature, whereas a 4 °C wet storage (chilling) has a retarding effect.

The function of the seed-coat in the dormancy of the seeds was determined with the method of removing of both seed-coat layers ("fully operated seeds") or only the outer seed-coat layer ("half-operated seeds") in a small area overlying the extreme point of the radicle (KARSSEN 1968). The method was applied to the seeds of the 1968a experiment, at different moments after harvest. It can be seen (*table 4*) that almost all the "fully operated seeds" can germinate both in light and darkness, even when the operation takes place two days after harvest. A part of the "half-operated seeds", however, can not germinate at that moment. The effect of this treatment is clearly related to the dormancy degree of the undamaged controls. After 55 days of dry storage this treatment still did not completely break the dormancy in the LLL-seeds. It does so, however, in the other groups.

4. DISCUSSION

4.1. Dormancy induction

The addition in the present study of a short-day cycle with a red light interruption of one hour in the middle of the long-night to the long-and short-day conditions, which were already tested before, has revealed some new aspects of this type of dormancy induction. It is possible, in our opinion, to distinguish between two types of dormancy, present at different moments after harvest, and induced in different ways.

The first type is present immediately after harvest in the seeds grown on plants, which during the period after full flowering were cultivated in LD or SDR (see LLL and RRR in *fig. 1*; LSL in *fig. 4*; LRR, LRL and LLR in *fig. 5*). It is not present, or only during a very short period, in the seeds from plants which stayed in SD during that last period of their life cycle (SSS in *fig. 1*; LSS and LLS in *fig. 4*).

The delaying or inhibiting action of a red light interruption of the long-night on the flowering response of SD-plants, is explained by its effect on the relative level of the active form of phytochrome (Pfr). The SD-response can only be obtained when a low relative level of Pfr is present during the second half of the long-night. This is prevented in LD and SDR (LANG 1965; EVANS & KING 1969). Because this SDR effect on the flowering response was also observed in the present experiments, it can be concluded that the induction of this first type of dormancy in LD and SDR is probably also regulated by the Pfr level. It seems therefore that the phytochrome system has an important function during the induction as well as the breaking of the dormancy (i.e. germination) in the *C. album* seeds (KARSSEN 1967).

A second type of dormancy can be discerned after about three months of dry storage. The germination percentages of the different seed lots at that postharvest moment are only related to the lenght of the period during which the plants stayed in LD conditions. Whether the plants stayed during the remaining part of their life cycle either in SD or SDR has no influence at all (*fig. 3*). The induction of this second type of dormancy – which in contrast with the first one shows a good correlation with the morphological properties of the seeds – seems therefore to depend on the total length of the daily light-period.

So it can be concluded that the different effect of LD and SD on the dormancy of the produced seeds is partly regulated by the phytochrome system and partly by the photosynthetic activity of the plants. CUMMING (1969) concludes from experiments on the induction of flowering in *C. rubrum* plants that Pfr as well as photosynthates have a promotive effect during the normal inductive dark period. In the present experiments these two factors cause different responses.

WENTLAND (1965) excluded an influence of the total light energy on the induction of seed dormancy in *C. album*, because a 17 hours photoperiod of 8 hours high and 9 hours very low intensity had the same effect as a 17 hours high intensity light period. The absence of data about the morphological characteristics of these seeds and about the after-ripening behaviour in all his experiments does not allow a comparison with the present results.

4.2. Nature of the two types of dormancy

The good correlation between the germination percentages after three months of dry storage and the thickness of the seed-coat (*fig. 6*) suggests that this layer is the most important limiting factor for the germination response at that moment. A continuous irradiation with white fluorescent light antagonises this limiting factor to some degree (see also KARSSEN 1970). Whether the seed-coat acts merely as a mechanical barrier against the elongation forces of the embryo (LONA 1947; IKUMA & THIMANN 1963) can not be decided on base of the present results. It was observed before (KARSSEN 1968) that the inner layers have, at least for some part, such a function.

It is not clear whether the volume of the embryo-perisperm complex, which increases more or less proportional with the germination percentages (*fig. 3*) has also an influence on the germinability of the seeds. Because the differences

between the seed-weight of the RRR- and LRR-seeds on the one side and the SSS- and LSS-seeds on the other side do not cause a difference in the germination percentages, this factor seems to be of minor importance.

The limited germination capacity of the LLL- and RRR-seeds (we restrict ourselves to these two basic groups) during the first months after harvest evidently is caused by some other factor than these morphological ones. WENTLAND (1965) found a much higher level of the inhibitor-ß complex in the LD- than in the SD-seeds of *C. album*, therefore it will be discussed whether the assumption of the presence of such a factor forms a reasonable explanation for this first type of dormancy. The localisation of the inhibitor in the embryo-perisperm complex (Wentland) agrees with the lack of correlation between germination capacity and the seed-coat thickness. It was shown, moreover, several times that differences in photoperiods – phytochrome regulated – caused differences in inhibitor content. Although it was mostly observed that SD-photoperiods caused a higher inhibitor level than LD (HEMBERG 1965; EAGLES & WAREING 1964), also the reverse was demonstrated. BOGORAD & MCILRATH (1959) found that the SD-plant *Xanthium pennsylvanicum* produced in LD a higher level of a substance – which inhibited the germination of lettuce seeds – than in SD. The dormancy breaking effect of an operation of the outer or both seedcoat layers (*table 4*) can result in the leaking of such an inhibitor from within the seeds.

The observed delaying effect of a chilling treatment on the rate of the after-ripening processes (*fig. 8*) – in contrast with KRUG (1929), WILLIAMS & HARPER (1965), and JACQUES (1968), who found a stimulation by chilling in the same and related species – forms, however, an argument against the presence of an inhibitor. The promotive effects of such a chilling treatment could be correlated several times with a decrease of the inhibitor content of the seeds (JACKSON 1968; SONDHEIMER *c.s.* 1968; RUDNICKI 1969).

The promotive effect of dry storage at somewhat elevated temperatures, also observed in this study, could, however, never be correlated with such a decrease in inhibitor content. It was assumed that this treatment increases the permeability of the seed-coats for oxygen (FUJII & YOKOHAMA 1965), and thus, among other things, increases the rate of a (possible non-enzymatic) oxidation reaction, which must occur before the seeds can germinate (ROBERTS 1964; MAJOR & ROBERTS 1968). As the rate of the after-ripening processes does not depend on the thickness of the seed-coat (*figs. 1, 4* and *5*) it is not reasonable to suppose that these storage conditions in the present experiments decrease some limiting action of the seed-coat, unless the properties of the inner seedcoat layer and the underlying endosperm layer (KARSSEN 1968) have changed by the LD and SDR conditions in a not directly observable way.

4.3. Polyspermy

The observation that one plant produces several groups of anatomically different seeds (poly- or heterospermy) was made for several species. BAAR (1912), KRUG (1929), and WILLIAMS & HARPER (1965) described this phenomenon for *C. album* seeds. NETOLITZKY (1926) gives more examples in other species. It is

quite obvious, in view of the present results and those of other investigators, that the presence of non-dormant big brown seeds and dormant small black seeds, which they observed, depends on a phenotypic polymorphism, regulated by daylength.

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REFERENCES

BAAR, H. (1912): Zur Anatomie und Keimungsphysiologie heteromorpher Samen von Chenopodium album und Atriplex nitens. *Sitz.ber. Kais. Akad. Wiss. Wien. Math.-Naturw. Kl.* Bd. C. XXII, Abt. 1.

BOGORAD, L. & W. J. MCILRATH (1959): A correlation of photoperiodic response of Xanthium and germination of implanted lettuce seed. In: *Photoperiodism and related phenomena in plants and animals.* Am. Assoc. Adv. Sci., Washington, D.C. R. B. WITHROW (ed.).

CUMMING, B. C. (1969): Photoperiodism and rhythmic flower induction: complete substitution of inductive darkness by light. *Canad. J. Bot.* **47**: 1241–1250.

EAGLES, C. F. & P. F. WAREING (1964): The role of growth substances in the regulation of bud dormancy. *Physiol. Plant.* **17**: 697–709.

EVANS, L. T. & R. W. KING (1969): Role of phytochrome in photoperiodic induction of Pharbitis nil. *Z. Pflanzenphysiol.* **60**: 277–288.

FUJII, T. & Y. YOKOHAMA (1965): Physiology of light requiring germination of Eragrostis seeds. *Plant Cell Physiol.* **6**: 135–145.

GRANT LIPP, A. E. & L. A. T. BALLARD (1963): Germination patterns shown by the light-sensitive seed of Anagallis arvensis. *Austr. J. Biol. Sci.* **16**: 572–584.

HARRINGTON, J. F. & R. C. THOMPSON (1952): Effect of variety and area of production on subsequent germination of lettuce seed at high temperatures. *Proc. Amer. Soc. Hort. Sci.* **59**: 445–450.

HEMBERG, T. (1965): The significance of inhibitors and other chemical factors of plant origin in the induction and breaking of rest periods, in W. RUHLAND, *Encyclopedia of Plant Physiology* **15/2**: 669–698. Springer, Berlin-Göttingen-Heidelberg.

HESLOP-HARRISON, J. (1959): Photoperiodic effects on sexuality, breeding system and seed germinability in Rottboellia exaltata. (Abstr.) *Proc. IX. Internat. Bot. Congr.*, Vol. II: 162–163.

IKUMA, H. & K. V. THIMANN (1963): The role of the seed-coats in germination of photosensitive lettuce seeds. *Plant Cell Physiol.* **4**: 169–185.

JACKSON, G. A. D. (1968): Hormonal control of fruit development, seed dormancy and germination with particular reference to Rosa. In: Plant Growth Regulators. *Soc. Chem. Ind. Monogr.* **31**: 127–156.

JACQUES, R. (1957): Quelques données sur le photopériodisme de Chenopodium polyspermum L.; influence sur la germination des graines. Colloque International sur le Photo-thermopériodisme, *Publ.* **34**, *Série B., I.U.B.S.*, Parma, 125–130.

— (1968): Action de la lumière par l'intermédiaire du phytochrome sur la germination, la croissance et le développement de Chenopodium polyspermum L. *Physiol. Vég.* **6**: 137–164.

KARSSEN, C. M. (1967): The light promoted germination of the seeds of Chenopodium album L. I. The influence of the incubation time on quantity and rate of the response to red light. *Acta Bot. Neerl.* **16**: 156–160.

— (1968): —. II. Effects of (RS)-abscisic acid. *Acta Bot. Neerl.* **17**: 293–308.

— (1970): —. IV. Effects of red, far-red and white light on non-photoblastic seeds incubated in mannitol. *Acta Bot. Neerl.* **19**: 95–108.

KODOLENKO, B. G. (1952): Formation of the seeds of Axyris amaranthoides L. and Atriplex hortensis L. (in Russian). *Agrobiologia* **7**: 135–138.

KOLLER, D. (1962): Preconditioning of germination in lettuce at time of fruit ripening. *Amer. Jour. Bot.* **49**: 841–844.

KRUG, H. (1929): Beiträge zur Keimungsphysiologie und Bekämpfung von Samenunkräutern. *Bot. Archiv.* **27**: 420–518.

LANG, A. (1965): Physiology of flower induction, in W. RUHLAND, *Encyclopedia of Plant Physiology* **15/1**: 1380–1536. Springer, Berlin-Göttingen-Heidelberg.

LONA, F. (1947): L'influenza delle condizioni ambientali, durante l'embriogenesi, sulla caratteristiche del seme e della pianta che ne deriva. *Lavori di Botanica.* Vol. pubbl. in occasione del 70° genetliaco del Prof. Gola: 313–352.

MAJOR, W. & E. H. ROBERTS (1968): Dormancy in cereals seeds. 1. The effects of oxygen and respiratory inhibitors. *J. Exp. Bot.* **19**: 77–89.

NETOLITZKY, F. (1926): Anatomie der Angiospermen-Samen in: K. LINSBAUER, *Handbuch der Pflanzenanatomie* **II/2**, Bd. *K.* Borntraeger, Berlin.

ROBERTS, E. H. (1964): A survey of the effects of chemical treatments on dormancy in rice seeds. *Physiol. Plant.* **17**: 33–43.

RUDNICKI, R. (1969): Studies on abscisic acid in apple seeds. *Planta (Berl.)* **86**: 63–68.

SONDHEIMER, E., D. S. TZOU & E. C. GALSON (1968): Abscisic acid levels and seed dormancy. *Plant Physiol.* **43**: 1443–1447.

VEGIS, A. (1965): Die Bedeutung von physikalischen und chemischen Auszenfaktoren bei der Induktion und Beendigung von Ruhezuständen bei Organen und Geweben höherer Pflanzen. In: W. RUHLAND, *Encyclopedia of Plant Physiology* **15/2**: 534–668.

VON ABRAMS, G. F. & M. E. HAND (1956): Seed dormancy in Rosa as a function of climate. *Am. J. Bot.* **43**: 7–12.

WENTLAND, M. J. (1965): *The effect of photoperiod on the seed dormancy of Chenopodium album.* Thesis, University of Wisconsin, U.S.A.

WILLIAMS, J. T. & J. L. HARPER (1965): Seed polymorphism and germination. I. The influence of nitrates and low temperatures on the germination of Chenopodium album. *Weed Res.* **5**: 141–150.