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The germination characteristics of phytochrome-deficient *aurea* mutant tomato seeds

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The germination of tomato (*Lycopersicon esculentum* Mill.) cv. Moneymaker seeds of a phytochrome-deficient *aurea* (*au*) mutant and its isogenic wild types were investigated. In contrast to the wild type whose seeds germinate in darkness, those of the *au* mutant have a low dark germination level. Continuous far-red light (FR) inhibits the germination of the wild type, whereas in *au*-mutant seed batches exhibiting some dark germination, no inhibition of these dark-germinating seeds was observed. Germination of the *au* mutant was promoted by continuous red light (R). Intermittent pulses of R were also effective and phytochrome was implicated as the photoreceptor, since cyclic treatments of 2 min R/ 2 min FR/ 26 min darkness led to a significantly lower germination than the control receiving 2 min R/ 28 min darkness. Germination of the *au* mutant in darkness increased with the period of post-harvest storage in paper packets at laboratory temperature. Germination could also be induced in darkness at 25°C by treatment of the imbibed seeds for a period of time at a lower or higher temperature. Germination was also promoted by the presence of nitrate ions in the imbibition medium. In this case simultaneous irradiation with FR failed to inhibit germination of the *au* mutant, whilst germination of the wild-type controls was strongly inhibited. In the case of a highly dormant *au* seed batch where continuous R, low temperature treatment and nitrate ions were partially effective (promotive), full germination could be induced by the combination of continuous R with one of the other factors. The stable pool of phytochrome is predicted to be the pool involved in the promotion of seed germination in darkness as a result of residual P_{fr} being present in it during dehydration. The *au*-mutant seeds are more dormant than wild type seeds and therefore require more of the active FR-absorbing form of phytochrome (P_{fr}) to achieve germination. Since the *au* mutant exhibits a phytochrome-controlled promotion of germination, it must contain phytochrome and it is speculated that this is the stable pool of phytochrome which has been demonstrated to be present in the light-grown *au* mutant plants.

Key words – Dormancy, *Lycopersicon esculentum*, physiological mutants, phytochrome, seed germination, tomato.

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Introduction

The *aurea* (*au*) mutants of tomato are phytochrome photoreceptor mutants lacking at least 95% of the spectrophotometrically (Koornneef et al. 1985, Adamse et al. 1988, Lipucci Di Paola et al. 1988) and immunologically (Parks et al. 1987) detectable phytochrome in dark-grown seedlings. Light-grown seedlings have a pleiotropic phenotype consistent with reduced phytochrome function during de-etiolation: long hypocotyls, reduced chlorophyll accumulation and reduced anthocyanin. The *au* mutant is therefore a very useful genotype for studying the function of the bulk phytochrome pool present in etiolated seedlings by quantitative comparison to the isogenic wild type. Adult plants of the *au* mutant have been demonstrated to contain about 50% of the phytochrome level observed in the wild type (Adamse et al. 1988, López-Juez et al. 1990) and they

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exhibit a normal phytochrome regulated end-of-day far-red light (FR) growth response. More than one type of phytochrome has now been demonstrated (Furuya 1989, Tomizawa et al. 1990) and it has been speculated that the *au* mutant lacks only the labile pool or type I phytochrome (Adamse et al. 1988, Peters et al. 1991). An additional element of the *au* phenotype is its poor seed germination compared to wild type (Koornneef et al. 1985, Lipucci Di Paola et al. 1988). This means that the *au*-mutant seedlings obtained as a result of germination in darkness are representative of a very small proportion of the seed population. Treatment of the dark-dormant *au*-mutant seeds with gibberellic acid (GA_3) results in very high germination (Koornneef et al. 1985). Such a treatment appears to have little influence on the phytochrome content in darkness (Parks et al. 1987) or the phytochrome regulation of gene expression (Sharrock et al. 1988, Oelmüller et al. 1989). However the photocontrol of hypocotyl growth and anthocyanin synthesis during de-etiolation are both strongly influenced by GA_3. The current investigation was initiated in an endeavour to obtain high germination in darkness of *au*-mutant seed batches. Tomato is an example of dark-germinating species, but phytochrome has been implicated in the germination process (Mancinelli et al. 1966) since FR inhibits germination and the effects of FR can be negated by red light (R). In this paper, results are reported on the germination behaviour of several seed batches of an *au* mutant and its isogenic wild type.

Abbreviations – D, darkness; FR, far-red light; GA_3, gibberellic acid; GA_{4+7}, a mixture of gibberellins A_4 and A_7; HIR, high irradiance response; HTT, high temperature treatment; LTT, low temperature treatment; P_{fr}, FR-absorbing form of phytochrome; R, red light.

Materials and methods

Seed batches used

Several different batches of an *au* mutant (au^w/au^w) of tomato (*Lycopersicon esculentum* Mill.) cv. Moneymaker (Koornneef et al. 1985 and references therein) and its isogenic wild type were used. After harvest the seeds were stored at room temperature.

Germination procedure

Seeds were sown on one layer of thick filter paper (Papierfabriek, Schut B. V., Heelsum, the Netherlands) moistened with 2 ml of distilled water or the appropriate solution in 5 cm plastic Petri dishes. Twenty-five seeds were sown in each dish and 4 dishes were used for each treatment within individual experiments.

A mixture of gibberellins A_4 and A_7 (GA_{4+7}) (ICI, Yalding, UK) at 100 μM was used in some experiments. Low temperature treatment (LTT) consisted of transferring the Petri dishes wrapped in aluminium foil to a temperature controlled room at 4 or 14°C for the desired period. High temperature treatment (HTT) consisted of floating the Petri dishes wrapped in aluminium foil on a water bath at the desired temperature. Where necessary seeds were manipulated under a dim green safelight (40 nmol m^{-2} s^{-1}) (Adamse et al. 1988).

Light sources

The broad band R and FR light sources (3 µmol m^{-2} s^{-1}) used for continuous and pulse irradiations were those described by Koornneef et al. (1980). In addition a light emitting diode light source (Nijssen Koeling, Leiden, the Netherlands) was used (emission maximum 660 nm, band width 10 nm at 50% of the emission maximum, 8 µmol m^{-2} s^{-1}) in the light cycle experiments.

Presentation of results

All experiments were repeated at least twice with qualitatively and quantitatively similar results and are presented as the final (i.e. the germination remained constant upon examination under green safelight for several days) mean germination ± SE. For clarity the error bars have been omitted from the figures, but the errors were of a comparable magnitude in all experiments as indicated in the tables.

Results

The *au* mutant (Tab. 1) exhibits lower germination than the isogenic wild type. Whilst the final germination of the wild type in darkness is high and unaffected by

Tab. 1. Final germination percent ± SE of wild type and labile-phytochrome deficient *au* mutant tomato seeds cv. Moneymaker, imbibed in H_2O under different light conditions (cR: continuous red light; cFR, continuous far-red light; D, darkness) or in GA_{4+7} at 25°C. NA, not available.

Harvest year	Wild type		*au* Mutant			
	D H_2O	cFR H_2O	D H_2O	cR H_2O	cFR H_2O	D GA_{4+7}
1983	NA	NA	45±3	97±2	44±3	98±2
1984	NA	NA	13±1	60±2	12±1	95±2
1985	NA	NA	15±3	90±1	13±3	92±4
1988	96±2	7±2	22±2	96±1	28±3	95±3
1989	89±3	8±3	5±1	18±2	4±2	95±2

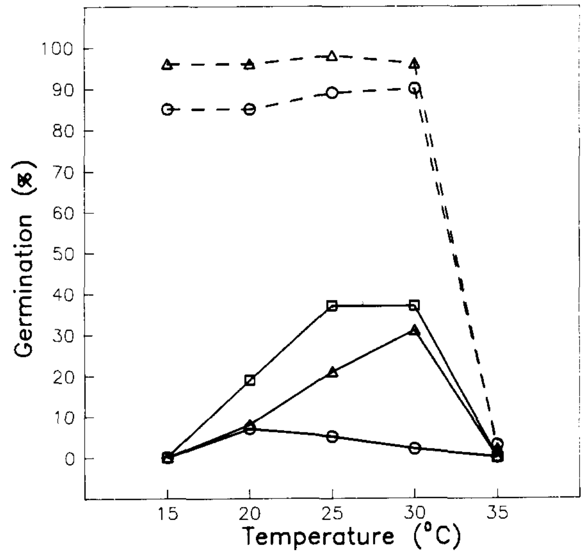

Fig. 1. Final germination percent of wild type (broken lines) and *au* mutant (solid lines) of tomato seeds cv. Moneymaker as a function of temperature. Seeds were harvested in 1983 (□), 1988 (△) and 1989 (○).

temperature in the range 15–30°C, that of the *au* mutant is low, but shows an optimum in the range 25–30°C (Fig. 1). The most recently harvested seed batch of the *au* mutant (1989), measured within 2 months of harvest, was the most dormant and the oldest seed batch (1983) the least dormant. However, even in the latter case less than half of the seed population germinates in darkness.

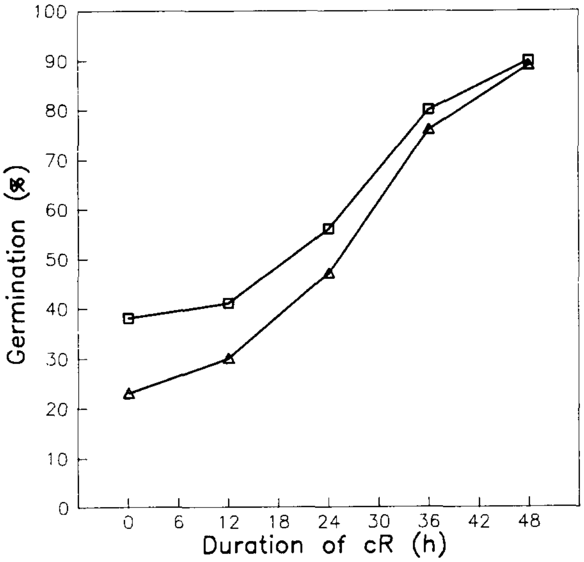

Fig. 2. Germination induction of *au* mutant tomato seeds cv. Moneymaker by continuous red light (cR) at 25°C. Seeds were exposed to cR for increasing periods of time from sowing and subsequently they were transferred to darkness. The final germination percent achieved is presented. Seeds harvested in 1983 (□) and 1988 (△).

That all the *au* mutant seeds are viable is shown by their stimulation to germinate by GA_{4+7} (Tab. 1). Exposure of the seeds to continuous FR resulted in a strong inhibition of the wild type (Tab. 1), whereas seeds of all the *au* mutant seed batches germinating in darkness were unaffected by such a treatment. All the *au* mutant seed batches exhibited a stimulation of germination under continuous R (Tab. 1).

The necessity for continuous R for promotion of the germination of the *au* mutant seed batches 1983 and 1988 is shown in Fig. 2. To attain maximum germination

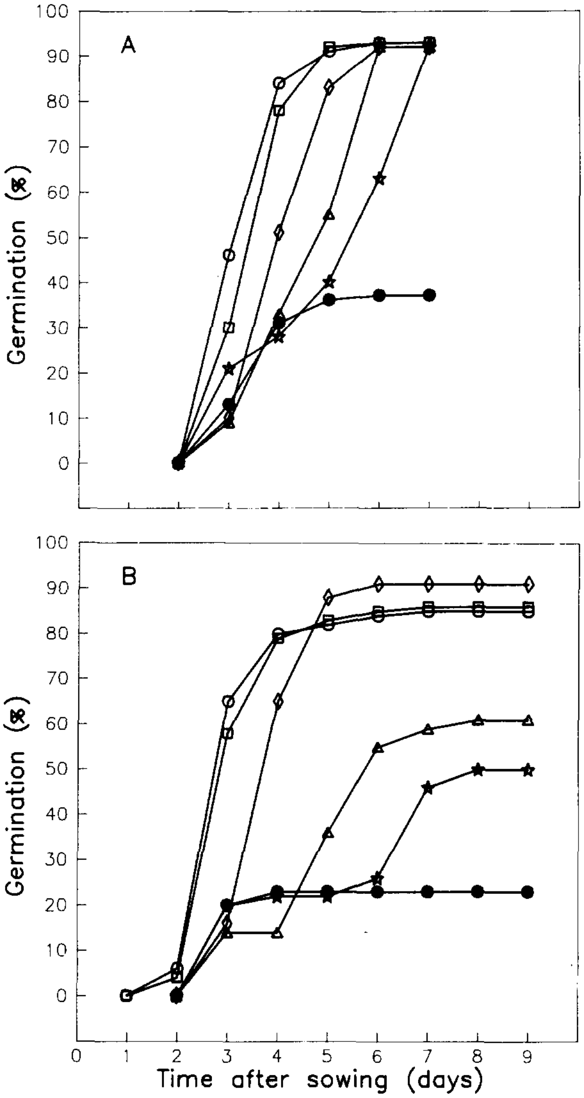

Fig. 3. The effectiveness of continuous red light (cR) in promoting germination of *au* mutant tomato seeds cv. Moneymaker after different periods of imbibition in darkness at 25°C. Seeds of the 1983 (A) and 1988 (B) harvests were imbibed in darkness for 1 (□), 2 (◊), 3 (△) and 4 (☆) days before exposure to cR. Also shown are the germination curves for seeds exposed to cR from the beginning of imbibition (○) and those maintained in darkness (●).

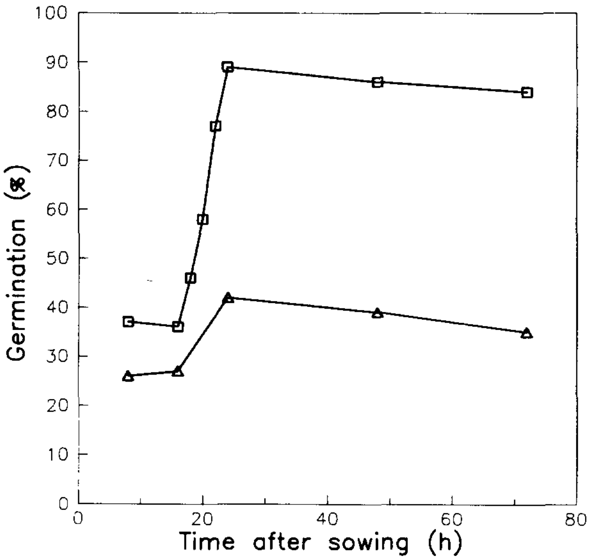

Fig. 4. The effect of 2 h high temperature treatment at 35°C on the final germination percent of *au* mutant tomato seeds cv. Moneymaker given after different periods of imbibition in darkness at 25°C. Seeds were kept in darkness throughout and after the high temperature treatment returned to 25°C. Seeds harvested in 1983 (□) and 1988 (△).

48 h irradiation is required. Figure 3 shows the effect of transferring seeds of the same seed batches to continuous R after various periods of dark imbibition. One day of darkness before continuous R results in very little, if any, delay in germination compared to the continuous R controls. However, while the 1983 seed batch (the least dormant) still achieves maximum germination even after 4 days imbibition in darkness (Fig. 3A), periods of darkness longer than 2 days in the case of the 1988 seed batch result in the appearance of secondary dormancy, the so called 'skotodormancy' (Fig. 3B).

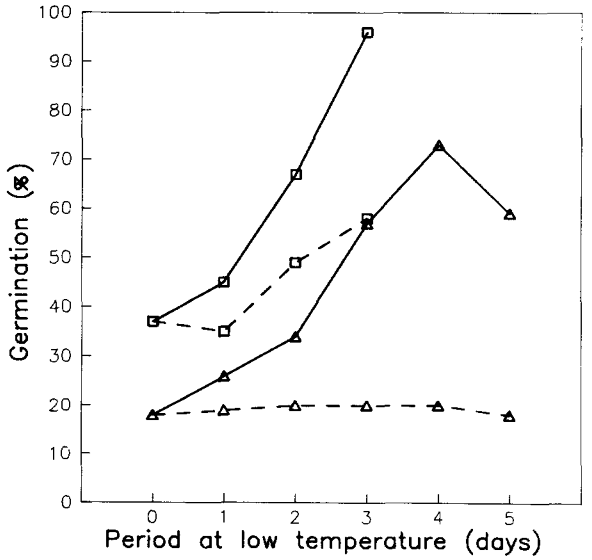

Fig. 5. The effect of chilling on the final germination percent of *au* mutant tomato seeds cv. Moneymaker. Seeds of the 1983 (□) and 1988 (△) harvests were imbibed for increasing periods of time from sowing at 14 (solid lines) or 4°C (broken lines) and subsequently transferred to 25°C until the final germination percent was achieved. The seeds were maintained in darkness throughout.

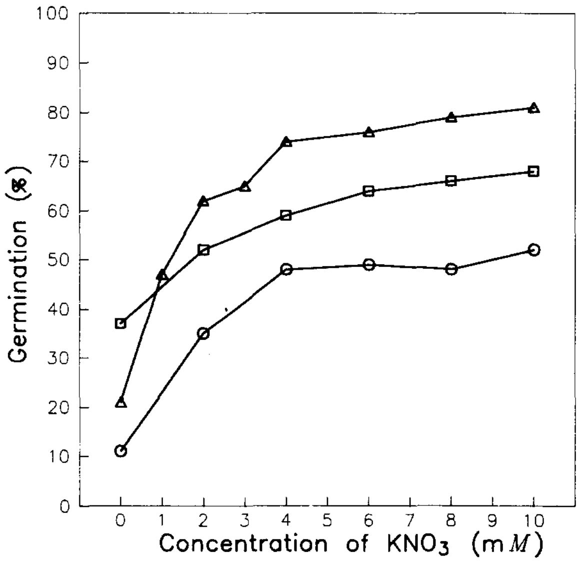

Fig. 6. The effect of increasing concentrations of KNO_3 on the final germination percent of *au* mutant tomato seeds cv. Moneymaker in darkness at 25°C. Seeds harvested in 1983 (□), 1988 (△) and 1989 (○).

The effect of a 2-h HTT at 35°C to seeds maintained in darkness on the germination of *au* mutant seed batches 1983 and 1988 is shown in Fig. 4. The 1983 batch is particularly sensitive to such treatments and the appearance of responsiveness is very sharp at 18 h after sowing and has achieved its maximum effect at 24 h. Responsiveness is retained for at least 3 days after sowing. The 1988 seed batch exhibited a similar, but much reduced response. Increased germination percentages in *au* mutant seeds of the 1983 batch were observed even with shorter periods of incubation at 35°C or a 2-h incubation at temperatures between 27.5 and 35°C (data not shown). A LTT of 14°C given from sowing induces germination of a large proportion of the population of

Tab. 2. Final germination percent ± SE of wild type and labile-phytochrome deficient *au* mutant tomato seeds (1988 harvest cv. Moneymaker) imbibed in H_2O or KNO_3 solution (5 mM) either in darkness (D) or under continuous far-red light (cFR), at 25°C.

Genotype	H_2O		KNO_3	
	D	cFR	D	cFR
Wild type	99±1	3±1	97±1	34±4
au Mutant	24±2	27±1	82±3	83±1

Tab. 3. The effect of 10 min red light (R) and 10 min R followed by a 10 min far-red light (R/FR) given 24 h after the start of imbibition on the final germination percent ± SE of the labile-phytochrome deficient *au* tomato seeds cv. Moneymaker, imbibed in either H_2O or KNO_3, at 25°C (D, darkness).

Seed harvest	Imbibition medium	D	R	R/FR
1983	H_2O	42±3	55±2	46±3
	KNO_3 (5 m*M*)	64±3	79±1	70±3
1988	H_2O	20±2	29±2	19±2
	KNO_3 (1 m*M*)	54±3	67±3	57±2
1989	H_2O	11±3	17±3	12±2
	KNO_3 (5 m*M*)	49±2	62±1	45±3

the *au* mutant seed batches 1983 and 1988 in darkness, a period of 3–4 days resulting in the maximum effect (Fig. 5). A LTT of 4°C was less effective than 14°C for the 1983 seed batch and was without effect in the case of the 1988 seed batch.

Imbibition of the seeds on a medium containing nitrate resulted in a promotion of large proportion of the seeds of all the *au* mutant seed batches in darkness (Fig. 6). The 1988 batch was particularly responsive to such a treatment, but all cases were saturated at 10 m*M* nitrate. Seeds of the 1988 seed batch induced to germinate by nitrate are not inhibited by continuous FR, although the wild-type control seeds are still strongly inhibited in the presence of nitrate (Tab. 2). To test if the nitrate treatment increases the responsiveness to the FR-absorbing form of phytochrome (P_{fr}) an experiment was conducted with the *au* mutant 1983, 1988 and 1989 seed batches at the appropriate nitrate concentration to result in approximately 50% of the maximum nitrate effect. The seeds were then exposed to a single R pulse or a R pulse followed by a FR pulse (Tab. 3).The results demonstrate that phytochrome is involved in the promotion of seed germination of all *au* batches, even those imbibed on water. However, the proportion of the population exhibiting R/FR reversibility is small. To test further the involvement of phytochrome in the promotion of germination, seeds of the *au* mutant seed batches 1983 and 1988 were imbibed on water and exposed to intermittent pulses of R or R followed by FR in a 30 or 60 min cycle (Tab. 4). Of the intermittent R treatments given, 2 min R/ 28 min dark was the most effective. A treatment of 2 min R/ 2 min FR/ 26 min dark resulted in almost complete reversion of the promotive effect of R pulses.

Tab. 4. Final germination percent ± SE of the labile-phytochrome deficient *au* mutant tomato seeds cv. Moneymaker under intermittent irradiation (R, red light; FR, far-red light; D, darkness) at 25°C. *, Light emitting diode source.

Light cycle	Harvest	
	1983	1988
D	42±2	22±2
1 min R/ 59 min D	58±4	27±2
2 min R/ 58 min D	64±2	39±4
1 min R/ 29 min D	60±3	41±4
2 min R/ 28 min D	71±2	50±3
2 min R*/ 28 min D	63±3	49±3
2 min R*/ 2 min FR/ 26 min D	45±2	29±2

In a final experiment the effectiveness of continuous R, LTT, HTT and nitrate in promoting the germinating of the *au* mutant seed batch 1989 was investigated as a function of post-harvest storage in paper packets at laboratory temperature (Tab. 5). One month after harvest this seed batch was highly dormant and only 18% germination was attained under continuous R, LTT was slightly less effective and there was no response to HTT. Over a 4-month period, the dark germination level slightly increased (5→12%), as well as the response to continuous R and LTT. Nitrate was the most effective treatment after 3 months post-harvest storage and this increased to 54% at 4 months. Combining continuous R with LTT, HTT and nitrate after 4 months storage resulted in 97, 61 and 99% of seeds germinating, respectively.

Discussion

The results in Tab. 1, and those published previously (Koornneef et al. 1985, Lipucci Di Paola et al. 1988), demonstrate that one aspect of the pleiotropic phenotype resulting from the *au* mutation is the relatively poor germination in darkness compared to the isogenic wild types. The *au* mutants lack spectrophotometrically detectable phytochrome in seeds (Koornneef et al. 1985, Lipucci Di Paola et al. 1988) and dark-grown seedlings (Koornneef et al. 1985, Parks et al. 1987): they are deficient in the 'bulk' labile phytochrome pool which accumulates in dark-grown seedlings. This pool is predominantly composed of type I phytochrome (Furuya, 1989, Tomizawa et al. 1990) or phytochrome A (Sharrock and Quail 1989). Tomato is an example of a dark-germinating species, but despite this there is evi-

Tab. 5. The effect of different treatments (D, darkness; cR, continuous red light; LTT, 4-days low temperature treatment at 14°C given from sowing; HTT, 2 h high temperature treatment at 35°C given 1 day after sowing, 5 m*M* KNO_3) on the final germination percent ± SE of *au* mutant tomato seeds (1989 harvest cv. Moneymaker) at 25°C as a function of the post-harvest storage period. ND, not determined.

Treatment	Period of storage (months)			
	1	2	3	4
D	5±1	6±1	7±1	12±2
cR	18±2	26±3	31±2	41±3
LTT	15±2	ND	28±3	52±4
cR + LTT	ND	ND	ND	97±1
HTT	7±4	ND	11±1	11±2
cR + HTT	ND	ND	ND	61±3
KNO_3	ND	ND	30±3	54±3
cR + KNO_3	ND	ND	ND	99±1

dence that P_{fr} present in the seed, is a prerequisite for germination. Continuous FR inhibits germination and intermittent FR is also very effective (Mancinelli et al. 1966). Therefore the requirement for continuous FR to inhibit germination is to prevent the accumulation of P_{fr}, which arises either as a result of hydration directly or indirectly from intermediates which accumulated during dehydration of the seeds. Dark-germinating seeds of species such as tomato (Mancinelli et al. 1966) and *Amaranthus caudatus* (Kendrick and Frankland 1969) have a P_{fr} dependent step for germination and can be inhibited by maintaining the P_{fr} level at a low value by intermittent FR irradiation. It can therefore be thought of as prolonged low fluence response, not a high irradiance response. However, dark-germinating seeds can also be blocked at a late stage by a cycling-dependent process which has all the characteristics of an HIR (Frankland 1986) and simultaneously induces a low fluence response requirement for germination (Cone and Kendrick 1985). The pool of P_{fr} involved in conveying the capacity for the seeds to germinate in darkness appears to be limiting in the *au* mutant.

If the *au* mutant fails to germinate in darkness because it has a phytochrome deficiency, this also explains why those seeds which do germinate are not inhibited by continuous FR. It is possible that the seeds germinating in darkness are no longer dormant i.e. they have no phytochrome limiting step. Such seeds could still have a phytochrome requirement, but be so sensitive to P_{fr} in the very low fluence response range (Kronenberg and Kendrick 1986) so that FR can no longer result in their inhibition. The fact that intermittent or continuous R results in a marked stimulation of germination of the *au* mutant indicates conversion of the low level (below detection limits by in vivo spectrophotometry) of residual phytochrome or newly synthesized phytochrome to P_{fr} is required. The question of interest is, which pool or phytochrome type is involved in this process? If the *au* mutant only misses the labile phytochrome pool then the promotive effects could be triggered by the stable type of phytochrome. At present we cannot provide a definitive answer to this suggestion. New tools are urgently required to enable us to identify the pools of phytochrome present in light-grown plants and seeds. Unfortunately the antibodies so far tested are unable to do this in tomato (López-Juez et al. 1990) and we hope that appropriate antibodies will soon be produced. In other species the pool of phytochrome detected in seeds appears to be of the light-stable type (Hilton and Thomas 1985) or is present in equal proportion with the labile type (Konomi et al. 1987).

It is possible that the *au*-mutant seeds are more dormant than the wild type and therefore require extra P_{fr} in the stable phytochrome pool above that endogenously present in the seeds to enable germination. The phytochrome-deficient long-hypocotyl mutants of the light-requiring species *Arabidopsis thaliana,* were demonstrated to show normal phytochrome control of germination (Cone and Kendrick 1985). In that study, it was also proposed that it was the stable pool of phytochrome that was involved in the promotion of seed germination.

Despite the lack of inhibition by FR, the majority of *au*-mutant seeds dormant in darkness can be stimulated to germinate by continuous R, a process that appears to be a prolonged low fluence response, since intermittent R is almost as effective as continuous irradiation. In addition, a fraction of the population exhibits R/FR reversibility of germination in the light-cycle experiments (Tab. 4). We have never observed a promotion of *au*-mutant cv. Moneymaker germination by continuous FR, which has been reported by Lipucci Di Paola et al. (1988) for cv. UC 105. This difference could be due to differences in sensitivity to P_{fr} or depth of dormancy determined by the cultivar or a quantitative difference between the two *au* alleles.

Temperature shocks such as LTT or HTT have been demonstrated to result in the germination of light-requiring seeds of many species (Frankland and Taylorson 1983). It has been proposed that this results in the induction of the very low fluence response (Kronenberg and Kendrick 1986), so that the low endogenous level of P_{fr}, although not enough to satisfy a low fluence response, is now more than sufficient to satisfy the germination requirement. Such seeds would then be anticipated to germinate under continuous low fluence rate FR. It is interesting to note that osmoconditioned tomato seeds which germinate in darkness are also not inhibited by continuous FR (Georghiou et al. 1982, Thanos and Georghiou 1988).

Inclusion of nitrate in the imbibition medium is known strongly to influence the light requirement of seeds for germination (Hilhorst and Karssen 1988). There is no evidence that nitrate induces a very low fluence response, but it can result in a shift in sensitivity of seeds to lower fluences within the low fluence range (Hilhorst and Karssen 1988). Nitrate treatment could therefore bring a larger proportion of the seed population within the range of the low fluence response. Recently, *Paulonia tomentosa* seeds which required two R pulses separated by a dark interval to achieve germination, have been shown to require only a single pulse in the presence of nitrate (Grubišić and Konjević 1990).

In conclusion, germination of a high proportion of the *au*-mutant seed population in darkness, for all our seed batches, is most conveniently achieved by treatment with nitrate. Experiments are currently in progress with such seedlings to study the quantitative role played by the 'bulk' labile pool of phytochrome during de-etiolation.

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