# ANALYSIS OF THE RESPONSE OF PHOTOMORPHOGENETIC TOMATO MUTANTS TO END-OF-DAY FAR-RED LIGHT

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**Refereed**

Abstract

The response was studied to end-of-day (EOD) far-red light (FR) of light-grown plants of: photomorphogenetic mutants aurea (*au*), high pigment (*hp*) and double mutant (*au,hp*); the potential photomorphogenetic mutant procera (*pro*) and the isogenic wild type of tomato (*Lycopersicon esculentum* Mill.) cv. Ailsa Craig. All of the genotypes tested exhibited a strong EODFR response resulting in an increase in plant height, fresh weight of internodes and in the case of wild-type and *hp*-mutant plants a reduction in anthocyanin accumulation. However, it had no effect on their leaf area and chlorophyll content. Interposing a dark period at the end of the white light photoperiod before exposure to FR demonstrated that 50% of the EODFR response on elongation growth and anthocyanin content was obtained for a dark period of 4 h. This indicates that the phytochrome species regulating anthocyanin synthesis in the wild type and *hp* mutant and growth in wild type, *au*, *hp*, and *au,hp* has the same characteristics, being stable in the active FR-absorbing form. The EODFR response on anthocyanin synthesis, determined by measurement of the anthocyanin content of young leaves at the same physiological stage of development demonstrated that the level of anthocyanin reached a minimum after 5 days EODFR treatment. The potential of photomorphogenetic mutants, either selected by conventional means or genetically engineered, for the control of plant growth is discussed.

Keywords: anthocyanin, chlorophyll, growth, *Lycopersicon*, phytochrome.

## 1. Introduction

The control of plant development by light (photomorphogenesis), involves at least three different groups of photoreceptors, including phytochrome (P), a blue light BL/UV-A photoreceptor (cryptochrome) and a UV-B photoreceptor (Mohr, 1986). Smith (1986) has proposed that one specific function of P in light-grown plants is related to the perception of an increased proportion of far-red light (FR) occurring in canopy shade light. This results in promotion of stem elongation in order to avoid shade light. One of the methods often used to trigger the P-mediated shade adaptation process is to briefly irradiate plants with end-of-day-FR (EODFR) (Downs *et al.*, 1957). The assignment of specific functions to the distinct photoreceptors is being studied with the aid of photomorphogenetic mutants in which certain parts of the morphogenetic pathway are eliminated or altered (Koornneef and Kendrick, 1986; Adamse *et al.*, 1988a). The existence of multiple types of P: light-labile P (PI) and light-stable P (PII), adds to the complexity (Furuya, 1989, Tomizawa *et al.*, 1990). Photomorphogenetic mutants have been isolated

for a number of species, but the best characterized is the aurea (*au*) mutant of tomato (Adamse *et al.,* 1988a, b). Compared to its isogenic wild type (WT) it has no spectrophotometrically and immunochemically detectable P (<5%) in dark(D)-grown tissues (Koornneef *et al.,* 1985; Parks *et al.,* 1987) and exhibits reduced photoregulation of seed germination, anthocyanin synthesis, hypocotyl elongation and chlorophyll synthesis. At the molecular level it has greatly reduced P control of the chlorophyll *a/b*-binding protein (CAB) gene expression (Sharrock *et al.,* 1988; Oelmüller *et al.,* 1989). In light-grown *au* plants about 50% of the WT level of P has been reported on the basis of *in vivo* dual-wavelength spectrophotometry (Adamse *et al.,* 1988b; López-Juez *et al.,* 1990b). Both WT and the *au* mutant adult light-grown plants exhibit a quantitatively similar elongation growth response to EODFR treatment (Downs *et al.*, 1957) indicating the presence of functional P in light-grown *au*-mutant plants (Adamse *et al.*, 1988b; López-Juez *et al.*, 1990b and Table 1). Although the most plausible inference is to ascribe this response to PII, which is predicted to accumulate in the mutant, the molecular nature of P detected in light-grown tissues (Adamse *et al.*, 1988b; López-Juez *et al.*, 1990b) has not yet been positively identified, since PI and PII specific antibodies are not yet available for tomato.

The monogenic recessive high pigment (*hp*) mutant shows characteristics opposite to the *au* phenotype: seedlings have an increased anthocyanin content (Adamse *et al.*, 1989; Peters *et al.*, 1989) and a reduced hypocotyl length in red light (RL), BL, UV-A (Peters *et al.*, 1989) and yellow light (Mochizuki and Kamimura, 1985) compared to WT. Moreover, in light-grown plants the chlorophyll content is particularly high in immature fruit tissues (Sanders *et al.*, 1975) and mature fruits have a higher lycopene and carotenoid content than WT (Kerr, 1965). Unlike WT, the *hp* mutant does not require the activation of the B photoreceptor to exhibit high levels of anthocyanin synthesis and enables complete de-etiolation under R (Peters *et al.*, 1989). Since etiolated *au*-mutant and *au,hp*-double mutant seedlings, both deficient in PI, show respectively, no or a small (3% compared to *hp*) R/FR reversible anthocyanin response after a BL pretreatment (Adamse *et al.*, 1989), it has been concluded that the PI pool regulates anthocyanin synthesis at the seedling stage and that the *hp* mutation does not result in the constitutive expression of genes involved in anthocyanin synthesis. The nature of the processes influenced by the *hp* mutation is unknown. The P content of comparable samples of *hp* and WT etiolated seedlings is similar (Peters *et al.*, 1989). Therefore the difference observed can not be explained by a higher absolute level of the active FR-absorbing form of P (Pfr). Peters *et al.* (1989) proposed that the *hp* mutation increases the responsiveness to Pfr.

This study investigates the influence of EODFR treatment on the growth and pigmentation of the newly formed internodes and leaves of six tomato genotypes: (i) a *hp* mutant which has the same P content and a very high level of anthocyanin compared to WT in seedlings; (ii) an *au* mutant deficient in the light-labile type of PI (Koornneef *et al.*, 1985); (iii) the *au,hp* double mutant; (iv) a *pro* mutant having a phenotype similar to WT treated with gibberellic acid (GA) (Jones, 1987; Jupe *et al,*. 1988) and (v) the isogenic WT.

## 2. Materials and methods

### 2.1. Plant material

Seeds of the mutants and near isogenic WT of *Lycopersicon esculentum* Mill. cv. Ailsa Craig were harvested from plants grown in a greenhouse at the Department of Genetics, Wageningen Agricultural University.

Seeds were then sown in sand with underlying compost, in earthenware seed pans. In experiments with the *au* and *au,hp* mutants all genotypes were pretreated on filter paper moistened with 25 $\mu M$ gibberellin $A_4$ and $A_7$ (ICI, Yalding UK) for 24 h at 25 ± 1° C. Seedlings were initially grown under a daily photoperiod of 14 h white light (WL) and 10 h D, at 20 ± 1° C and 70 % relative humidity. After 8 days, uniform seedlings were selected and potted in 10 cm diameter plastic pots filled with potting compost. After a further 3 to 7 days seedlings were again selected, resulting in about 60% of the seedlings being used and the seedlings were transferred to a growth room at 23 ± 1 or 25 ± 1 °C maintaining the same light regime. After a further 20 to 28 days EODFR treatment was begun and repeated for up to 20 consecutive days. This consisted of transferring plants to a cabinet situated in the same growth room for a 20 min FR (+FR) irradiation at the end of the 14 h WL period, before replacing the plants on the staging. A dim green safelight was used when manipulating the plant material. The control plants received no EODFR (-FR).

### 2.2. Growth measurement

At 0, 7 or 20 days from the start of EODFR treatment the length of every internode was measured with a ruler. Total leaf area and fresh weight (fr wt) of the stems and leaves were determined. Leaf area was estimated with a leaf surface meter as described by Pieters (1984). The mature internode lengths of plants of the different genotypes growing in a greenhouse were measured with a ruler.

### 2.3. Anthocyanin assay

Samples of the youngest leaf were harvested, weighed and extracted with 1.2 ml acidified (1 % HCl, w/v) methanol for 48 h in D with shaking. A Folch partitioning was performed after adding 0.9 ml $H_2O$ and 2.4 ml chloroform to the extracts and centrifugation for 30 min at 4800 rpm. The absorbance of the top phase was determined with a Beckman DU-64 spectrophotometer at 535 nm (A535). The results are expressed on a fresh-weight basis.

### 2.4. Chlorophyll assay

Chlorophyll contents were determined spectrophotometrically in 80% (v/v) acetone/water extracts, according to Bruinsma (1963). The comparably developed leaves were cut into small pieces and extracted. Further details are described in López-Juez *et al.* (1990a).

## 2.5. Light sources

White light was obtained from Philips TL 135/33 fluorescent tubes. The irradiance was 25 W $m^{-2}$; photosynthetically active radiation (400-700 nm) being 120 $\mu$mol $m^{-2}$ $s^{-1}$. The emission spectrum of the tubes was determined with a spectral analyzer (Rofin-Sinar Laser UK Ltd., Weybridge), controlled by a microcomputer system. The P photoequilibrium ($\phi$) = Pfr/RL-absorbing form of P (Pr) + Pfr, i.e. the proportion of total P maintained as Pfr at equilibrium by the light sources was calculated with the absorption coefficients of P and the formula given by Mancinelli (1986). The calculated value established by the WL source was 0.82. Broad-band FR was produced by filtering the light from tungsten filament lamps through one layer of blue (No 627) and one layer of red (No 501) 3 mm plexiglas (Röhm u. Haas, Darmstadt). The irradiance was 14 $\mu$mol $m^{-2}$ $s^{-1}$ in the range 700-780 nm and the 20 min exposure was sufficient to establish a value of $\phi$ = 0.05. Irradiance was measured with a photodiode meter, Optometer, type 80X (United Detector Technology Inc., Santa Maria, CA).

## 2.6. Presentation of results

All experiments have been repeated with qualitatively similar results. The results presented are the mean ± standard error (SE) for individual or pooled experiments.

## 3. Results

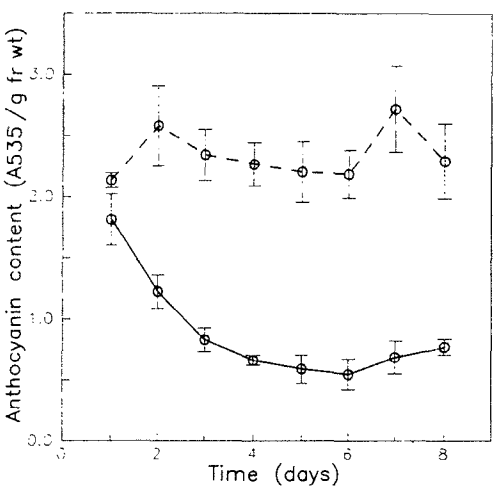
Table 1 shows that the *hp* mutant and WT have similar chlorophyll contents while the *au* and the *au,hp* mutants had about half of the chlorophyll content and were yellower in appearance. The chlorophyll *a/b* ratio was 5.0, 4.5, 3.0 and 3.1 for *au*, *au,hp*, *hp*, and WT, respectively. However, despite the difference in anthocyanin observed between WT and the *hp* mutant at the seedling stage, they contained similar levels at the end of the present experiments (Table 1). Clearly the *au,hp* double mutant is more like the *au* than the *hp* phenotype with respect to both chlorophyll and anthocyanin content. Therefore there is a clear correlation between these effects and the *au* mutation. However, despite these differences, all the genotypes responded to EODFR with an increase in elongation growth (Table 1). In both the *hp* mutant and WT there was a dramatic effect on the anthocyanin content of comparably developed leaves (Table 1). The time course of loss of anthocyanin content probably represents the kinetics of anthocyanin dilution due to growth (Fig. 1) after a rapid inhibition of biosynthesis. Although smaller in magnitude, a reduction in anthocyanin was also observed in older leaves (data not shown).

Table 1. Comparison of the effect of a 20 min far-red light (+FR) pulse at the end of 7 daily photoperiods of 14 h white light (25 $Wm^{-2}$) at 25 °C with control plants (-FR) on chlorophyll and anthocyanin content of comparable leaf samples and increase (Δ) in plant height of wild-type (WT), *au*, *hp* and *au,hp* tomato plants (cv. Ailsa Craig).

| Parameter | | Genotype | | | |
|---|---|---|---|---|---|
| | | WT | *hp* | *au* | *au,hp* |
| Δ height | +FR | 146.3 ± 4.6 | 90.0 ± 2.0 | 200.7 ± 4.5 | 160.7 ± 5.1 |
| (mm) | -FR | 76.3 ± 2.4 | 39.0 ± 2.6 | 103.6 ± 2.5 | 82.0 ± 4.9 |
| Chlorophyll | +FR | 3.70 ± 0.38 | 3.40 ± 0.21 | 1.32 ± 0.03 | 1.85 ± 0.02 |
| (mg/g fr wt) | -FR | 3.12 ± 0.18 | 3.02 ± 0.22 | 1.62 ± 0.12 | 1.79 ± 0.16 |
| Anthocyanin | +FR | 0.57 ± 0.05 | 0.43 ± 0.04 | ND* | ND |
| (A535/g fr wt) | -FR | 1.79 ± 0.15 | 1.67 ± 0.13 | ND | ND |

*ND = not detectable

Figure 1. Anthocyanin content (A535/g fr wt) of comparably developed young leaves of wild-type tomato plants (cv. Ailsa Craig) grown under a daily photoperiod of 14 h white fluorescent light (25 W $m^{-2}$) at 25 °C with (o——o) and without (o- - -o) 20 min end-of-day far-red light treatment.




The characteristics of phytochrome regulation of the EOD-FR response were further studied by interposing a dark period at the end of the day before exposure to FR. A delay of 4 h still results in approximately 50 % of the EODFR response on elongation growth (Fig. 2) for *au*, *au,hp*, *hp* and WT and anthocyanin content for *hp* and WT (Fig. 3). This means that Pfr, involved in this response must still be present at that time; i.e. the pool of phytochrome regulating the EODFR response is by definition, relatively stable in the Pfr form.

Figure 2 -The effect of a 20 min far-red light (FR) pulse at different times after the end of 7 daily photoperiods of 14 h white fluorescent light (25 W $m^{-2}$) at 25 °C on the increase in plant height of tomato wild-type (○), *au* (△), *hp* (●) and *au,hp* (▲) tomato plants (cv. Ailsa Craig). Control without FR (WL).

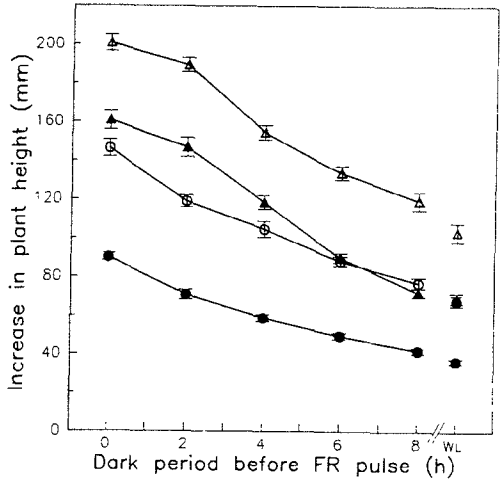
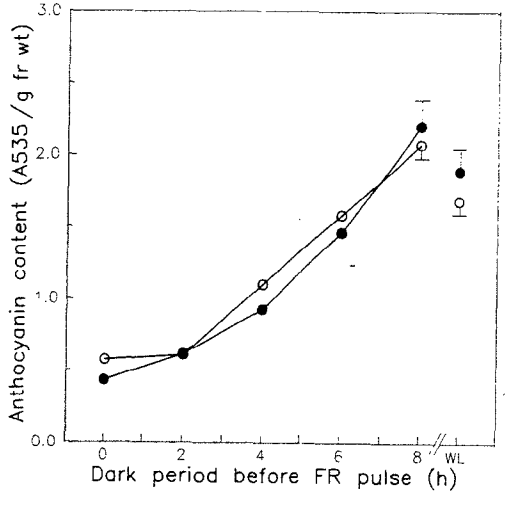



Figure 3 -The effect of a 20 min far-red light (FR) pulse at different times after the end of 7 daily photoperiods of 14 h white fluorescent light (25 W $m^{-2}$) at 25 °C on the anthocyanin content (A535/g fr wt) of tomato wild-type (○) and *hp* (●) tomato plants (cv. Ailsa Craig). Control without FR (WL).



In a subsequent series of experiments we also studied the influence of EODFR, not only on the *hp* mutant and WT, but also on the *pro* mutant. In addition to an increase in internode length during the experimental period, increase in stem fr wt, leaf area and leaf fr wt were determined (Table 2). The *pro* mutant exhibited a normal EODFR response on elongation growth. There was no influence of EODFR on leaf area and leaf fr wt of the three genotypes studied (Table 2). The increase in stem fr wt and plant height results from an increase in stem water content and a decrease in stem diameter of the EODFR-treated plants.

The mean internode lengths of plants growing in the greenhouse during the summer was also determined (Table 3). The *hp* mutant had the shortest internode length but it was not significantly different from that of WT. The *pro* mutant had the longest internode length followed by the *au* mutant and the *au,hp* double mutant, which has slightly longer internodes than WT.

The phenotype of the *pro* mutant is remarkably similar to that of the WT treated with GA (Jones, 1987; Jupe *et al.*, 1988). However, this mutant does not have increased GA levels (Jones, 1987). It was suggested by Adamse *et al.* (1988a) that the *pro* mutant could be similar to the cucumber *lh* mutant and is a possible candidate for a mutant deficient in the function of light-stable P. However, in contradiction to this possibility, *pro* exhibits an EODFR elongation response (Table 2), not shown by the *lh* mutant cucumber (López-Juez *et al.*, 1990a).

If the proposal of García-Martínez *et al.* (1987) that GAs are involved in the EODFR response is correct, the *pro* mutant can not be saturated for the particular GA response involved, since it exhibits a typical EODFR response (Table 2).

Table 2 -Comparison of the effect of a 20 min far-red light (+FR) pulse at the end of 20 daily photoperiods of 14 h white light (25 $W^{-2}$) at 23 °C with control plants (-FR) on the increase (Δ) in plant height, stem growth rate, Δ stem fr wt and leaf area of wild-type (WT), *hp* and *pro* tomato plants (cv. Ailsa Craig).

| Parameter | | Genotype | | |
|---|---|---|---|---|
| | | WT | *hp* | *pro* |
| Δ height | +FR | 123.4 ± 6.0 | 96.3 ± 5.6 | 421.7 ± 15.6 |
| (mm) | -FR | 80.9 ± 4.0 | 73.9 ± 5.6 | 285.3 ± 9.1 |
| Stem growth | +FR | 6.0 ± 0.3 | 4.3 ± 0.3 | 21.9 ± 0.8 |
| rate (mm/day) | -FR | 4.0 ± 0.2 | 3.7 ± 0.3 | 14.3 ± 0.5 |
| Δ stem fr wt | +FR | 5.95 ± 0.73 | 4.03 ± 0.33 | 14.91 ± 2.00 |
| (g) | -FR | 4.60 ± 0.56 | 3.32 ± 0.28 | 11.90 ± 1.59 |
| Leaf area | +FR | 481.3 ± 41.1 | 523.3 ± 60.2 | 645.2 ± 61.6 |
| ($cm^2$) | -FR | 464.8 ± 38.9 | 507.7 ± 58.3 | 675.9 ± 66.2 |
| Leaf fr wt | +FR | 16.30 ± 1.89 | 14.35 ± 1.64 | 18.58 ± 1.94 |
| (g) | -FR | 15.00 ± 1.66 | 13.14 ± 1.49 | 17.77 ± 1.81 |

Table 3 -The mean internode length of mature wild-type (WT), *hp*, *au,hp*, *au* and *pro* tomato plants (cv. Ailsa Craig) growing in a greenhouse during the summer.

| Genotype | Internode length (cm) |
|---|---|
| WT | 5.30 ± 0.27 |
| *hp* | 5.23 ± 0.35 |
| *au,hp* | 5.85 ± 0.28 |
| *au* | 6.96 ± 0.29 |
| *pro* | 7.38 ± 0.47 |

## 4. Discussion

Despite the inefficient de-etiolation process of the *au* mutant, light-grown plants exhibit an apparently normal EODFR response in terms of elongation growth (Table 1). However, the *au* mutant has yellow leaves, lacks detectable anthocyanin (Table 1) and is slightly longer than WT under greenhouse conditions (Table 3). This suggests that the P regulating these processes is deficient in light-grown plants. These observations lend support to the hypothesis that chlorophyll biosynthesis and the EODFR responses are under the control of different P pools. These pools, which are thought to be light labile and light stable may be PI and PII, respectively. Since the P regulating the EODFR is apparently stable in the Pfr form, it is tempting to speculate that the EODFR response is regulated by PII.

The *hp* mutant is in many ways opposite to the *au* mutant and resembles tomato plants which have been genetically engineered to overexpress the oat PI gene (Boylan and Quail, 1989). However, the P content of the *hp* mutant is the same as WT and studies at the de-etiolation stage have led to the conclusion that the *hp* mutant is more responsive for P action (Peters *et al.*, 1989). During normal development of tomato, de-etiolation is achieved, not only as a result of photoactivation of P, but also by its coaction with the BL photoreceptor. It appears that activation of the BL photoreceptor results in an amplification of the P response. In fact, it is the coaction of the BL-photoreceptor and P which enables the *au* mutant to become sufficiently de-etiolated so that it can survive (Peters *et al.*, 1991; Oelmüller and Kendrick, 1991). However, the *au* mutation has a strong residual effect as indicated by its reduced chlorophyll levels and its inability to form anthocyanin in light-grown plants. Taken together, these observations give credence to the notion of discrete functional P pools in plants. While PII may be a type of P which functions predominantly in light-grown plants, PI is essential for plastid development during de-etiolation and it can be envisaged that this role is maintained in light-grown plants.

Plants with *hp* characteristics at the seedling stage (*i.e.* short hypocotyls with high anthocyanin levels) were obtained when high levels of an oat PI gene was expressed in tomato (Boylan and Quail, 1989). Light-grown transgenic plants classified as either null or as low-level expressors resembled WT, while high-level expressors, in contrast to *hp*, were extreme dwarfs, with dark-green foliage and fruits. Regardless of whether the height of the adult plant was normal or dwarf, seedlings expressing oat PI all had short

hypocotyls at the seedling stage. The overproduction of oat PI results in the persistence of oat PI in light-grown plants, demonstrating that PI can be biologically active in fully green tissue. This does not necessarily mean that tomato PI plays a dominant role in elongation growth of light-grown WT plants, since quantitative differences in the rate and the extent of degradation of the Pfr forms of tomato and oat PI in the transgenic plants were observed. Boylan and Quail (1989) point out that the *au* mutant, WT and transgenic PI overexpressors represent a continuum of phenotypic expression in response to increasing levels of PI. Although the *hp* mutant shows characteristics at the seedling stage similar to the transgenic PI overexpressors, it does not have an elevated PI level.

What possibilities do these studies of photomorphogenetic mutants and transgenic plants provide for the regulation of plant growth and development in horticulture? With an increase in the use of supplementary lighting in greenhouses (Vince-Prue and Canham, 1983) and the use of plastic mulches (Decoteau *et al.*, 1988) dramatic deviations from the spectral quality of daylight can occur which can be perceived by P or the BL photoreceptor. Since most recessive mutations are deletions, the observations that a group of mutants of *Arabidopsis* called *det* (Chory *et al.*, 1989) which initiate de-etiolation in D and that the *hp* mutant which at face value no longer requires BL for normal development, suggest that there is a negative control of growth. In other words the photoreceptors can be envisaged as functioning by the removal of some inhibitory substance. One possible scenario is that the mutations result in a reduced rate of synthesis of this hypothetical inhibitor. It has been known for a long time that the spectral quality of light used for supplementary irradiation can result in abnormal growth and development of many species. However, the potential variation seen here for photomorphogenetic mutants suggests that using conventional breeding techniques, or genetic engineering, it should be possible to produce plants which exhibit 'normal' growth under light sources such as high-pressure sodium, which are deficient in BL compared to normal daylight.

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## 5. References

Adamse, P., Kendrick, R.E., and Koornneef, M., 1988a. Photomorphogenic mutants of higher plants. Photochem. Photobiol. 48:833-841.

Adamse, P., Jaspers, P.A.P.M., Bakker, J.A., Wesselius, J.C., Heeringa, G.H., Kendrick, R.E., and Koornneef, M., 1988b. Photoregulation of a tomato mutant deficient in labile phytochrome. J. Plant Physiol. 133:436-440.

Adamse, P., Peters, J.L., Jaspers, P.A.P.M., van Tuinen, A., Koornneef, M., and Kendrick, R.E., 1989. Photocontrol of anthocyanin synthesis in tomato seedlings: A genetic approach. Photochem. Photobiol. 50:107-111.

Boylan, M.T., and Quail, P.H., 1989. Oat phytochrome is biologically active in transgenic tomatoes. The Plant Cell 1:765-773.

Bruinsma, J., 1963. The quantitative analysis of chlorophylls *a* and *b* in plant extracts. Photochem. Photobiol. 2:241-249.

Chory, J., Peto, C.A., Feinbaum, R., Pratt, L.H., and Ausubel, F., 1989. *Arabidopsis thaliana* mutant that develops as a light-grown plant in the absence of light. Cell 58:991-999.

Decoteau, D.R., Kasperbauer, M.J., Daniels. D.D., and Hunt, P.G., 1988. Plastic mulch effects on reflected light and tomato growth. Sci. Hort. (Amst.) 34:169-176.

Downs, R.J., Hendricks, S.B., and Borthwick, H.A., 1957. Photoreversible control of elongation in pinto beans and other plants under normal conditions of growth. Bot. Gaz. 118:199-208.

Furuya, M., 1989. Molecular properties and biogenesis of phytochrome I and II. Adv. Biophys. 25:133-167.

García-Martínez, J.L., Keith, B., Bonner, B.A., Stafford, A.E., and Rappaport, L., 1987. Phytochrome regulation of the response to exogenous gibberellins by epicotyls of *Vignor sinensis*. Plant Physiol. 85:212-216.

Jones, M.G., 1987. Gibberellins and the *procera* mutant of tomato. Planta 172:280-284.

Jupe, S.C., Causton, D.R., and Scott, I.M., 1988. Cellular basis of the effects of gibberellin and the *pro* gene on stem growth in tomato. Planta 174:106-111.

Kerr, E.A., 1965. Identification of high-pigment, *hp*, tomatoes in the seedling stage. Can. J. Plant Sci. 45:104-105.

Koornneef, M., Cone, J.W., Dekens, R.G.,, O'Herne-Robers, E.G., Spruit, C.J.P., and Kendrick, R.E., 1985. Photomorphogenic responses of long-hypocotyl mutants of tomato. J. Plant Physiol. 120:153-165.

Koornneef, M., and Kendrick, R.E., 1986. A genetic approach to photomorphogenesis. In: Photomorphogenesis in Plants, pp.521-547. (Eds R.E. Kendrick and G.H.M. Kronenberg). Martinus Nijhoff Publ., Dordrecht.

López-Juez, E., Buurmeijer, W.F., Heeringa, G.H., Kendrick, R.E., and Wesselius, J.C., 1990a. Response of light-grown wild-type and long-hypocotyl mutant cucumber plants to end-of-day far-red light. Photochem. Photobiol. 52:143-150.

López-Juez, E., Nagatani, A., Buurmeijer, W.F., Peters, J.L., Furuya, M., Kendrick, R.E., and Wesselius, J.C., 1990b. Response of light-grown wild-type and *aurea*-mutant tomato plants to end-of-day far-red light. J. Photochem. Photobiol. B Biology 4:391-405.

Mancinelli, A.L., 1986. Comparison of spectral properties of phytochromes from different preparations. Plant Physiol. 82:956-961.

Mochizuki, T., and Kamimura, S., 1985. Photoselective method for selection of *hp* at the cotyledon stage. Tomato Genet. Coop. Rpt. 35:12-13.

Mohr, H., 1986. Coaction between pigment systems In: Photomorphogenesis in Plants, pp.547-564. (Eds R.E. Kendrick and G.H.M. Kronenberg). Martinus Nijhoff Publ., Dordrecht.

Oelmüller, R., and Kendrick, R.E., and Briggs, W.R., 1989. Blue-light mediated accumulation of nuclear-encoded transcripts coding for proteins of the thylakoid membrane is absent in the phytochrome-deficient *aurea*-mutant of tomato. Plant Mol. Biol. 13:223-232.

Oelmüller, R., Kendrick, R.E., (1991). Blue light is required for survival of the tomato phytochrome-deficient *aurea* mutant and the expression of four nuclear genes coding for plastidic proteins. Plant Mol. Biol. 16:293-299.

Parks, B.M., Jones, A.M., Adamse, P., Koornneef, M., Kendrick, R.E., and Quail, P.H., 1987. The *aurea* mutant of tomato is deficient in spectrophotometrically and immunocytochemically detectable phytochrome. Plant Mol. Biol. 9:97-107.

Peters, J.L., van Tuinen, A., Adamse, P., Kendrick, R.E., and Koornneef, M., 1989. High pigment mutants of tomato exhibit high sensitivity for phytochrome action. J. Plant Physiol. 134:661-666.

Peters, J.L., Wesselius, J.C., Georghiou, K., Kendrick, R.E., Van Tuinen, A., and Koornneef, M., (1991). The physiology of photomorphogenetic tomato mutants. In: Phytochrome Properties and Biological Action, pp. 237-247. NATO ASI Series, Vol H 50. (Eds B. Thomas and C.G. Johnson). Springer-Verlag, Heidelberg.

Pieters, G.A., 1984. A television leaf area meter. Photosynthetica 18:454-458.

Sanders, D.C., Pharr, D.M., and Konsler, T.R., 1975. Chlorophyll content of a dark-green mutant of 'Manapal' tomato. Hort. Science 10: 262-264.

Sharrock, R.A., Parks, B.M., Koornneef, M., and Quail, P.H., 1988. Molecular analysis of the phytochrome deficiency in an *aurea* mutant of tomato. Mol. Gen. Genet. 213:9-145.

Smith, H., 1986. The perception of kight quality. In: Photomorphogenesis in Plants, pp. 187-217. (Eds R.E. Kendrick and G.H.M. Kronenberg). Martinus Nijhoff Publ., Dordrecht.

Soressi, G.P., 1975. New spontaneous or chemically-induced fruit- ripening tomato mutants. Tomato Genet. Coop. Rpt. 25:21-22.

Tomizawa, K., Nagatani, A., and Furuya, M., 1990. Phytochrome genes: Studies using the tools of molecular biology and photomorphogenetic mutants. Photochem. Photobiol. 52:265-275.

Vince-Prue, D., and Canham, A.E., 1983. Horticultural significance of photomorphogenesis. In: Encyclopedia of Plant Physiology, pp. 518- 544. (Eds W. Shropshire, Jr. and H. Mohr). Springer-Verlag, Berlin.