The Relationship between Phytochrome Photoequilibrium and Development in Light Grown Chenopodium album L.*

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Abstract. Chenopodium album seedlings were grown in light environments in which supplementary far-red light was mixed with white fluorescent light during various parts of the photoperiod. Both the logarithmic rate constant of stem extension and the leaf dry weight:stem dry weight ratio were linearly related to estimated phytochrome photoequilibrium ($\phi$) in each treatment regime. These data are taken to be indicative of a functional link between phytochrome and development in the green plant. A layer of chlorophyllous tissue only affected the linearity between calculated $\phi$ and the logarithmic stem extension rate at high chlorophyll concentrations, whilst even low concentrations—equivalent to the levels found in stem tissue—caused a significant shift in measured $\phi$. End-of-day supplementary far-red (FR) light induced between 0–35 per cent of the response elicited by all-day supplementary FR, whilst daytime supplementary FR (with a white fluorescent light end-of-day treatment) induced approximately 90 per cent. The ecological significance of this difference is discussed with respect to shade detection.

Key words: Chenopodium — Far-red — Photoequilibrium — Phytochrome — Stem extension.

Introduction

Phytochrome, the red/far-red (R/FR) photoreversible plant photoreceptor, has been rigorously investigated in dark grown tissue, and its role in seedling de- etiolation well documented. Its function in green plants is less clear. The previous papers in this series have expounded the hypothesis that in nature phytochrome mediates the developmental responses to shade light quality (Holmes and Smith, 1977a, b, c; Smith and Holmes, 1977; Tasker and Smith, 1977)—that is the change in R/FR ratio ($\zeta$) due to attenuation of daylight by the shading vegetation. Most striking is the increased internode extension (Morgan and Smith, 1976), which can be explained ecologically as an adaptation for avoiding shade. In their previous paper the authors briefly reported a linear relationship between phytochrome photoequilibrium ($\phi$), estimated from etiolated tissue, and stem extension rate in green Chenopodium album. These experiments are fully reported here, together with two related investigations.

Firstly, chlorophyll screening is known to shift phytochrome absorption maxima (Grill, 1972), and unless the photoreceptor is located in the upper epidermis this could well affect the response linearity. Therefore, the effect of a layer of chlorophyllous tissue on calculated and measured $\phi$, and their relationship with stem extension, was investigated. Secondly, several workers have proposed that in nature the end-of-day spectrum determines the phytochrome-controlled response to shade (Kasperbauer, 1971; Shropshire, 1973; Vince-Prue, 1977), mainly because in the controlled environment plants readily react to a FR light treatment at the end of the daily white light period. Two points make this hypothesis less plausible than daytime detection, these being: (a) daytime detection offers more complete information; and (b) the non-vegetational change in $\zeta$ at dusk (Shropshire, 1973; Holmes and Smith, 1977a) would complicate end-of-day shade detection. Therefore, the relative responses of C. album to daytime and end-of-day supplementary FR were investigated.
Materials and Methods

Light Measurements and Phytochrome Determinations

Light quality was measured using a Gamma Scientific (San Diego) spectroradiometer, and light quantity, defined as the spectral photon flux of the 400–700 nm waveband (photosynthetically active radiation; McCree, 1972), was measured with a Lambda Instruments (Lincoln, Nebraska) quantum meter. Both instruments have been fully described before (Holmes and Smith, 1977a).

Phytochrome photoequilibrium ($\phi$) was determined by two indirect methods, both of which gave estimates relating to etiolated tissue. The first, estimated $\phi (\phi_d)$, is determined from $\zeta$ (the 660 nm:730 nm ratio of spectral photon flux rate) by using Smith and Holmes' (1977) plot of the $\phi/\zeta$ relationship. The second, calculated $\phi (\phi_c)$, is calculated from the spectral photon distribution of the 400–800 nm waveband using an expansion of Hartmann's (1966) formula, which will be described in detail by Tasker and Smith later on. Direct determination, which was used in the screening experiments, is described below.

Plant Material and Light Sources

*C. album* seed was collected from Field 12, on the Experimental Farm, Sutton Bonington. Seedlings were grown up to the third leaf pair stage in 6.35 cm pots in John Innes potting compost in a 12 h:12 h light:dark cycle. The pretreatment environment was lit by a bank of 1525 mm long 80 W Philips “Warm White” fluorescent tubes ($\zeta = 9.0$; PAR = 180 ± 11 $\mu$mol m$^{-2}$ s$^{-1}$). The photo- and thermo-periods were 16 h:0 h (day:night) and 13 ± 1 °C respectively. The highest temperature invariably occurred at the end of a night in a range of light environments, differing only in the light treatment being given over the whole of the photo-period (‘all day’; Fig. 1), for 21 d. The immediate and large developmental response to FR irradiance is readily apparent (Fig. 2). It should be noted that no attempt was made to equalise the photosynthetically active radiation as the supplementary-FR treated plants grew taller. By day 9 the difference between the tops of the two sets of plants in terms of photosynthetically active radiation and temperature was 7 $\mu$mol m$^{-2}$ s$^{-1}$ and 6 °C respectively. These differences are small and considered unimportant. However, by day 21 the differentials were 49 $\mu$mol m$^{-2}$ s$^{-1}$ and 2 °C, and these will have been responsible for some of the observed increase in height.

(i) Effect of Added FR on Stem Extension Rate

Batches of 15 plants were grown in low and high $\zeta$, the treatment being given over the whole of the photoperiod (‘all day’; Fig. 1), for 21 d. The immediate and large developmental response to FR irradiance is readily apparent (Fig. 2). It should be noted that no attempt was made to equalise the photosynthetically active radiation as the supplementary-FR treated plants grew taller. By day 9 the difference between the tops of the two sets of plants in terms of photosynthetically active radiation and temperature was 7 $\mu$mol m$^{-2}$ s$^{-1}$ and 6 °C respectively. These differences are small and considered unimportant. However, by day 21 the differentials were 49 $\mu$mol m$^{-2}$ s$^{-1}$ and 2 °C, and these will have been responsible for some of the observed increase in height.

(ii) Effect of a Range of $\zeta$ on Extension Rate, and its Relationship to $\phi$

Batches of between 10 and 15 seedlings were grown in a range of light environments, differing only in their FR irradiance, for 9 d (the period over which stem extension is exponential (Fig. 2) and during which differences in photosynthetically active radiation and temperature at the plant apices are insignificant). The light treatment was given over the whole day (‘all day’; Fig. 1). Over the 9 d period the extension rate was graded according to $\zeta$, and since it was exponential it could be accurately quantified as the logarithmic rate constant, which is referred to as the logarithmic stem extension rate (Fig. 3). Analysis of variance indicates a significant difference ($P < 0.001$) between the extension rates of the different treatments. The relationships between $\phi$, and the logarithmic stem extension rate, and $\phi_c$ and the leaf dry weight:stem dry weight ratio are linear (Fig. 4). That both of these extension related parameters are linearly related to $\phi$, is thought to be strong, although circumstantial, evidence for a functional link between phytochrome and development in the green plant.