Biomass Partitioning and Root-Knot Nematode Development in Tomato Plants under End-of-Day Red or Far-Red Light

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ABSTRACT

The ratio of far-red to red light received by a growing plant alters the photoequilibrium of the phytochrome system and regulates partitioning of photosynthate among stems, leaves, and roots. This study was conducted in a controlled environment to determine whether red or far-red light received by tomato (*Lycopersicon esculentum* Mill. cv. Rutgers) shoots can affect activity of root-knot nematode, *Meloidogyne incognita* (Kofoid and White). Nematode-inoculated and noninoculated plants received 5 min of red (a low far-red to red ratio) or 5 min of far-red (a high ratio) light at the end of the daily 12-h photosynthetic period for 32 d consecutively, after which plant parameters and nematode presence were measured. The red or far-red light treatments altered plant growth patterns and the reproduction of *M. incognita*. Plants that received the far-red light treatment were taller, heavier, and had a greater leaf area than red light–treated plants. Also, the far-red light–treated plants were lighter green in color, developed longer internodes, had greater leaf mass and a higher shoot/root biomass ratio than plants treated with red light. *Meloidogyne incognita*–inoculated plants that received the far-red light had fewer eggs and fewer egg masses than plants that received red light. Crop production procedures such as use of plant residues, colored mulches, and other practices that affect the ratio of far-red relative to red light in growing plant canopies might influence nematode parasitism of tomato.

ROOT-KNOT nematodes elicit a metabolic sink reaction in host plants in which nutrient flow to the root system is increased (Bergeson, 1966; McClure, 1977; Melakeberhan and Ferris, 1988). In tomato, *M. incognita* infection results in an increase in root weight and a decrease in shoot weight which shifts the shoot to root balance. Nematode-infected tomato plants have thinner leaves and accumulate proportionately less mass in the stem tissues than in the leaf lamina (Fortnum et al., 1991). Plant growth regulators have been implicated in nematode–host responses and disease development (Bird and Loveys, 1980; Fortnum and Lewis, 1983; Glazer et al., 1983; Hussey, 1985; Kochba and Samish, 1971).

Photomorphogenesis in many plants is regulated by light in the red (R) and far-red (FR) portion of the spectrum (Schopfer, 1984). The R–FR photoreversible pigment, phytochrome, is extremely sensitive to light of low irradiances. The R-absorbing form of phytochrome (Pr) absorbs R and becomes the FR-absorbing form (Pfr), and vice versa. Thus the FR/R ratio in incoming light regulates the photoequilibrium level between the two forms of phytochrome and this regulates many developmental processes (Kasperbauer, 1988). A brief end-of-day exposure to R (a low FR/R ratio) or to FR (a high FR/R ratio) alters the photoequilibrium of phytochrome and influences the partitioning of photosynthate among stems, leaves, and roots during the subsequent dark period (Kasperbauer and Peaslee, 1973). A brief end-of-day exposure to R results in a plant that has a shorter stem and a larger root system (i.e., smaller shoot-to-root biomass ratio). Conversely, a plant that receives a short end-of-day exposure to FR develops a longer stem and a smaller root system (i.e., larger shoot-to-root biomass ratio). It has been suggested that the phytochrome system initiates events that modify the balance of endogenous growth regulators (Kasperbauer, 1971) and functions in adaptation of the growing plant to changing light environments under field conditions (Kasperbauer et al., 1984; Kasperbauer and Karlen, 1986; Kasperbauer, 1987, 1988).

Phytochrome-mediated shifts in photosynthate par-

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Abbreviations: FR, far-red light; Pfr, far-red light–absorbing phytochrome; Pr, red light–absorbing phytochrome; R, red light.

titioning have been shown to affect the symbiotic relationship between *Rhizobium japonicum* and soybean (Kasperbauer et al., 1984). Soybean plants that received end-of-day R had more rhizobium-induced nodules, with a greater dry weight, than plants that received FR. Also, the light source used during the photosynthetic period can affect the development of *M. javanica* (Bird et al., 1980), suggesting that a combination of irradiance and spectral balance received by the growing shoots might be involved.

The purpose of this study was to determine the effect of phytochrome-mediated shifts in photosynthate partitioning on the development of *M. incognita* on tomato roots when total light energy and temperature were held constant among all plants, and brief R or FR treatments shifted phytochrome equilibrium toward the Pfr or Pr form, respectively, at the end of the photosynthetic period.

MATERIALS AND METHODS

Culture of Plants and Preparation of Inoculum

Rutgers tomato seeds were germinated in vermiculite. Five-centimeter-tall seedlings were transplanted into 15-cm plastic pots containing 1-L heat-pasteurized mixture (2:1, v/v) of a Varina sandy loam soil (clayey, kaolinitic, thermic Plinthic Paleudult) and vermiculite pH 6.2. The plants were maintained in a greenhouse without supplemental lighting until a height of 12 cm was reached. Uniformly sized seedlings were selected and placed in a growth chamber maintained at 25°C for 48 h prior to receiving nematodes and starting the end-of-day light treatments. The *M. incognita* Race 3 population was isolated from field plots at the Clemson University Pee Dee Research and Education Center (Florence, SC) and cultured on tomato seedlings. Nematode eggs from roots of 50-d-old tomato plants (extracted in 0.5% NaOCl and washed in tap water) served as the inoculum (Hussey and Barker, 1973). Ten milliliters of inoculum, containing ≈750 eggs in developmental stages A to H (Taylor and Sasser, 1978), was pipetted into each of two 5-cm-deep holes on opposite sides of each inoculated tomato plant and the holes were filled with soil. A root suspension filtrate obtained from uninfected tomato plants was added to the control plants, so each plant received a total of 20 mL of suspension. All plants were watered with quarter-strength Hoagland's nutrient solution every 7 d (Hoagland and Arnon, 1950).

Effect of Light Treatment of Shoots on Root-Knot Development

All plants were grown in a controlled-environment chamber at 25°C with 12-h days of cool-white fluorescent light at 450 μmol m^{-2} s^{-1} between 400 and 700 nm. At the end of the daily photosynthetic period, plants received 5 min of R or FR in a treatment room, then were returned in darkness to the dark, controlled-environment chamber for the remainder of the 12-h night. The R (360 μw cm^{-2} in the 600- to 700-nm waveband) was obtained by filtering radiation from cool-white fluorescent lamps through two layers of red cellophane. The FR (360 μw cm^{-2} in the 700- to 770-nm waveband) was obtained by filtering radiation from internal reflector incandescent-filament flood lamps through two layers of red and two layers of dark blue cellophane. The R and FR treatments began when the seedlings were inoculated with *M. incognita* and were continued each day for 32 consecutive days. Plants were harvested on the day following the last light treatment. Shoots were cut at the soil surface and then divided into stems (stem + petiole + rachis) and leaflets. The roots were washed free of soil. Plant parts were weighed and leaf areas determined using a Li-Cor 3100 area meter (LI-COR, Lincoln, NE).[1] Root galling was rated on a 0 to 10 scale in which 0 = no galls and 10 = 100% of the root tissue galled (Barker et al., 1986). Egg masses were counted and the roots were then extracted for the enumeration of nematode eggs using the NaOCl treatment previously described. Roots were stained using the NaOCl–acid–fuchsin method (Byrd et al., 1983) and the total number of nematodes and their developmental stages were recorded. A randomized complete-block design with four replications was used in each of two growth chamber experiments. Data were pooled and analyzed using analysis of variance and factorial techniques.

RESULTS AND DISCUSSION

Growth Responses

Brief end-of-day irradiation with R or FR affected the relative amount of photosynthate partitioned to shoots and roots (P = 0.01; Table). The FR-treated plants had a larger shoot/root ratio than R-treated plants. Plants treated with FR (a high FR/R ratio) were taller, had a greater shoot weight and leaf area than those treated with R (a low FR/R ratio) (P = 0.01, Table 1). The FR-irradiated plants were lighter green in color, developed longer internodes (P = 0.05), and had greater leaf mass (P = 0.01) than plants irradiated with R (Table 1).

Phytochrome regulation of photomorphogenesis is extremely sensitive to light of low photon flux densities. Our brief end-of-day exposures to R or FR allowed experiments to be performed under controlled conditions in which all plants received the same light and temperature for 23 h and 55 min d^{-1}; and the 5 min R or FR irradiations were at the same energy level, but poised phytochrome predominately in the FR- or R-absorbing form, respectively, at the beginning of the night. Phytochrome form during the night is known to regulate partitioning of photosynthate to developing plant parts and regulate shoot/root ratios (Kasperbauer, 1971; Kasperbauer et al., 1984).

Partitioning of photosynthate among leaves, stems and roots may be controlled by a shift in endogenous growth regulator balance controlled through the phytochrome system (Kasperbauer, 1971). Phytochrome has been shown to interact with hormonal regulation of plant growth and development (Tucker, 1981) which may alter the association between plants and obligate parasites. The impact of R and FR on the symbiotic relationship between soybean and *Rhizobium japonicum* (nodulation) (Kasperbauer et al., 1984) may be due in part to this altered growth regulator balance.

Reproduction of *Meloidogyne incognita*

In a preliminary experiment, plants inoculated with *M. incognita* and harvested after 10 d of R or FR treatments had similar numbers of second-stage juvenile larvae (J2) within their roots regardless of the

[1]Mention of a trademark, proprietary product, or vendor does not constitute a guarantee or warranty of the product by Clemson University, the South Carolina Agricultural Experiment Station, or the USDA and does not imply its approval to the exclusion of other products or vendors that may also be suitable.

Table 1. Biomass distribution (per-plant means) in tomato plants that received red (R) or 5 min far red (FR) light at the end of the daily photosynthetic period for 32 consecutive days.

End-of-day light (5 min)			Biomass distribution				Plant size		
			Shoots						
Color	FR/R	Nematode† presence	Stems	Leaf	Roots	Shoot/root	Height	Internode length	Leaf area
			g				cm		cm²
R	Low	−	28.7	18.8	20.7	2.3	35.5	3.1	619
R	Low	+	26.6	17.8	18.6	2.4	36.1	3.0	587
FR	High	−	33.3	25.1	21.2	2.8	39.2	3.5	875
FR	High	+	34.1	26.6	21.9	2.8	38.9	3.3	887
Light (L)			**	**	NS	**	**	*	**
Nematode (N)			NS	NS	NS	NS	NS	NS	NS
L × N			NS	NS	NS	NS	NS	NS	NS

*,** Significant at the 0.05 and 0.01 probability levels, respectively.
† Initial population density of *Meloidogyne incognita* of 1500 eggs pot^{-1} (+) or not inoculated (−).

Table 2. Effect of end-of-day red (R) or far red (FR) light treatment of shoots on the reproduction of *Meloidogyne incognita* on roots of tomato plants after 32 consecutive days of treatment.†

End-of-day light (5 min)		Root-gall index	Eggs	Egg masses	Eggs per egg mass	Adult females	Juvenile larvae (J3–J4)
Color	FR/R						
			no. × 10³‡	no.			
R	low	2.0	33.9	87	437	496	22
FR	high	2.1	20.5	46	472	475	20
Significance		NS	*	**	NS	NS	NS

*,** Significant at the 0.05 and 0.01 probability levels, respectively.
† Values are expressed as means per plant. Initial population density of *Meloidogyne incognita* was 1500 eggs pot^{-1}.
‡ Multiply value shown by this to get actual value.

light treatments. Thus, initial entry of the J2 larvae into the roots was not significantly affected by R or FR treatment of the shoots; however, a longer treatment period showed that light environment of the shoots could affect reproductivity of the adult nematode. After 32 d of R and FR treatment, the number of mature females within the roots, the root gall index, and the number of eggs per egg mass did not differ (P = 0.05) between the light treatments (Table 2). However, *M. incognita*–inoculated plants that received the end-of-day FR (high FR/R ratio) had fewer eggs (P = 0.05) and egg masses (P = 0.01) than plants that received R (low FR/R ratio) (Table 2). Clearly, the reproductivity (number of eggs and egg masses) of nematodes in roots was influenced by the light environment of the shoot.

Root-knot nematodes alter biomass partitioning in tomato (Fortnum et al., 1991) when nutrients produced in the shoots are rapidly mobilized to the roots to support nematode development (Bergeson, 1966; McClure, 1977; Melakeberhan and Ferris, 1988). In the present study, a low inoculum level was chosen to minimize the effect of the nematodes on the host physiology, and nematode inoculations did not alter the biomass distribution in tomato plants receiving end-of-day R or FR (Table 1). It is probable that nutrient mobilization from the shoots to the nematode-modified polyploid feeding cells (giant cells) plays an important role in the rate of maturation of root-knot nematodes.

Plant growth regulators have been implicated in the development of root-knot nematode–host interactions (Bird and Loveys, 1980; Fortnum and Lewis, 1983; Glazer et al., 1983; Hussey, 1985; Kochba and Samish, 1971). However, the physiological processes that sequester nutrients to nematode-altered plant structures (feeding cells, giant cells) have not been clearly defined. An altered growth regulator balance, initiated by the phytochrome system, might play a role in the observed changes in *M. incognita* reproduction observed under the different light treatments (Table 2).

Crop production procedures, such as the use of colored mulches, plant spacing and row orientation have been shown to alter the amount of reflected FR and the ratio of FR to R received by the growing plant canopy (Decoteau et al., 1986, 1989; Kasperbauer et al., 1984). The end-of-day light treatments used in the present study produced growth patterns typical of field grown plants that receive different FR/R ratios. The alterations in amounts of reflected FR and R affect the partitioning of photosynthate into shoots, roots, and fruit. Thus, use of production practices, such as colored mulches, may provide a means to minimize nematode reproduction and disease development. Experiments are underway to study the effects of reflective films on root-knot development.

CONCLUSIONS

1. The FR/R ratio received by growing shoots influenced plant height, leaf area and the shoot/root biomass ratio.
2. Second stage juvenile larvae (J2) infection of the roots was not significantly altered by the FR/R ratio received by the shoots.
3. However, plants whose shoots received a high FR/R ratio and developed a larger shoot/root bi-

omass ratio had fewer nematode eggs and egg masses after 32 d.

4. Crop production procedures that alter the FR/R ratio in light received by shoots of growing plants might affect nematode reproductivity in the roots.

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