Competition Responses of *Populus alba* Clone 'Bolleana' to red:far-red light

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ABSTRACT

The reduced ratio of red:far-red (R:FR) light acts as a measure of the proximity of competitors and plants can detect the potentially competing neighbor plants by perceiving reflected R:FR signals and initiate the response of "shade avoidance" before actual shading occurs. The phytochrome system is responsible for monitoring the changes in the R:FR and initiating the shade avoidance response. The response to low R:FR ratio was studied in a white aspen *Populus alba* clone 'Bolleana' using two filter systems: a clear plastic filter system that allows a R:FR ratio less than 1.0 to pass from adjacent border plant reflection; and a special commercial plastic that blocks FR light and creates a R:FR ratio above 3.0. The reduced R:FR signals enhanced the stem elongation in response to competition at the expense of relative stem diameter growth. Trees grown inside clear chambers were 27% taller than trees grown inside the FR-blocking filter chambers. Stem taper of clear chamber trees was 16% less than the FR-blocking filter trees. Low R:FR also induced 22% more stem dry weight and 13% greater petiole length per leaf compared to the FR-blocking filter trees. There were no statistically significant differences in leaf area, leaf number increment, and total dry weight between the two light filter treatments.

Key words **:** red:far-red light, *Populus alba*, phytochrome, shade-avoidance

INTRODUCTION

Plants use light as energy, information to detect neighbors, and to keep track of time throughout the seasonal growth cycle. Plants can detect their neighbors by sensing the spectral properties of light reflected from the foliage of nearby plants and initiate the response of "shade avoidance" before actual shading occurs (Ballar *et al.*, 1987, 1990, 1994; Smith *et al.*, 1990). Ambient light has a ratio of red to far-red light (R:FR at ~660 nm to ~730 nm) of about 1.2 (Kendrick and Kronenberg, 1994). The photosynthetic pigments absorb R light preferentially, but reflect or transmit FR light, which reduces the R:FR photon ratio below 1.0 and acts as a

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signal for detection of neighbors (Ballar *et al.*, 1987, 1990, 1994; Ritchie, 1997; Smith *et al.*, 1990; Smith and Whitelam, 1997). The changes in the R:FR ratio function as a measure of the proximity of competitors and acts as an "early warning signal"(Ballar *et al.*, 1987). The shade avoidance includes enhanced stem elongation and other morphological changes to increase the chance of receiving direct sunlight. The shade avoidance reaction varies according to the species and genetic background. Most studies have been done with herbaceous plants (reviewed in Kendrick and Kronenberg, 1994). The most common response of shade avoidance is extra elongation growth in internodes. The elongation growth is also observed in the hypocotyl and petioles. Most herbaceous plants show the elongation growth at the expense of leaf development and branching. However, different shade avoidance responses have been reported in some tree species. In coastal Douglas-fir (*Pseudotsuga menziesii*) seedlings, crown biomass and branch number increased with decreasing growing space (Ritchie, 1997). Although leaf numbers were reduced in more dense canopies in *Populus trichocarpa* X *P. deltoides* clone 'Beaupr' trees, increased leaf area and dry weight were reported (Gilbert *et al.*, 1995). In accordance with the above results, other studies reported that young trees in high density plantations usually show rapid height growth that occurs long before actual shading (Cameron *et al.*, 1991; DeBell and Giordano, 1994; Knowe and Hibbs, 1996; Scott *et al.*, 1992).

Many experiments have shown that the phytochrome pigment system is responsible for monitoring the changes in the R:FR and initiating the shade avoidance response (reviewed in Kendrick and Kronenberg, 1994). Phytochromes are blue protein photo-reversible pigments that absorb R and FR light most strongly. They have important roles in light-regulated vegetative and reproductive development. Phytochromes are encoded by a multigene family and each phytochrome controls a different process with overlapping functions. While five genes (*PHYA, B, C, D* and *E*) have been reported in *Arabidopsis*, only three genes (*PHYA, B1* and *B2*) have been reported in *Populus trichocarpa* and *Populus balsamifera* (Sharrock and Quail, 1989; Howe *et al.*, 1998). There are two types of phytochromes: type I is light labile (phytochrome A) and type II (phytochrome B-E) is light stable. In dark-grown plants, phytochrome A is the most abundant phytochrome. Expression of phytochrome A is negatively regulated in the light and the protein is degraded in the light (Kendrick and Kronenberg, 1994).

The involvement of multiple phytochromes in response to shade avoidance has been reported through the studies of phytochrome deficient mutants. For example, light-grown phytochrome B deficient mutants of *Arabidopsis* showed elongated growth and early flowering that are characteristics of the shade avoidance syndrome of wild type seedlings grown under a low R:FR light environment (Nagatani *et al.*, 1991; Reed *et al.*, 1993). This indicates that the phytochrome B signal is responsible for the inhibition of hypocotyl elongation and has a major role in the shade avoidance response. Under FR-rich light, *Arabidopsis* phytochrome B null mutants showed additional elongation growth and even earlier flowering than phytochrome B null mutants grown in a normal light environment. This indicates that other phytochromes are also involved in the shade avoidance response (Smith and Whitelam, 1997). According to the analyses of other phytochrome null mutants, phytochrome B, D and E regulate the shade avoidance response (Aukerman *et al.*, 1997; Devlin *et al.*, 1998, 1999). Normally, phytochrome A has little effect on shade avoidance, probably due to the property of light instability of phytochrome A. The function of phytochrome C is still unknown in the shade avoidance response due to the lack of phytochrome C null mutants (Morelli and Ruberti, 2000). However, a reduced level of phytochrome C was detected in the *Arabidopsis*

phytochrome B mutant, which indicates that the mutant phenotype may result in part from the reduced phytochrome C (Hirschfeld *et al.*, 1998).

Phytochrome is produced in the R light-absorbing form called Pr in dark-grown plants. Pr is converted by R light to the FR light-absorbing form called Pfr, which is the physiologically active form of phytochrome and the two forms are photoreversible (reviewed in Kendrick and Kronenberg, 1994). It has been suggested that the ratio between Pfr and the total amount of phytochrome (Pfr/Ptotal) determines the magnitude of the response. Lower ratios of R:FR convert greater portions of Pfr into the Pr form generating reduced ratios of Pfr/Ptotal. The changes were also reported in tree experiments: lower Pfr/Ptotal was detected with higher canopy density of *Populus trichocarpa* X P. *deltoides* clone 'Beaupr'and Douglas-fir seedlings (Gilbert *et al.*, 1995; Ritchie, 1997). They found negative linear relationships between stem height growth rate and plant spacing or Pfr/Ptotal. Therefore, the R and FR wavelengths of light function as a signal for plants to adjust to the competition environment through modification in growth.

The objective of this study was to understand the growth changes in *Populus alba* clone 'Bolleana' in its juvenile stage in response to the changes in R:FR. The long term objective is to develop a controlled-environment assay to study genetic variation in the shade avoidance response of *Populus* clones. A commercial plastic filter system that selectively absorbs FR light was used to produce a high ratio of R:FR (van Haeringen *et al.*, 1998). Although many studies have been performed on the response to the different R:FR light conditions, most of the data are from herbaceous plants. An understanding of the shade avoidance response of poplar trees would be useful for the management of poplar stands in the field to maximize production through genetic selection for the best growth response and to choose optimal spacings.

MATERIALS AND METHODS

Plant Material and Growth Conditions

The white aspen *Populus alba* clone 'Bolleana' was used to study the effect of R:FR on growth as a competition signal. Ramets were propagated through a greenwood cutting method (Faltonson *et al.*, 1983). Stems were cut into small sizes that contained two internodes with two fully-expanded leaves. The lower leaf was removed and the base of the stem was dipped into 1,000 mg/L of indole 3-butyric acid (IBA) to induce rooting. The IBA-treated stem segments were inserted into Jiffy-7 Peat Pellets (Jiffy Products of America, Batavia, IL) that were moisturized overnight before use. The stem cuttings were placed in a mist chamber for rooting over a 20-day period. The rooted stem cuttings were potted in a mixture of peat:perlite: vermiculite (1:1:1) and used for the R:FR light treatment when plant height reached around 14 -19 cm. All plants were fertilized once a week with a mixture of Miracle-Gro Excel All Purpose (21:5:20, Scotts, Columbus, OH) and watered daily. Plants were grown in the Forestry Greenhouse at Iowa State University under 20℃ and 16-h light period.

Light Treatment and Growth Measurements

Two plants of similar height were randomly assigned to one of two filter chambers. Trees in the filter chambers were surrounded by four border trees arranged in a 40cm square to create the reflected light environment. Four more border trees were added at the 12th day of treatment to reduce the R:FR ratio inside the clear filter chamber below 1.0, which is the threshold light condition that induces the shade avoidance response (Fig. 1). Open toped chambers constructed from plastic films (30 cm diameter and 50 cm height) were used to establish the two different R:FR ratios. A special FR-blocking plastic filter was used to create a ratio of above 3.0 for a plant grown

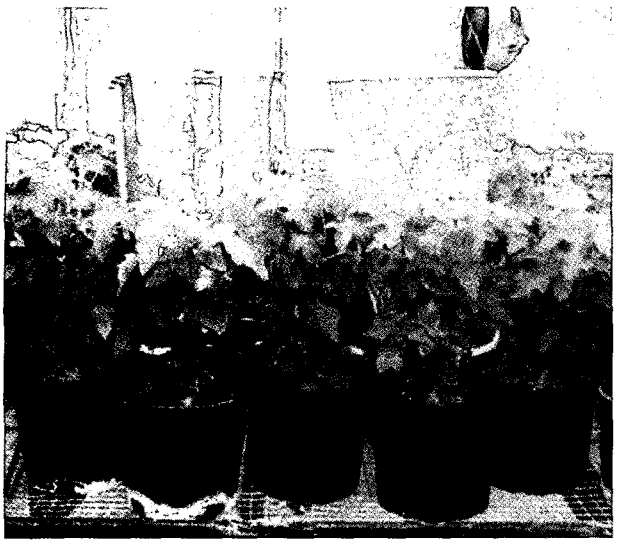

Fig. 1. Arrangement of two filter chambers in greenhouse experiment. Left chamber is clear filter and right chamber is FR-blocking filter. Trees in the filter chambers were surrounded by eight border trees to create the reflected light environment. To maintain the same level of photosynthetically active radiation for the two filter chambers, six 3.7 cm width strips of duct tape were attached to the sides of the clear filter chambers to reduce light penetration.

inside (Visqueen, Cleveland, UK; van Haeringen *et al.*, 1998). The FR filter selectively blocks FR light and thereby increases the R:FR ratio. A transparent plastic filter was used as a control, transmitting a R:FR ratio of below 1.0 produced by the border trees. The filter chambers surrounded whole plants during the treatment period that continued for 27 days. Photosynthetically active radiation (PAR, 400-700 nm) inside the two filter chambers was measured using a LI-1000 spectroradiometer (LI-COR, Lincoln, NE). According to preliminary measurements, the clear filter chambers allowed ~25% more PAR to pass through than the FR filter chambers. To maintain the same level of PAR for the two filter chambers, six 3.7-cm width strips of duct tape were attached vertically to the sides of the clear filter chambers at every 60 around the circumference of a chamber to reduce light penetration. To homogenize the growing conditions in the greenhouse, plants were rotated into different positions on different benches every six days. The R:FR was measured horizontally at the mid-height of the filter chamber with an integrating cylinder, on loan from Weyerhaeuser Company (Ballar *et al.*, 1987). This integrating cylinder has a cylindrical bar of transparent acrylic with a 45 cone removed from the upper end to focus light entering from the sides on to the filter optic cable of a LI-COR remote sensing attachment on a LI-1800 spectroradiometer (LI-COR, Lincoln, NE). The R:FR ratios were calculated as the ratio of photon irradiance between 655 and 665 nm (R) over photon irradiance between 725 and 735 nm (FR) (Smith, 1994).

To study the effect of R:FR light on plant growth, the following traits were measured on five replications. Plant height was measured during the treatment at 3-day intervals. At the end of the treatment period, height, internode length, stem diameter at every internode, leaf area, leaf number, and petiole length were measured from LPI 0 (Leaf Plastochron Index, first leaf 3.0 cm) to the base of each tree (Larson and Isebrands, 1971). Leaf area was measured using a LI 3000 area meter (Li-Cor, Lincoln, NE). Stem tapers were calculated as follows: stem taper = (D2-D1) / L, where D1 = diameter at the LPI 2 (mm), D2 = diameter at the LPI nearest to 25 cm basipetal from D1 (mm), and L = actual stem distance between D1 and D2 (cm). The potted root mass was soaked in water in a cold room at 4°C overnight and then washed clean of potting debris. Dry weights were determined for leaf, stem, petiole and root after drying in an oven at 70°C for 72 h.

One-way analysis of variance (ANOVA) was used to compare treatment means with a threshold of $P = 0.05$ used to classify statistical significance. The SAS statistical package program version 6.12 was used to compute the analysis of variance (SAS institute, 1996).

RESULTS AND DISCUSSION

Table 1. Effect of different red:far-red light on tree morphological characteristics. All numbers are average of five replications after 27 days of filter chamber treatment. The *P* values from the ANOVA are shown for each trait in the bottom row. Top dry weight is the combined dry weight of leaf, stem and petiole. Total dry weight is the combined dry weight of top and root. NS, not significant.

Filter system	Growth increment (cm)	Stem taper	Petiole length (cm)	Leaf No. increment	Leaf area (cm^2)	Leaf dry weight (g)	Stem dry weight (g)	Petiole dry weight (g)	Top dry weight (g)	Root dry weight (g)	Top/root dry weight (g)	Total dry weight (g)
Clear	25.7	0.066	2.94	6.2	602	1.60	0.78	0.11	2.49	0.69	3.85	3.18
FR-blocking	18.8	0.079	2.57	6.0	613	1.64	0.61	0.10	2.35	0.75	3.09	3.10
Increment for the clear filter trees (%)	27% (+)	19% (-)	13% (+)	NS	NS	NS	22% (+)	NS	NS	NS	NS	NS
P value	0.011	0.004	0.014	0.749	0.885	0.749	0.005	0.675	0.430	0.307	0.112	0.884

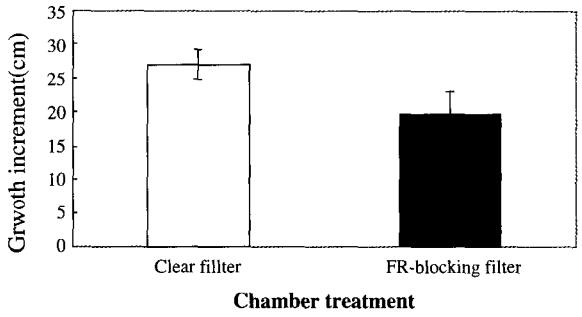

Fig. 2. Average growth increment after 27-day treatment of five replications exposed to different red:far-red light under two different filter chambers. Trees inside clear filter chambers (R:FR = 0.8) were 27% taller than trees inside the FR-blocking filter chambers (R:FR = 3.2, P = 0.01). The vertical bars represent standard error.

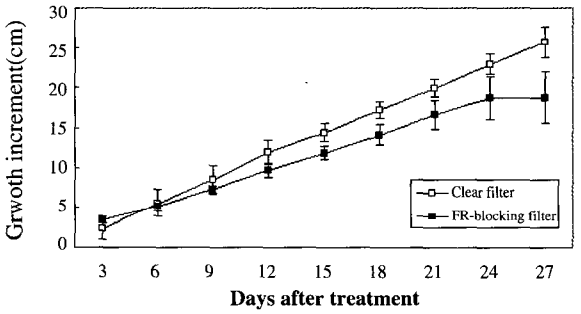

Fig. 3. Increase in cumulative stem growth in response to low red:far-red light (clear filter, R:FR = 0.8) during 27 days of treatment. Growth increments are averages of five replications for each treatment exposed to two different red:far- red light. The vertical bars represent standard error.

The R:FR ratio averaged 1.0 inside the clear filter chambers and 3.7 inside FR-blocking filter chambers when the filter chambers were surrounded by four border trees. An additional four border trees were added at the 12th day of treatment and the ratios were decreased to 0.8 and 3.3, respectively. The temperatures inside the two types of filter chambers were not significantly different (Sin, 2000). PAR levels were similar inside both filter chambers during the period of treatment. The major response to low R:FR was the enhanced stem growth. Trees inside clear filter chambers were taller than trees inside the FR-blocking filter chambers (Table 1 and Fig. 2; *P* = 0.01). The difference in growth increment between the two filter systems became significant after 15 days of treatment and reached a maximum at the end of the treatment (Fig. 3). Average stem growth inside the clear filter chamber was 6.9 cm (27%) taller than trees inside the FR-blocking filter chambers through 27 days of treatment. Average internode lengths were greater for trees in the clear chambers at all positions except the lowest one that would have formed at the beginning of the treatment. LPI 0-1 and LPI 5-6 of the clear filter trees showed the most significant length advantage over

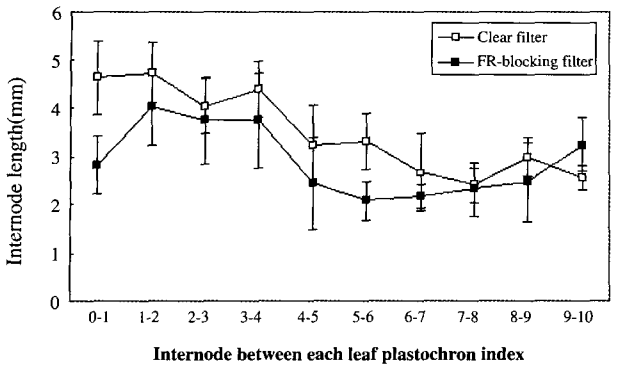

Fig. 4. Average internode length after 27-day filter treatment of five replications exposed to two different red:far-red light under two different filter chambers. Leaf plastochron index (LPI) was used to compare the leaves between the two treatment in the same stage of development and same age of leaves (LPI 0 3.0 cm). The vertical bars represent standard error.

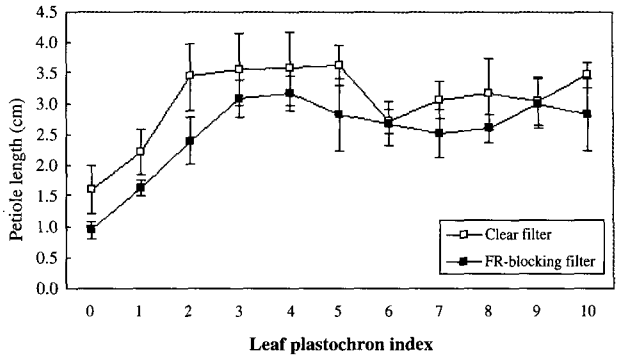

Fig. 5. Average petiole length at each leaf plastochron index (LPI 0 3.0 cm) after 27-day treatment of five replications exposed to two different red:far-red light under two different filter chambers. The vertical bars represent standard error.

trees inside the FR filter chambers (Fig. 4).

Stem taper showed a significant difference between the two filter treatments (P = 0.004). Average stem taper for the FR-blocking filter treatment was 16% greater than the clear filter treatment. Stem dry weight showed a significant difference between the two filter treatments in the reverse direction (P = 0.005). Average stem dry weight of the clear filter trees was 22% heavier than the stem dry weight of the FR-blocking filter trees.

Average petiole length also showed a significant difference between the two filter treatments (P = 0.01). Petioles of clear filter trees averaged 13% longer than petioles of FR-blocking filter trees. However, the difference in total petiole dry weight did not show a significant difference between the two filter treatments. Average petiole length of the clear filter trees between LPI 0 and LPI 2 was significantly longer than the FR-blocking filter trees and this trend was present in older leaves as well (Fig. 5). The pattern of petiole length development at each LPI was similar between the two filter treatments.

There were no significant differences in leaf number increment, leaf area, leaf dry weight, and root dry weight (Table 1). Total biomass was not significantly different between the two filter chambers. In addition, the ratio of top dry weight (leaf, stem and petiole) to root dry weight was not significantly different between the two filter chambers.

Two different filter systems were used to analyze the effect of the R:FR ratio on the stem elongation and other growth traits in a poplar clone. Not many studies have been done with tree species and most work has been performed in the field. The field studies used different plant spacings to analyze the effect of changed R:RF. However, different spacings influence many other variables, such as light intensity, root competition, water use efficiency and gas exchange. So, it is not usually clear from field studies what the direct effect of R:FR is on growth traits. The filter system we used gives better conditions to study the effect of R:FR on growth and morphological changes because the filters modify only the R:FR ratios.

The results of this study indicate that R:FR signals change stem elongation, stem taper, stem dry weight, and petiole length in young *Populus alba* clone 'Bolleana' trees. However, other traits, such as leaf

number increment, leaf area, and dry weight (leaf, petiole and root) showed no significant differences. The main effect of low R:FR is to induce the competition response that enhances stem elongation. While the reduction in R:FR inside filter chambers appears to be the cause of stem elongation, we have checked for other possible conditions that might affect the changes, such as differences in temperature and PAR. However, no differences were found in temperature and PAR in the two filter chambers. The two filter chambers act the same in reducing air movement. Air movement does affect the allocation of photosynthate to mechanically support stems, reducing stem height and increasing stem taper (Cleugh *et al.*, 1998).

The combined dry weight of leaf, stem and petiole (top dry weight) in each treatment was not significantly different. This suggests that elongated stem growth was due to enhanced allocation of resources to stem internode elongation at the expense of other growth centers, not the result of increased photosynthesis. This result is consistent with previous studies in herbaceous species, in which reduced R:FR redirected dry mass towards stem and petioles and away from leaves, although the difference in leaf dry weight was not statistically significant in our experiment (Morgan and Smith, 1979; Keiller and Smith, 1989). However, the response to changed R:FR is dependent on genetic background, which suggests that the allocation of biomass in different tissues is controlled through genetic mechanisms.

At day 12, an additional four trees were added around the filter chambers to reduce R:FR. Over the next three days, growth differences in the two filter chambers became significantly different and stayed that way (days 15-27 of the combined treatment schedule in Fig. 3). This is supportive evidence that the competition response occurs quickly in the low R:FR condition. R:FR less than 1.0 is known as the starting point of inducing competition response. From day 15, the growth increment difference between the two treatments kept getting larger until the last day of treatment.

Gibberellin production is increased under low R:FR, which leads to the internode elongation, cell extension and cell division, and leaf development (Weller *et al*, 1994; Beall *et al.*, 1996). Stem elongation and cell expansion are strongly correlated with gibberellin levels, but dry weight deposition is not related to gibberellin concentration (Potter *et al.*, 1999). Auxin is also an important component of the elongation process that is induced by shade (Behringer and Davies, 1992; Steindler *et al.*, 1999). It has been hypothesized that higher lateral transport of auxin to epidermal and cortical cells occurs in the hypocotyl of shaded seedlings at the expense of auxin transport through the developing vascular system. This leads to elongation of these tissues and reduction of the vascular differentiation and root auxin concentration, which causes a reduction in lateral root formation and eventually primary root growth (Morelli and Ruberti, 2000). We did not find significant root dry weight reduction in our low R:FR treatment, but the trend in the data was in that direction. The control of hormonal effects is probably dependent on genetic background and/or developmental stage, showing different competition responses.

The average leaf areas at LPI 0 and LPI 1 for clear filter trees were larger than FR-blocking filter trees. This may be an adaptation of leaves in the fast growing region of the stem to produce leaf area more rapidly at the top region of elongating stems in the competition condition. Enhanced stem elongation and reduced stemtaper in response to reduced R:FR is consistent with the previous studies (Casal *et al.*, 1990; Ritchie, 1997). Stem taper is an important indicator of mechanical support of trees and also indicates the relative allocation to height and diameter growth. This kind of plant response to reduced R:FR is probably a

physiological process for better light harvest, which increases the possibility of survival during competition.

Through this study, we found that there was large variability in the response of trees during the treatment for the same filter chamber. Even though the starting plants were similar in terms of height and leaf number, the subsequent growth rate fluctuated tree by tree. This indicates that the physiological condition of each tree was not the same although they looked the same. To eliminate this problem, trees need to be grown for a longer period of time under the same growth conditions and then monitored for their growth rate to be sure they have similar potential once treatment starts. Finally, we should choose trees that show similar growth rate and have the same height and leaf number.

This study provides clear evidence that competition conditions (low R:FR) alter tree biomass allocation to stem elongation. However, this study was performed using the juvenile trees, which might respond differently as they age. This phenomenon is common in other physiological processes. Therefore, further experiments with plants of various ages are needed.

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