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Elevated CO_2 changes the moderate shade tolerance of yellow birch seedlings

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Abstract

To demonstrate the existence of light thresholds in plant growth and to examine the effects of elevated CO_2 on the shade tolerance of a tree species, an experiment consisting of a completely randomized design for a total of 96 yellow birch (*Betula alleghaniensis* Britton) seedlings was conducted with 3 light levels (2.9%, 7.7%, 26.1% of full sunlight) × 2 CO_2 levels (350 and 700±10 ppm) with 4 replications in a phytotron. The study proved that thresholds exist and they vary in different plant organs. In ambient CO_2, the thresholds were 13.3%, 18.7%, 15.0%, 15.2%, and 15.6% of full sunlight for stem, leaf, root, total plant biomass, and the averaged value, respectively. In 700 ppm CO_2, the corresponding thresholds were 16.7%, 21.3%, 18.1%, 21.7% and 19.5% for stem, leaf, root, total plant biomass, and the averaged value, respectively. The lowest threshold in the stem is an indicator of the minimal light intensity for regular growth for seedlings of this species. Below this threshold, light-stressful growth occurs. The result of a paired *t*-test indicated that the thresholds in elevated CO_2 were significantly higher than in ambient CO_2. This suggests that yellow birch will lose its moderate shade tolerance, evolutionally becoming a shade-intolerant species, and that it may become more difficult to naturally regenerate in the future.

Key words: elevated CO_2; light threshold; phytotron; plant biomass; yellow birch

Introduction

From the 1860s to the year 2000, atmospheric CO_2 concentration increased from 280 to 350 ppm (NRC, 2000). In the same period, the average surface temperature of the earth increased by 0.57°C (NRC, 2000). If global warming continues, the average July soil temperature in temperate regions will increase to 19°C by the 2070s (Wegley, 1999) from the present value of 15°C (Stathers and Spittlehouse, 1990). This increased temperature will be within the optimal soil temperature range of 16 to 27°C for many tree species in North America (Cheng, 1999; Cai and Dang, 2002; Peng and Dang, 2003; Dang and Cheng, 2004). For example, the net photosynthesis and total biomass of white spruce (*Picea glauce* (Moench) Voss.), aspen (*Populus tremuloides* Michx.), black spruce (*Picea Mariana* (Mill.) and jack pine (*Pinus banksiana* Lamb.) seedlings are the highest at soil temperatures of 16.0 to 25.4°C (Cheng, 1999; Peng and Dang, 2003; Dang and Cheng, 2004). It is predicted that the area of temperate forest will expand by 193% to 251%. Its northern and southern boundaries in North America will move northward (Environment Canada, 1988, 1997), and the forest may play a more important role in the future than in the present.

The temperate forest structure will change in the future (Environment Canada, 1988, 1997). Global climate change will induce a higher mortality rate for softwoods, will increase growth for hardwoods and shrubs in the temperate regions, and increase density of vegetation (Environment Canada, 1988, 1997). This will result in higher competition among plants for resources such as light while increasing difficulties in the natural generation of all temperate plant species (Rajaniemi, 2002).

Yellow birch (*Betula alleghaniensis* Britton) is a commercially important and moderately shade-tolerant species in the temperate forest of eastern North America (Burns and Honkala, 1990). The species grows difficultly in low light. Natural regeneration of the species depends on canopy opening caused by natural and artificial disturbances such as fire, wind, and cutting.

Light has a positive relationship with plant growth. When light is below a specific intensity, the growth decrease is accelerated since the rate of change is not constant (Hirose *et al*., 1997; Beaudet and Messier, 1998; Claveau *et al*., 2005; Cheng *et al*., 2005). That specific intensity is supposed to be a light threshold. Cheng (1999) explained ecologically that the threshold of an abiotic factor is the point at which the direction of the rate of change in ecophysiological traits (e.g. net photosynthesis, stomatal conductance, transpiration, respiration etc.) and tree growth changes inversely with changing the factor from high to low or from low to high. Below the threshold, the traits and growth are restricted, and more seriously as the factor continues to decrease. In calculus, such a threshold is a point on the graph of a function at which

the direction of concavity changes is called an inflection point (Leithold, 1976; Cheng, 1999). So far, no study has been conducted to determine the light threshold exactly.

Light threshold is different from light compensation point (at which the amount of photosynthate plant assimilates by photosynthesis equals the amount that the plant uses for respiration). The light compensation point is changeable and decreases with soil drying, lower temperature, and elevated CO_2 levels (Zou and Gao, 2002; Zhao *et al*., 2004). Whether elevated CO_2 level changes the light threshold has not been studied.

Study on the threshold of an abiotic factor is important in plant ecology, silviculture and forest management. For example, Bassman (1989) has stated that the threshold of low soil temperature is between 2–10°C for some boreal tree species, between 12–13°C for Monterey pine (*Pinus radiata*) (Kaufmann, 1977) and at 9°C for whiter spruce (Goldstein *et al*., 1985). Increase in soil temperature by silvicultural treatments, such as scarification, mounding, prescribed fire, ripping, etc., can promote the natural generation of the forests (McMinn, 1982; Sutton, 1984; Brand, 1990; Orlander, 1987; Fleming *et al*., 1998).

This phytotron study, therefore, was undertaken to examine the effects of elevated CO_2 on the light threshold in yellow birch seedlings. The data were used to test the hypotheses that: (1) there is a light threshold in tree growth; and (2) elevated CO_2 increases the light tolerance of yellow birch seedlings by decreasing the light threshold, since there are more carbohydrates available from the accelerated photosynthesis for plant survival and growth.

1 Materials and methods

1.1 Experimental design

The experiment was established as a completely randomized design with 2 CO_2 concentrations and 3 light levels in the McGill University Phytotron in Canada. Two chambers (multi-function TC30 chambers, Controlled Environments Limited, Winnipeg, Canada) were maintained at 350±10 ppm CO_2 and two others at 700±10 ppm CO_2 concentrations (Romer, 2001). However, the four chambers could not be used randomly for the two CO_2 levels. In the chambers, fluorescent lamps were used for plant growth. Their spectral photon distribution ranged within photosynthetic radiation activation (PRA) (Tsegay *et al*., 2005) and the red light to far-red light ratio was about 1:2, similar to natural daylight (Cober and Voldeng, 2001). In each of the growth chambers, 3 light levels (46.62±0.93; 122.92±2.46; 417.66±9.49 μmol/(m^2·s) were established. The low and medium light levels were created by 78 cm wide × 130 cm long frames covered by two or four layers of black colored shade and nylon cloths. For the high light treatment, plants were placed on a platform (78 cm wide × 130 cm long × 25 cm high) without shading in each chamber. Based on the average full sunlight of 1600 μmol/(m^2·s) measured in a dominant yellow birch forest at Riviére à Pierre in the Réserve Faunique de Portneuf 47°04′N and 72°15′W, Québec, Canada, the relative light of the three levels were calculated as 2.9%, 7.7% and 26.1% to mimic closed, small, and large canopy gaps in natural forests (⩽5%, >5%–<10% and >20% of full sunlight) (Tang, 1997). Those lights represented either diffusion irradiation in closed and small gaps or mean irradiation of direct and diffuse light in a large gap. Under each light level, 4 seedlings were placed both randomly and uniformly. The 4 growth chambers were used twice for 4 replications of each treatment.

Due to the different heights of the seedlings, the relative light availability for all the seedlings changed during the experiment. The light levels were finally divided into 0–3% (heavily closed gaps), >3%–5% (lightly closed gaps), >5%–10% (small gaps), >10%–20% (medium gaps), >20% (large gaps) (Tang, 1997), based on the light measurement for each seedling before harvesting.

1.2 Soil collection and treatment

One cubic meter of natural soil was collected from the A1H horizon in a yellow birch and sugar maple forest in the Duchesnay Forest Experimental Station in Quebec, Canada. The soil was an ortho-humo-ferric podzol with the average pH of 5.4 and average NO_3-N content of 2.917 mg/g, NH_4-N of 35.513 mg/g, P of 0.072 mg/g, Ca of 0.381 mg/g, K of 1.970 mg/g and Mg of 0.151 mg/g. After removing stones and coarse root fragments, and homogeneous mixture, the soil was stored in a cold room at 4°C before use.

1.3 Plant material and germination

Yellow birch seeds were obtained from the Quebec Ministry of Natural Resources. The germination rate and dry-weight percentage of the seeds were 72.5% and 75.8% with a high relative growth rate (Villar *et al*., 1998). Yellow birch was germinated twice, in January and April, respectively. Before the germination, the seeds were placed in a beaker and covered with water for 20 d at room temperature. The water in the beaker changed every week. After the soaking period, yellow birch seeds were sown in propagation plug trays (28 cm wide × 55 cm long × 6 cm high, Plant Products Co. Ltd, Brampton, Canada). Each tray contained 72 plugs (6 rows × 12 columns) filled with the natural soil. The trays of the seeds were placed in the McGill University greenhouse with a 16-h photoperiod and 25±3°C/15±2°C daytime/nighttime temperatures for germination. In the greenhouse, these seedlings were watered once per week and grew in the greenhouse for 64 d. During that time they were in the phase of rapid growth and strongly responded to abiotic and biotic factors (Landis *et al*., 1993). Before being placed in the growth chambers, the seedlings were transplanted to 12 cm diameter × 12 cm high pots with a 3-cm diameter hole in the bottom, and kept in the greenhouse for a further 3 d to minimize the disturbance and mortality due to environmental change after the transplantation.

1.4 Growth chamber environment

In all of the growth chambers, the air temperature was maintained at 25±0.05°C/15±0.04°C daytime/nighttime,

the relative humidity at (60±0.86)%/(65±0.58)% daytime/nighttime, and the photoperiod at 16 h (6:00 a.m. to 10:00 p.m.). During the light period, the light gradually increased to the maximum and decreased to zero to mimic sunrise and sunset and minimize the potential disturbance of plant processes by changing the light suddenly. All the plant pots under the high light were covered by aluminum foil with a 3-cm diameter hole at the center to reduce the possible increase in soil temperature by heat energy from the lights in the chambers. The foil was approximately 2 cm above the soil surface in the pots so as not to affect ventilation, soil humidity, or respired CO_2. The soil temperatures under the high and low lights were monitored by thermometers, and the difference during the experiment was between 0.5 and 1°C. All the pots under each of the light levels in each growth chamber were placed in a tray that was 120 cm long × 60 cm wide × 10 cm high. The trays were filled with 4 cm height of water, which was automatically taken up by the capillarity of the soil in the pots. Soil moisture under the different light treatments in each chamber was monitored by soil moisture meters with wet, medium and dry marks. When the meter arrows pointed to the medium mark, water was filled up to the 4 cm height again in all the trays.

At the beginning of the treatment, the initial height and base diameter of all the seedlings were measured. After 55 d, the height and diameter of the seedlings had responded to the elevated CO_2 based on the measurement of 20 seedlings selected randomly in each chamber. All the seedlings grew in the chambers for 62 d.

1.5 Light measurement

Light intensity at the top of the crown in each seedling was measured by a LI-1000 datalogger (LI-COR, Lincoln, Nebraska, USA). The relative light for each seedling was calculated as the light received by the seedling divided by the average full sunlight (1600 μmol/(m^2·s)).

1.6 Harvesting of the seedlings

After the light measurement, 96 yellow birch seedlings were harvested, 48 from 350 ppm CO_2 chambers and 48 from 700 ppm CO_2 chambers. Sixteen seedlings were taken from each of the low, medium, and high light treatments at each of the CO_2 levels. The leaves, stem (including branches), and root system of each seedling were separated. The roots were washed using tap water.

1.7 Growth traits investigated

Height and base diameter, stem biomass (including branch biomass), leaf biomass and root biomass were measured during or after harvesting. The organ biomass was weighed using a digital balance after drying at 70°C for 48 h. Total plant biomass was calculated.

1.8 Data analyses

Analysis of covariance (ANCOVA) was used to test effects of elevated CO_2 on stem, leaf, root, and total plant biomass (Fu, 1979; Huitema, 1980). Tree height and light (as a continuous variable in the ANCOVA), which significantly affected all the organ and plant growth, were used as covariates to remove their effects on the analyses. A cubic regression model was used to simulate the relationships of all individual organ and whole plant biomass with light. This model is better for fitting observed data (Thornley, 1976); recently it has been used in many studies of plant ecology (Cheng, 1999; Cai and Dang, 2002; Sullivan *et al*., 2002; Peng and Dang, 2003; Uddin *et al*., 2003; Dang and Cheng, 2004). The light threshold was calculated as follows: (1) the first derivative function derived from the cubic model described the rate of change; (2) the second derivative function of the cubic model equaled zero for the threshold point as described by Leithold (1976) and Cheng (1999).

$$\text{Cubic model}: \ T = B_0 + B_1L + B_2L^2 + B_3L^3 \quad (1)$$

$$\text{Rate of change}: \ \mathrm{d}(T)/\mathrm{d}(L) = C_0 + C_1L + C_2L^2 \quad (2)$$

$$\text{Light threshold}: \ \mathrm{d}(\mathrm{d}(T)/\mathrm{d}(L)) = 0 \quad (3)$$

Where, B_0, B_1, B_2, B_3, C_0, C_1 and C_2 are the coefficients of the equations; T is the biomass of leaves or stem or roots or total plant; L is the relative light intensity.

A paired *t*-test (Fu, 1979) was used to test whether the light thresholds in 700 and 350 ppm CO_2 were significantly different, if they existed.

All the variables were graphically examined for normality using histograms and for homogeneity of variance using scatter plots. If necessary, variables were transformed logarithmically. All the data were tested and found to satisfy the assumptions for ANCOVA and regression analyses. SPSS (version 10) statistical software (SPSS Inc., USA) was used to perform the analyses.

2 Results

2.1 Effects of elevated CO_2 on plant biomass

Elevated CO_2 significantly affected the seedling growth. It increased leaf, stem, root and total plant biomass in the seedlings as shown in Table 1.

2.2 Rates of change in plant growth with light gradient

The biomass was a function of light and strongly followed the cubic model (Table 2, Fig.1). Rates of change

Table 1 Analysis of covariance for the effects of elevated CO_2 on stem, leaf, root, total plant biomass (g) in yellow birch seedlings

Source	Stem biomass	Leaf biomass	Root biomass	Total plant biomass
CO_2 (700 ppm)	1.674±0.056*	4.139±0.148*	3.902±0.171*	10.295±0.323*
(350 ppm)	1.362 ±0.054	3.549 ±0.149	3.329±0.172	8.767 ±0.322
Height *(p)*	0.000*	0.001*	0.000*	0.000*
Light *(p)*	0.000*	0.000*	0.000*	0.000*

Tree height and light gradient are the covariates. *p*: possibility; the number of samples is 96; *significant difference at 95%.

Table 2 Cubic models for the relationships of stem, leaf, root and total plant biomass with light gradient for yellow birch seedlings growing in CO_2

CO_2 concentration (ppm)	Cubic model	R^2
700	$S = 0.258 + 0.307L - 0.015L^2 + 0.0003L^3$	0.99*
350	$S = 0.413 + 0.199L - 0.012L^2 + 0.0003L^3$	0.99*
700	$L_f = 0.519 + 0.745L - 0.032L^2 + 0.0005L^3$	0.99*
350	$L_f = 0.741 + 0.564L - 0.028L^2 + 0.0005L^3$	0.98*
700	$R = 0.762 + 0.809L - 0.038L^2 + 0.0007L^3$	0.99*
350	$R = 1.388 + 0.413L - 0.018L^2 + 0.0004L^3$	0.97*
700	$T = 2.575 + 1.537L - 0.052L^2 + 0.0008L^3$	0.99*
350	$T = 2.189 + 1.371L - 0.073L^2 + 0.0016L^3$	0.99*

R^2 is the coefficient of determination; *significant at 95%; S: stem; L: light; L_f: leaf; R: root; T: total plant biomass.

in stem, leaf, root and total plant biomass decreased from low to medium light. After reaching their lowest values, the rates increased as the light continued to increase (Fig. 2). Table 3 shows the first derivative functions for the rates of change.

2.3 Effects of elevated CO_2 on light thresholds

Light thresholds in all the organ and total plant biomass differed; elevated CO_2 increased the light thresholds. In the seedlings, the light thresholds were 16.7%, 21.3%, 18.1%, 21.7% and 19.5% of full sunlight for stem, leaf, root, total plant biomass, and the mean value of the thresholds in 700 ppm CO_2; 13.3%, 18.7%, 15.0%, 15.2% and 15.6% for

Table 3 The first derivative equations of the cubic models in Table 2 for the rates of change in stem, leaf, root, and total plant biomass with light gradient for yellow birch seedlings growing in CO_2

CO_2 concentration (ppm)	Rate of change
700	$d(S)/d(L) = 0.307 - 0.030L + 0.0009L^2$
350	$d(S)/d(L) = 0.199 - 0.024L + 0.0009L^2$
700	$d(L_f)/d(L) = 0.745 - 0.064L + 0.0015L^2$
350	$d(L_f)/d(L) = 0.564 - 0.056L + 0.0015L^2$
700	$d(R)/d(L) = 0.688 - 0.044L + 0.0015L^2$
350	$d(R)/d(L) = 0.413 - 0.036L + 0.0012L^2$
700	$d(T)/d(L) = 1.537 - 0.104L + 0.0024L^2$
350	$d(T)/d(L) = 1.371 - 0.146L + 0.0048L^2$

S: stem; L: light; L_f: leaf; R: root; T: total plant biomass.

them in 350 ppm CO_2 (Table 4). The result of the paired-*t* test showed that the thresholds in the two CO_2 levels were significantly different (Table 4).

3 Discussion

The study demonstrates that light thresholds exist in the growth of yellow birch seedlings; elevated CO_2 changes the light thresholds. This finding partially supports the hypotheses of the study.

3.1 Light thresholds and growth strategy

The variety of light thresholds reveals a growth strategy of a tree species. The study discovered that the light threshold in leaf biomass is the highest, followed by the

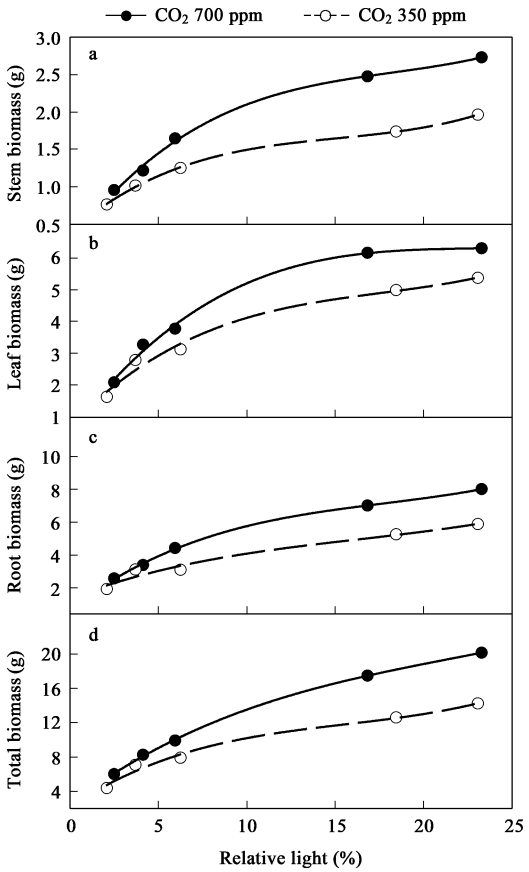

Fig. 1 Cubic models for the relationships of stem, leaf, root and total plant biomass with light gradient in yellow birch seedlings growing in both CO_2 levels. The equations are shown in Table 2.

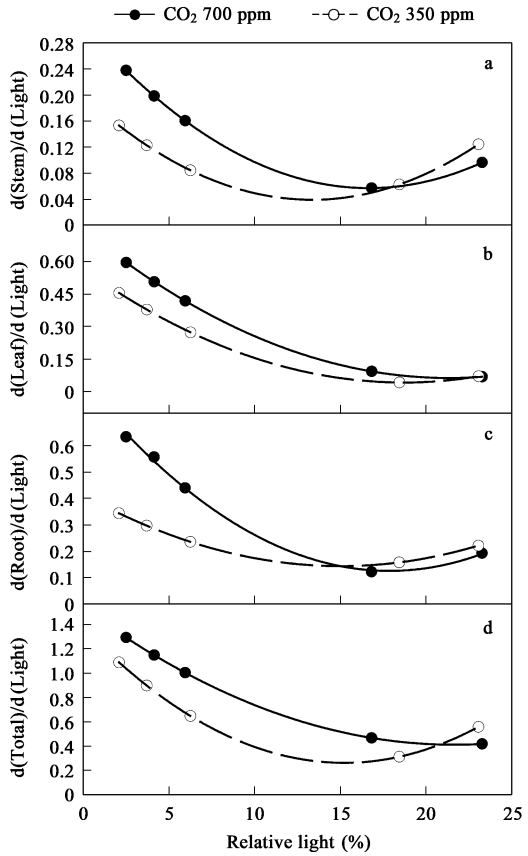

Fig. 2 Rates of change in individuals change with light gradient. The first derivative functions (Table 3) for the rates derive from the cubic models in Fig.1.

Table 4 The second derivative equations of the cubic models in Table 2 equal zero for light thresholds in stem, leaf, root, and total plant biomass of yellow birch seedlings

Infection point	Thresholds (%)		Difference (%)
	700 ppm CO_2	350 ppm CO_2	
d(d(S)/d(L)) = 0	16.7	13.3	3.4
d(d(L_f))/d(L)) = 0	21.3	18.7	2.6
d(d(R)/d(L)) = 0	18.1	15.0	3.1
d(d(T)/d(L)) = 0	21.7	15.2	6.5
Mean	19.5	15.6	3.9*
Paired *t*-test			(p = 0.021)

A paired *t*-test for examining whether the light thresholds in 700 and 350 ppm CO_2 are statistically different. p is possibility; *significantly different at 95%. S: stem; L: light; L_f: leaf; R: root; T: total plant biomass.

roots and stem in the seedlings (Table 4). This indicates that the leaf organ, as photosynthesitic tissue, is the most sensitive to change in light from high to low intensity. The gradient of the light thresholds is associated with the growth strategy of yellow birch seedlings. In low light caused by dense vegetation, the biomass of the plant is primarily allocated to stem for height growth to capture more light. As more light and carbohydrates are available, root biomass increases for more soil resource availability to enhance photosynthesis (Sheriff *et al*., 1986; Mitchell and Hinckley, 1993). Finally, leaf biomass increases in higher light for whole plant growth. Therefore, the light threshold in the stem is an indicator to represent the minimal light intensity for regular growth of the seedlings. Below the threshold, the plant grows stressfully. This study supports the result reported by Messier *et al*. (1999) and Claveau *et al*. (2002), which is that height, as an aspect of tree size, affects the ability of the tree to survive in low light, as the size determines changes in many aboveground traits of the tree. For example, tree canopy develops with increasing height. However, the study cannot address the question of whether light availability is more important than soil resource availability in the survival of yellow birch seedlings, since all the seedlings grew in an individual pot without belowground competition from other plants. Generally, belowground competition decreases height growth and aboveground biomass of the tree species (Natacha *et al*., 2001; Wang and Su, 2002), which might change the light thresholds in the plant organs. This is a potential issue for further research.

3.2 Effects of elevated CO_2 on light thresholds

Elevated CO_2 changes light thresholds in all the organ and total plant biomass. The light thresholds in elevated CO_2 were statistically higher than in the ambient CO_2 (Table 4). This is contrary to the second hypothesis of the study and implies that yellow birch may lose its moderate shade tolerance and evolutionarily become a shade-intolerant species as it adapts to the stronger aboveground competition caused by dense vegetation in the future. As a result, the natural regeneration of it would be more difficult in the future.

3.3 Light thresholds in natural environment

The light thresholds in artificial and natural environments should differ. In this study, the seedlings grew in an artificial environment with optimum air and soil temperatures, and photoperiod; stable light intensity during the daytime; available water; and no belowground competition. This environment is very different from a natural environment. Any of the above factors may result in a better growth response in the seedlings compared to their growth in a natural environment. Thus, the light thresholds in the phytotron are likely to be different from those to be found in nature.

In the study, the intensity used for full sunlight was 1600 μmol/(m^2·s). In many temperate forests, full sunlight is about 2000 μmol/(m^2·s). Therefore, the light thresholds should be lower in most temperate forest areas than that in the phytotron study.

4 Conclusions

This study first proposes and demonstrates the existence of light thresholds in plant growth. The threshold, as an indictor, exactly reveals the shade tolerance of a tree species. The higher the threshold is, the weaker the shade tolerance is. Elevated CO_2 increases the light thresholds in yellow birch seedlings, thus decreasing their shade tolerance.

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