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# Light competition within dense plant stands and their subsequent growth under illumination with different red:far-red ratios

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ABSTRACT

We evaluated the dynamics of light competition within dense cucumber (*Cucumis sativus* L.) plant stands and its relationship to subsequent growth under illumination with different red to far-red ratios (R:FRs). The plant stands containing seedlings with different initial degrees of mutual shading was grown under metal-halide lamps (MHLs) with spectra similar to that of sunlight (R:FR = 1.2) or fluorescent lamps (FLs) with high R:FR (11) for 6 days at a photosynthetic photon flux of 300 $\mu$mol m$^{-2}$ s$^{-1}$. The daily-integrated photosynthetic photon intercepted by individuals (daily PP; mol d$^{-1}$ per plant) were calculated once a day from the PPF, the photoperiod, and the directly irradiated leaf area. Under MHLs, differences in the daily PP values of individual seedlings with different initial shading degrees became non-significant within 2 days, whereas under FLs, differences were preserved throughout the experimental period, indicating that the unequal competition exists between neighbors under FLs. The daily PP on day 0 and dry-weight increase of the seedlings during the experimental period were positively correlated under FLs but not under MHLs, indicating that the initial dominance of light interception by individual seedlings is likely to affect their subsequent growth under FLs. The seedlings that had lost out to neighboring seedlings could not climb over the neighbors under FLs, probably because of insufficient stimulation of shade-avoidance responses caused by the higher R:FR illumination.

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## 1. Introduction

The shade-avoidance responses of plants are stimulated by a reduction in the red-to-far-red ratio (R:FR) that results from the absorption of red light by neighboring vegetation; for example, shoot elongation and leaf expansion increase and leaf thickness and chlorophyll synthesis decrease (Smith and Whitelam, 1997). Plants use these responses to tolerate or avoid shading (Franklin, 2008). The shade-avoidance responses both result from and subsequently affect the competitive interactions between neighboring plants, and therefore affect structure of plant stands. It is well known that equal light competition between neighboring plants can promote the development of uniform plant size (Nagashima and Hikosaka, 2011; Nagashima and Terashima, 1995; Vermeulen et al., 2008; Weiner and Thomas, 1992). Ballaré et al. (1994) demonstrated that shade-avoidance responses, which are mediated by phytochromes, play a central role in the size stabilization within the plant stands. To do so, they compared the responses of isogenic wild-type plants with those of transgenic plants that had an impaired response to changes in R:FR. In our previous research (Shibuya et al., 2013), we confirmed this previous finding by using artificial illumination to modify the proportion of active phytochromes. We found that the stabilization of plant height was greatly delayed under illumination with a higher-than-sunlight R:FR, because high R:FR mitigates the effects of the reductions in R:FR caused by light interception by neighboring plants and therefore decreases the magnitude of shade-avoidance responses.

The fact that competitive interactions among neighboring plants are affected by light quality would have important implications particularly for transplant production in closed systems (Kozai, 2007; Kozai et al., 2006, 2016) in which seedlings are grown densely under artificial illumination. These systems commonly use typical commercial fluorescent lamps with higher-than-sunlight R:FR. The effects of higher-than-sunlight R:FR on plant morphological and physiological traits have been investigated to control the plant growth and development (Li et al., 2003; Li and Kubota, 2009; Mata and Botto, 2009; Shibuya et al., 2010, 2011, 2014, 2016). These reports indicate that the higher R:FR can enhance biotic and abiotic stress tolerances, which are important criterions for the quality of transplants, at the expense of their growth rates. However, the effects of these manipulations on the competitive interactions have

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not been reported, with the exception of our previous preliminary study described above (Shibuya et al., 2013). This is an important omission, since understanding the responses of morphological and physiological traits to changes in R:FR at levels ranging from individual organs to whole plants and the resulting effects on the structure and productivity of vegetation communities is important for predicting the impacts on plant production (Anten, 2005). The dynamic relationships between the vegetation structure and light interception by plants have been investigated through dynamic models in an effort to clarify the ecophysiology of competitive interactions among neighbors (Hikosaka et al., 1999; Hikosaka, 2003, 2005; Hikosaka and Anten, 2012).

In the present study, we investigated the impacts of the illumination R:FR on the dynamics of light competition within cucumber (*Cucumis sativus* L.) seedlings by quantifying the light competition processes that occur under illumination with normal (similar to that of sunlight) and high R:FR, with the goal of understanding the competitive interactions that occur under higher-than-sunlight. To achieve this goal, we quantitatively described the light competition processes on the basis of light interception by individual plants, and then investigated the effects of the illumination R:FR on relationships between the initial degree of shading of individual plants and their subsequent growth. We hypothesized that the effects of initial shading would be sustained and would be strongly related to subsequent growth under high-R:FR illumination, which would not stimulate shade-avoidance responses by shaded plants, thereby preventing the size stabilization. The experimental approach used in the present study and the results will provide insights into how to optimize the competitive interactions and subsequent growth of individual plants that occurs in the transplant production under artificial illumination.

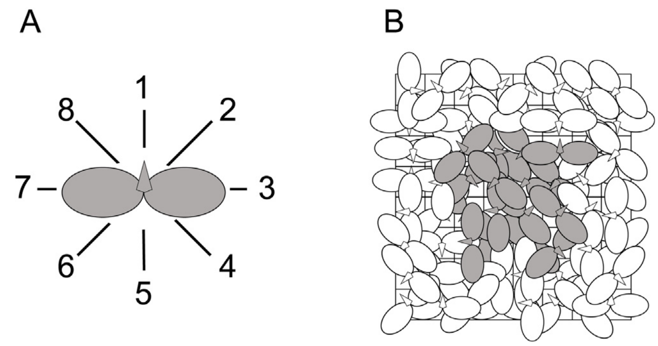


**Fig. 1.** Illustration of how seedlings were oriented at the time of planting. (A) Eight orientations, at 45° intervals, were defined. (B) An example of the initial plant stands. To avoid edge effects, only the 16 seedlings at the center of planting tray (gray filled seedlings in the figure) were used for evaluation of light competition processes and subsequent growth.

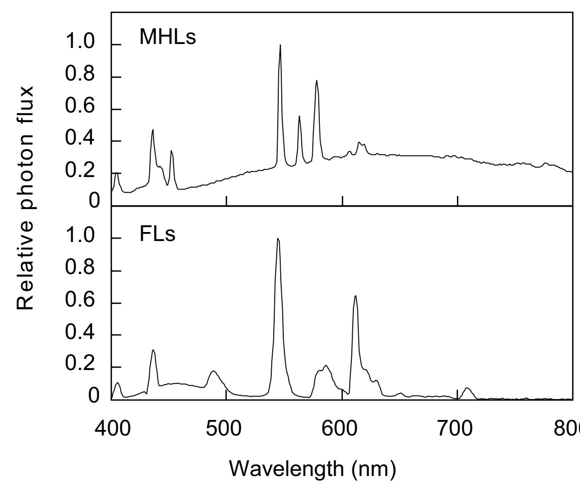


**Fig. 2.** Relative photon flux of spectra of the light produced by metal-halide lamps (MHLs) that provided a spectrum similar to that of sunlight, and fluorescent lamps (FLs) with a high R:FR. The seedlings were shielded from the metal-halide light by a water filter to avoid heat. Photon fluxes were measured at canopy level.

## 2. Materials and methods

### 2.1. Preparation of plant stands

Cucumber (cv. Hokushin) stands were prepared with randomized degrees of shading by randomizing both the planting orientation and the order of layering of seedlings transplanted at the growth stage with cotyledons and a bud of first true leaf (6 days after seeding). The growth conditions for germination and initial seedling growth before the transplantation were the same as for the MHL treatment (described below). Planting trays (200 mm × 200 mm, 40 mm deep) partitioned into 64 square cells that contained vermiculite growing medium were used for growing seedlings. The seedlings were planted one per cell, with different leaf orientations. The eight leaf orientations were defined at 45° intervals (Fig. 1A), and the bud of first true leaf was randomly oriented in one of these directions by choosing the orientation from a table of random numbers from 1 to 8. In addition, the layering order (i.e., transplantation order) of seedlings was determined. Thus, the plant stands containing seedlings with different mutual shading degrees were prepared (Fig. 1B). The height of all seedlings was adjusted to 20 mm in the transplantation. Both sets of random numbers were created in Microsoft Excel 2013, and new tables were created for each replicate ($n = 5$). To avoid edge effects, the light competition processes and subsequent growth of only the 16 seedlings at the center of each planting tray were evaluated. The planting density was 1600 plants $m^2$, and initial leaf area index (LAI) was approximately 1.2.

### 2.2. Growing conditions

The plant stands were grown in growth chambers under MHLs (DR400/TL; Toshiba Lighting & Technology Corp, Yokosuka, Japan) with a spectrum similar to that of sunlight and with an R:FR of 1.2, or under FLs (FPL55EX-N; Panasonic Corp., Kadoma, Japan) with an R:FR of 11 (Fig. 2). Here, R:FR was defined as the ratio of the photon flux at red wavelengths (600 to 700 nm) to that at far-red wavelengths (700 to 800 nm). The proportion of active phytochrome to total phytochrome, which was calculated from the spectra of illumination according to Sager et al. (1988), was 0.74 under the MHLs and 0.83 under the FLs. The percentage of blue (400–500 nm), green (500–600 nm) and red (600–700 nm) to the photosynthetically active radiation (400–700 nm) was 18.5%, 38.9% and 42.6%, respectively, in MHL illumination, 30.3%, 42.4% and 27.3%, respectively, in FL illumination. It was supposed that differences between plant morphological and physiological responses under FLs and MHLs are primarily due to difference in R:FR although the different percentages of blue, green, and red photon flux possibly influences the plant morphological responses. This is because similar relationships could be observed between FL illuminations with high and normal R:FR when modifying only the FR photon flux (Shibuya et al., 2010, 2011). A water filter (20 mm in depth) was placed under the metal-halide lamps to prevent biasing effects that could result from increases in leaf temperature caused by the long-wave radiation emitted by these lamps; the leaf-air temperature difference was within 0.5 °C under each illumination type. The PPF at the canopy height was maintained at 300 μmol $m^{-2}$ $s^{-1}$ by adjusting the distance between the lamps and the canopy surface

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