The aerial environment modulates plant responses to blue light

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Abstract

The optimal amount of BL in the light spectrum varies dependent on plant species, plant process, and the background environment. The aim of this study was to investigate plant responses to BL in different aerial environments. In controlled production systems, such as greenhouses with reduced ventilation and air movement, high relative air humidity (RH>85%) is common. Such an environment inhibits plant transpiration and nutrient uptake and may have a negative impact on stomatal function and plant quality. In a number of experiments, we investigated the response to BL in different air humidity regimes. The results show that plants grown under high RH (90%) use BL more efficiently compared with those grown under moderate RH (60%). At high RH, plant growth and leaf quality of basil (*Ocimum basilica*), cucumber (*Cucumis sativus*) and tomato (*Lycopersicon esculentum*) improved with increased amounts of BL (5→ 30%). We conclude that manipulation of BL can be used as a cultivation strategy to improve plant productivity and quality in an environment with high RH.

INTRODUCTION

Blue light (BL) controls many processes important for plant productivity, such as morphology, stomatal function and patterning, stimulation of chlorophyll synthesis and photosynthetic capacity (Hogewoning et al. 2010; Islam et al. 2012; Terfa et al. 2012; Terfa et al.

2013). In Northern Europe, supplementary lighting is common in greenhouses during periods with low natural radiation, and the dominating lamp type is high pressure sodium (HPS) with a low amount of BL (5-8%). Increased BL (>20%) has been shown to improve plant quality and stomatal function in different plant species (Islam et al. 2012; Terfa et al. 2012). Manipulating the amount of BL could therefore be a useful strategy for controlling transpiration, growth and morphology of plants.

In controlled production systems, such as greenhouses with reduced ventilation and air movement, a high relative air humidity (RH>85%) is common. High RH inhibits plant transpiration and nutrient uptake and can induce leaf yellowing and suppress growth and dry mass (DM) accumulation in some plants species (Gislerød et al. 1987; Gislerød & Mortensen 1990; Lihavainen et al. 2016). Stomata of plants developed under high RH show reduced ability to respond to closing signals such as darkness and drought, and are usually wide open during day and night (Arve et al. 2014; Torre et al. 2003). Several approaches to counteract the negative effect of high RH on stomatal function have been tested, and daily temperature and/or RH variation, application of abscisic acid, high wind speed, longer periods with darkness and BL have been shown to improve stomatal responsiveness to darkness (Fanourakis et al. 2016).

The aim of this study was to evaluate whether additional BL could be used as a cultivation strategy to improve growth and quality of herbaceous species produced under high RH. Thus, we tested the response to additional BL on transpiration. chlorophyll content, morphology and growth in three common greenhouse species: basil (*Ocimum basilica*), cucumber (*Cucumis sativus*) and tomato (*Lycopersicon esculentum*).

MATERIALS AND METHODS

Experimental set-up and plant material

Seeds of basil (*Ocimum basilica* 'Marian') from LOG A/S (Oslo, Norway) were sown in 12-cm pots in fertilized peat (Norway) in a greenhouse compartment with 20°C and 70% RH. After 14 days, pots with germinated seedlings were placed in controlled growth chambers at 20°C, RH of either 60% or 90% and ambient CO_2. Tomato (*Lysopersicon esculentum* 'Ailsa Craig') and cucumber (*Cucumis sativus* ´Quarto F1´) were seeded in 12-cm pots as described above. When the first true leaves were expanding, plants were placed in controlled growth chambers at 23°C with either 60% or 90% RH. In the growth chambers, all plants received 20 h of light at a total of 200 $\mu mol\ m^{-2}\ s^{-1}$ photosynthetically active radiation (PAR) from either HPS or a combination of HPS + BL (Figure 1), and 4 h of darkness per day. Chambers with BL received 50 µmol m^{-2} s^{-1} from light emitting diodes (LEDs) (400-500 nm, peak at 460 nm; Philips GreenPower LED module HF Blue) and 150 µmol m^{-2} s^{-1} from 400W HPS lamps (Gavita Superagro. Norway), as measured with a Li-COR LI 190 SA quantum sensor (LI-COR Inc., USA). The amount of BL in the HPS+BL treatment was 30%, calculated by adding the intensity of all wavelengths between 400 and 500 nm and then calculating the percentage of total intensity between 400 and 700 nm (Figure 1). The plants were watered when needed with 50/50 mixture of YaraLiva® Calcinit™ calcium nitrate solution (14.4% NO_3. 1.1% NH_4. 19.0% Ca. Yara Norge AS. Oslo. Norway) and Kristalon™ Indigo (7.5% NO_3. 1% NH_4. 4.9% P. 24.7% K. 4.2% Mg. 5.7% S. 0.027% B. 0.004% Cu. 0.06% Mn. 0.2% Fe. 0.004% Mo. 0.027% Zn. Yara Norge AS. Oslo. Norway). Electrical conductivity was 1.5 mS cm^{-1}.

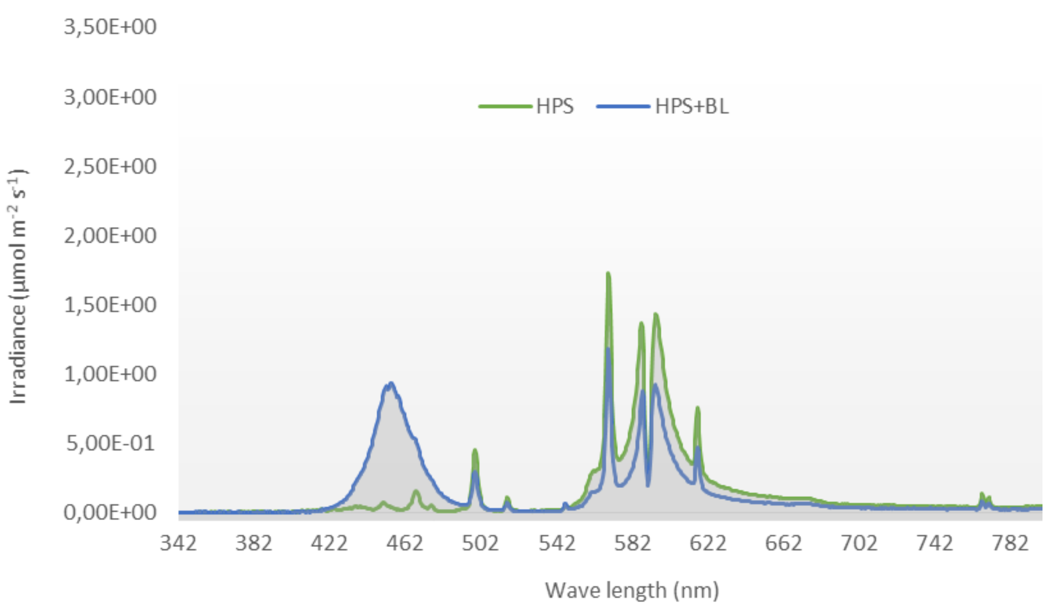

Figure 1. Light spectra of the lamps used in the experiments. High pressure sodium (HPS) lamps (Osram NAV T-400W), green line; HPS + Blue Light (BL) emitting diodes (Philips GreenPower LED module HF Blue), blue line.

Growth analysis, leaf color, chlorophyll and nutrient content

The growth and leaf color of basil were evaluated after 4 weeks of growth according to a scale from 3 to 0, where 3 = no visible yellowing, 2 = yellow spots in-between the veins and 1 = severe leaf yellowing. Growth of tomato and cucumber was evaluated after 3 weeks. The number of leaves (>1cm) was counted, and the total length was measured from the base of the shoot to the shoot apical meristem. Dry weight was determined after drying for 5 d at 70°C. Leaf area was measured with a leaf area meter (Li-3100, Li-Cor Inc.) The relative chlorophyll content was measured with a handheld chlorophyll content meter (model CL-0.1, Hansatech Instruments Ltd, UK).

Transpiration measurements

Leaf transpiration was measured at the end of the experimental period on fully expanded leaves using a porometer (AP4, Delta-T Devices Ltd., Cambridge, UK). The measurements were conducted in the middle of the dark period and 1-2 h after the light was turned on. Epidermal impressions were made of fresh, intact, fully expanded leaves from tomato and cucumber by Suzuki's universal micro-printing (SUMP) method using SUMP liquid and SUMP plate B (SUMP Laboratory, Tokyo, Japan) as described previously (Tanaka et al. 2005). All samples were taken interveinally close to the midrib on the abaxial side (tomato) or both abaxial and adaxial sides (cucumber). The copied SUMP images were observed under a light microscope, and the number of stomata was counted with UTHSCSA ImageTool for Windows version 3.00 (University of Texas Health Science Centre, San Antonio, TX, USA).

Statistics

Significant differences between means were tested for normally distributed data using general linear models (GLM) and Tukey's test. Differences with $p<0.05$ were considered significantly different. All statistical tests were performed in Minitab 16.1.1 (Windows version, State College, PA, USA).

RESULTS

At moderate RH, no signs of chlorosis or black spots on the basil leaves were observed. However, the plants grown in high RH with HPS developed severe leaf yellowing (Table 1). The symptoms first appeared as yellow spots in-between the veins, and on some plants the entire leaf turned yellow and small black spots appeared on the leaf surface. Additional BL improved the leaf quality of basil in high RH; the yellowing was less severe and the chlorophyll content increased significantly (Table 1). At moderate RH, rather small effects were observed when the plants received more BL compared to HPS alone, although the plants were slightly shorter and had more chlorophyll (Table 1). At moderate RH, BL reduced internode lengths but plants developed the same number of leaves as with HPS alone. However, under high RH the stem length increased with HPS+BL but the plants had a higher number of leaves compared to those grown with HPS alne (Table 1).

Table1. Effects of additional blue light (BL) on growth and leaf quality of basil grown at high (90%) and moderate (60%) RH. Visible leaf quality was evaluated according to a scale from 3 to 0 where 3 = no visible yellowing, 2 = yellow spots in-between the veins and 1 = severe leaf yellowing (n=10). HPS, High-pressure sodium lamps.

	Moderate RH (60 %)		High RH (90 %)	
	HPS + BL	HPS	HPS + BL	HPS
Plant height (cm)	25.00±1.21^{ab}	27.55±0.91^{a}	23.10±0.65^{b}	20.12±0.33^{c}
Number of leaves	12.80±0.27^{a}	12.10±0.22^{a}	12.00±0.25^{a}	10.80±0.23^{b}
Relative chlorophyll content	14.12±0.42^{a}	13.00±0.43^{a}	11.03±0.33^{b}	7.74±0.41^{c}
Leaf quality (0-3)	3.0	3.0	2.8	1.6

The suppressed growth and leaf unfolding rate observed in basil at high RH with HPS was not observed in tomato or cucumber but a tendency of leaf yellowing and a lower chlorophyll content were found (Tables 2 and 3). Furthermore, BL inhibited plant height and growth under both RH regimes but the effect was much stronger at moderate RH compared to high RH (Tables 2 and 3). In tomato grown at moderate RH, additional BL reduced plant height and total dry weight by 39 and 35%, respectively. However, with high RH the reduction in height and dry weight was only 22 and 13% (Table 2). Similarly, in cucumber grown at moderate RH, additional BL reduced plant height and total dry weight by 40 and 20%, respectively, while at high RH the reduction was only 20 and 2% (Table 3). Number of leaves followed a similar trend in both species (Tables 2 and 3). The number of fruits per cucumber plant and average fruit length were significantly larger with moderate RH and HPS alone and with high RH and HPS + BL than with moderate RH and HPS + BL and with high RH with HPS alone (Table 3).

Table 2. Growth and morphology of tomato grown under high (90%) and moderate (60%) RH with the traditional high-pressure sodium (HPS) lamp (200 $\mu molm^{-2}s^{-1}$) and HPS + blue LED (BL) (150 + 50 $\mu molm^{-2}s^{-1}$).

	Moderate RH (60 %)		High RH (90 %)	
	HPS + BL	HPS	HPS + BL	HPS
Plant height (cm)	16.50±0.58^{c}	27.0±1.03^{a}	20.94±0.65^{b}	27.38±0.79^{a}
Number of leaves	7.50±0.27^{b}	8.63±0.32^{a}	8.25±0.25^{ab}	9.13±0.23^{a}
Total dry weight (g)	2.82±0.24^{b}	4.3±0.47^{a}	3.84±0.23^{ab}	4.45±0.20^{a}
Relative chlorophyll content	23.12±1.07^{a}	17.90±0.63^{b}	23.89±1.22^{a}	17.44±0.92^{b}
Stomata number (50 μm^2)	14.00 a	14.92 a	13.51 ab	12.81 b

Different letters in the same row indicate significant differences at $p<0.05$ (n=8).

Table 3. Growth and morphology of cucumber grown under high (90%) and moderate (60%) RH with the traditional high-pressure sodium (HPS) lamp (200 $\mu mol m^{-2} s^{-1}$) and HPS + blue LED (BL) (150 + 50 $\mu mol m^{-2} s^{-1}$).

	Moderate RH (60 %)		High RH (90 %)	
	HPS + BL	HPS	HPS + BL	HPS
Plant height (cm)	35.0±1.16^{c}	59.38±1.27^{a}	47.81±1.84^{b}	62.81±1.86^{a}
Number of leaves	10.63±0.18^{c}	11.25±0.16^{b}	11.88±0.35^{a}	11.38±0.26^{b}
Dry weight (g)	6.31±0.12^{c}	7.84±0.26^{a}	6.86±0.21^{bc}	7.02±0.29^{b}
Fruit number per plant	7.40±0.25^{b}	9.00±0.32^{a}	9.00±0.32^{a}	7.20±0.59^{b}
Fruit length (cm)	2.45±0.07^{b}	2.60±0.15^{ab}	3.10±0.19^{a}	1.30±0.04^{c}
Relative chlorophyll content	28.26±1.99^{a}	20.55±0.75^{b}	25.93±0.96^{a}	17.55±0.80^{b}
[1]Stomata number (50 μm^2)	19.73 c	12.75 a	15.45 b	13.72 a

Different letters in the same row indicate significant differences at $p<0.05$ (n=8).

[1]merged stomata count adaxial and abaxial side

The transpiration rate of the three species was affected differently by BL dependent on the RH background. BL increased transpiration significantly at both moderate and high RH ($p<0.05$) in cucumber (results not shown). However, in basil, BL increased transpiration rate at moderate RH but not at high RH (Figure 2). In tomato, BL increased transpiration at high RH but not at moderate RH (results not shown).

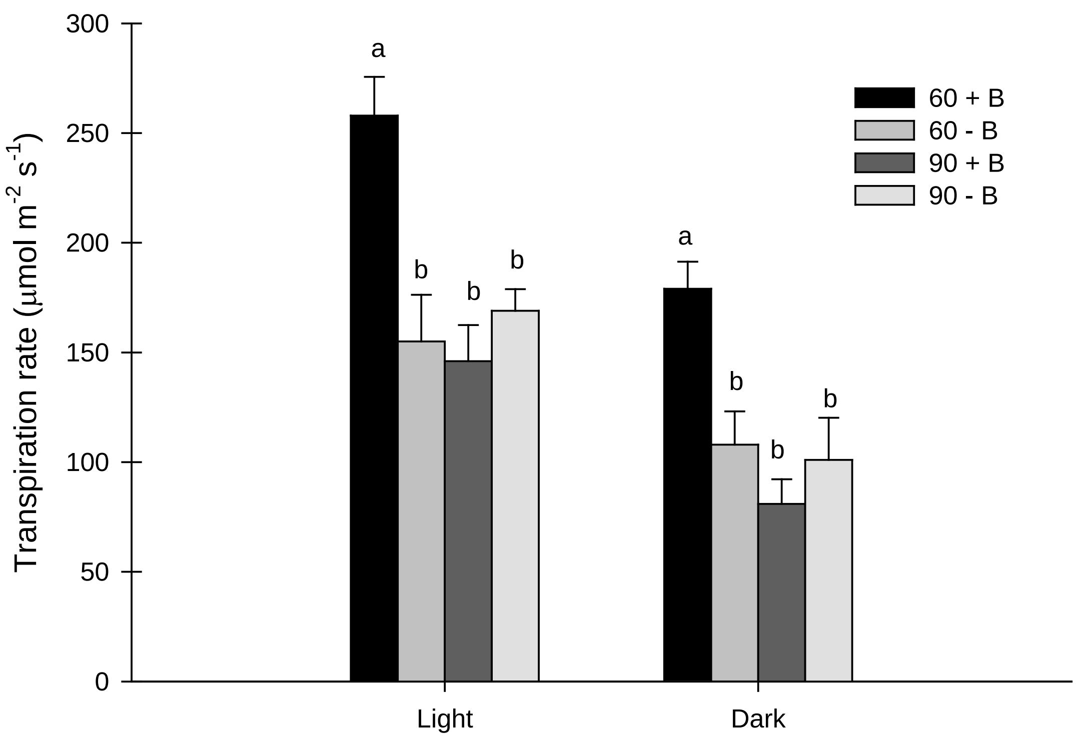

Figure 2. Transpiration rate (µmolm^{-2}s^{-1}) of basil leaves developed under 60% and 90% RH with HPS (200 µmol m^{-2}s^{-1}) or with HPS + blue LED lamps (150 + 50 µmolm^{-2}s^{-1}). Different letters within day and night indicate significantly different values. N=5. Mean ± SE.

The transpiration rate of the three species was affected differently by BL dependent on the RH background. BL increased transpiration significantly at both moderate and high RH ($p<0.05$) in cucumber (results not shown).

The ratio between transpiration rates during day and night was calculated to compare the responsiveness to darkness as a signal for closure (Table 4). In basil, the main difference in day/night transpiration rate ratio was found between moderate and high RH, but no significant difference was found between any of the treatments (Table 4). However, in cucumber and tomato a trend towards an increased day/night transpiration was observed at high RH when additional BL was added during the day, but the data was not statistically different (Table 4). Cucumber and tomato grown under high RH with HPS alone had a day/night transpiration rate ratio close to 1, which indicates almost no stomatal movement in response to darkness (Table 4).

Table 4. Ratio between day and night transpiration rate for basil, tomato and cucumber grown under high (90%) and moderate (60%) RH grown with the traditional high-pressure sodium (HPS) lamp (200 μmolm^{-2}s^{-1}) and HPS + blue LED (BL) (150 + 50 μmolm^{-2}s^{-1}). Transpiration was measured with a porometer (see Materials and Methods for details).

	Moderate RH (60 %)		High RH (90 %)	
	HPS + BL	HPS	HPS + BL	HPS
Basil	1.45±0.12^{a}	1.48±0.19^{a}	2.07±0.47^{a}	2.01±0.50^{a}
Tomato	1.51±0.14^{a}	1.54±0.12^{a}	1.27±0.15^{ab}	1.15±0.05^{b}
Cucumber	1.54±0.05^{ab}	1.82±0.15^{a}	1.24±0.05^{bc}	1.05±0.17^{c}

Different letters in the same row indicate significant differences at $p<0.05$ (n=8-10).

DISCUSSION

Additional blue light improves leaf quality and growth in high RH

Plant production under high RH (> 85%) is common during periods when ventilation is avoided to save energy. This is usually also the time when supplementary lighting is required to improve growth and yield of greenhouse crops at northern latitudes. In this study, we demonstrated that addition of BL increased chlorophyll content under both high and moderate RH in all three species, basil, cucumber and tomato (Tables 1-3), and improved growth and leaf quality under high RH. Thus, additional BL is a useful cultivation strategy for improving leaf quality and productivity under high RH.

The reason for leaf yellowing at high RH is proposed to be related to reduced transpiration and nutrient deficiencies (Gislerød et al. 1987; Gislerød & Mortensen 1990; Mortensen & Gislerød 1989). Reduced chlorophyll content is often connected to deficiencies in Mg, Fe or N (Engels et al. 2012). It is likely that the leaf yellowing observed in plants produced under high RH and HPS is due to insufficient N uptake and that the BL improves N uptake by increasing transpiration. However, different plant species may respond differently to BL and/or the BL may work via different mechanisms to increase chlorophyll content and improve leaf quality. The increased chlorophyll content found in leaves exposed to additional BL could also be due to a direct effect on chlorophyll biosynthesis. Senger and Bauer (1987) showed that plants grown under supplementary BL fluorescent lamps had higher Chl *a*/*b* ratios and more sun-like type chloroplasts than plants exposed to less BL. Furthermore, higher Chl content was reported in cucumber and roses produced with an increased proportion of BL and points towards a photosynthetic apparatus better adapted to high light levels (Evans 1987; Hogewoning et al. 2010; Terfa et al. 2013).

The effect of interaction between temperature and light quality on growth and morphology has been the subject in many studies (Bergstrand et al. 2016; Moe et al. 2002). However, less attention has been paid to the aerial environment and its interaction with light quality. In this study, additional BL reduced stem elongation and DM accumulation more strongly under moderate RH than under high RH (Tables 2 and 3). BL is involved in inhibition of growth of internodes and cell expansion or division (Dougher & Bugbee 2004; Folta et al. 2003). Furthermore, dry air (large vapor pressure deficit) is also known to be an abiotic stressor that induces stomatal closure and reduces growth and stem elongation in herbaceous plant species (Zhang et al. 2015). It has been well described in other growth studies that exposure to more than one stressor at the same time can have a synergistic effect on the growth response (Murali & Teramura 1985). However, the reason why BL confers stronger growth inhibition at moderate RH compared to high RH is not clear.

Additional BL increases transpiration but dependent on RH and plant species

Increased transpiration could be due to a higher number of stomata or an increased stomatal aperture. BL is known to promote both stomatal opening and stomata number (Terfa et al. 2013). In the present study. BL increased transpiration in basil, tomato and cucumber but the strength of the response varied with species and RH regime (Figure 2; Table 4). However, cucumber showed the strongest response to BL, and a significant increase in transpiration was found under both moderate and high RH when more BL was added (data not shown). Furthermore, a significantly larger number of stomata was found in cucumber on the upper and lower sides of the leaves when exposed to additional BL, as described earlier by Hogewoning et al. (2010). The increased number of stomata in cucumber in response to BL may explain the stronger effect on transpiration in this species compared to tomato. However, the day/night transpiration ratio increased in cucumber and tomato produced under high RH when BL was added, indicating an improved stomatal closure in darkness (Table 4). Previous experiments with pot roses (*Rosa* x *hybrida*) also showed that light with a higher proportion of BL than provided by the traditional HPS lamp improved dark-induced stomata closure and tolerance to drought (Terfa et al. 2012). On the contrary, cucumber and tomato grown under high RH with HPS alone had a day/night transpiration ratio close to 1.0, which indicates almost no stomatal movement in response to darkness. The reason for the lack of stomatal movement under high RH and HPS alone is not clear but could be due to a higher accumulation of starch in the guard cells. In a study with silver birch, increased starch accumulation and a higher C/N ratio was found in leaves developed under high RH compared to ambient RH levels (Lihavainen et al. 2016), and similar results have been obtained in *Hydrangea macrophylla* grown under high RH compared to moderate RH (S. Torre, unpublished data). Starch degradation in guard cells has an important role in plant growth by driving stomatal responses to light. Also, this degradation has been shown to be controlled by the phototropin-dependent blue-light receptor (Horrer et al. 2016). The fact that additional BL increased the ratio between day and night transpiration rates under high RH opens up the possibility that BL triggers stomatal function under high RH through starch degradation as described in Horrer et al. (2016) but further research is needed to confirm this theory.

CONCLUSION

When the proportion of BL increased from 5 to 30% under moderate RH (<60%), a strong growth inhibition and a significant reduction in dry weight was found in tomato and cucumber. However, under high RH, plant growth and quality was improved with increased amounts of BL (30 vs. 5%). We conclude that manipulation of BL can be used as a cultivation strategy to improve plant production and quality under high RH.

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