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Original article

The rosmarinic acid content of basil and borage correlates with the ratio of red and far-red light

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Summary

Rosmarinic acid (RA) and caffeic acid (CA) are potent antixodiants and show antimicrobial activity against many fungal plant pathogens. Their biosynthesis employs enzymes of the phenylpropanoid pathway, a pathway that in mustard is regulated by phytochrome. If RA biosynthesis is regulated by phytochromes one would expect that the RA level correlated with the ratio of red to far-red light. In this paper we tested this hypothesis by growing basil and borage under different ratios of red to far-red light. CA and RA contents were measured with state of the art LC-MS/MS. Regression analysis showed that there is a significant inverse correlation of the ratio of red to far-red light and the content of RA, but not of CA. Hence, we conclude that RA biosynthesis is regulated by phytochrome.

Keywords
far-red light, light emitting diodes, light regime, phenylpropanoid pathway

Significance of this study

What is already known on this subject?
- CA and RA are potent antioxidant and show antimicrobial activities.

What are the new findings?
- We show that RA biosynthesis is promoted by a low ratio of red to far-red light, indicating that it is regulated by phytochrome.

What is the expected impact on horticulture?
- Growers can use this information to design lighting strategies, which increases RA contents.

Introduction

Caffeic acid (CA) and rosmarinic acid (RA) are abundant polyphenolic compounds in basil (*Ocimum basilicum*) and borage (*Borago officinalis*) (Park, 2011; Bandoniene, 2005). Both are potent antioxidant (Jayasinghe, 2003; Chen and Ho, 1997). RA shows anti-inflammatory activity in animal models (Sanbongi, 2004) and CA and RA show antimicrobial activity against a variety of pathogenic fungi (Widmer and Laurent, 2006; Bais, 2002). In the future, a high content of antioxidants could become an additional selling argument for herbs. Therefore, a method to increase the content of CA and RA is of great interest for growers.

CA and RA are synthesised via the phenylpropanoid pathway, a chain of enzymatic reactions that is fairly well established (Petersen, 1993). One of its precursors is phenylalanine which is converted by phenylalanine ammonium lyase (PAL) to cinnamic acid. Cinnamic acid in turn is converted to 4-coumaryl-CoA and CA. A second precursor is tyrosine which is converted to 4-hydroxyphenylactic acid. RA synthase forms the ester bound of 4-coumaryl-CoA and 4-hydroxyphenylactic acid which gives rise to RA. In cell cultures of *Coleus blumei* RA content correlates with phenylalanine ammonium lyase (PAL) activity, indicating that it is a rate-limiting step (Razzaque, 1977).

RA and CA share large parts of their biosynthesis pathway with anthocyanins and quercetin, which also derive from cinnamic acid produced by PAL. In mustard (*Sinapis alba*) anthocyanin and quercetin biosynthesis is induced by a low ratio of red to far-red light (Lange, 1971). This data indicates that the pathway is regulated by the photoreceptor phytochrome (Beggs, 1987). Moreover, it was shown that in mustard PAL activity and proteins levels are regulated by phytochrome (Brödenfeldt, 1987). Phytochromes undergo light induced conformational changes between a red light perceiving P_r state and a far-red light perceiving Pf_r state. The ratio of red to far-red light defines the ratio of the two states. In mustard a shift to the P_r state promotes the expression and activity of PAL (Brödenfeldt, 1987). This data provide a possible molecular mechanism how phytochrome regulates anthocyanin biosynthesis.

Recently it was shown that the RA content of basil depends on the light regime (Shiga, 2009). However, from Shiga's experiment it was not clear which photoreceptors mediates the effect. Since CA and RA share much of its biosynthesis pathway with anthocyanins, we reckon that they are regulated by phytochrome. To test this hypothesis basil was grown under lamps emitting different ratios of red to far-red light. Moreover, we tested whether the effect of the light regime on RA content is the same in borage, a member of a distant family, to establish whether this is a common mechanism.

Materials and methods

Experiment 1

Experiments with basil were conducted during April and May 2013 on the campus of the University of Applied Sciences Weihenstephan-Triesdorf (48°24'6"N, 11°43'53"E). Plants were cultivated in pots (size 12) with a standard horticulture substrate. Germinated basil plants of the variety 'Aton' were grown in the institute of horticulture in the total absence of sunlight but with artificial lighting consisting of a

Table 1. Number of photons in the range of blue (400–500 nm), red (620–690 nm) and far-red light (720–740 nm) of the different fixtures. PAR (%) is the percentage of photosynthetic active radiation (400–700 nm) of the total photon flux.

Light regime	Blue	Red	Far-red	PAR (%)	Red/far-red
OF	34.3	49.0	4.6	94	10.6
G2	8.8	80.4	30.9	76	2.6
AP673	15.7	67.8	8.1	94	8.3

Fluora fluorescence lamp (OF), (Osram, Semiconductors, Regensburg, Germany), LED B150 spectrum G2 lamp (G2) and LED B150 spectrum AP673 lamp (AP673) (both from Valoya OY, Helsinki, Finland). Spectral composition of the lamps are summarised in Table 1. Plants were illuminated with a photosynthetically active radiation (PAR) of 120 µmol m^{-2} s^{-1} for 16 h per day. Plants were cultivated at room temperature without additional CO_2 and watered and fertilized (0.01% Ferty1, Planta, Regenstauf, Germany) using an automated system controlled by a tensiometer. Control plants were grown in a greenhouse at 18°C during the day and 16°C during the night. Experiments with borage were conducted during the month of October and November 2013 with similar settings.

Experiment 2

In a second experiment the effect of blue and red light, but without far-red light, on RA content of basil was tested with prototype red/blue LEDs (Osram Semiconductors, Regensburg, Germany). Therefore, basil plants were exposed to 0, 25, 50, 75 and 100% red light (the rest was blue light) in the absence of sunlight. For technical reasons the PAR was reduced to 60 µmol m^{-2} s^{-1}.

Measurement of plant and light quality

At the end of the cultivation period plants height was measured from the rim of the pot the most upper leave with a ruler. Internode length (distance between nodes) was measured also with a ruler. Then, plants were cut off and the fresh weight was recorded with a laboratory scale. The optical quality (compactness) of basil plants was rated by a professional grower on a scale ranging from 1 = not compact to 5 = very compact. Spectra were recorded with a Jaz spectrometer (Ocean Optics, Dunedin, USA). Percentage of photons in the wavebands 400–500 nm (blue), 620–690 nm (red) and 720–740 nm (far-red light) were extracted from the spectra and these numbers were used to correlate the CA and RA content with the wavelength (Sellaro, 2010). PAR was measured with a quantum sensor (LI-190, LiCOR Biosciences, Lincoln, USA). Daily light integrals in J cm^{-2} at the location Weihenstephan were provided by the Deutsche Wetterdienst and converted to PAR according to McCree (1981) using an average day length of 15.5 h (May) and 10.4 h (October). Transmission of the greenhouse glass is about 50%.

Measurement of CA and RA content with mass spectrometry

After one month of cultivation six leaves, taken randomly from different areas of the plant, were freeze-dried and stored at -80°C until further use (Mulinacci, 2011). Freeze-dried leaves were grinded in a ball mill and re-suspended in methanol at a concentration of 1 g dry weight L^{-1} solvent (Jayasinghe, 2003). RA and CA were extracted at room temperature for 30 minutes and stored at -20°C until further analysis. Samples were analysed on a 6490 triple-quadrupole LC-MS/MS equipped with a 1290 Infinity HPLC system (Agilent Technologies). CA and RA (Sigma, Germany) were used as standards. RA and CA were quantified in the negative mode using a multiple reaction monitoring protocol set on the key fragments of m/z 161 and m/z 197 (RA) and of m/z 135 (CA) in the MS2 spectra (Møller, 2007; Chua, 2011). RA and CA contents are given in g 100 g^{-1} dry weight (%w/w).

Statistical analysis

The number of basil plants per group was $n = 20$ and $n = 8$ for borage. Normality of RA and CA contents were tested with Kolmogorov-Smirnov-test. Homoscedasticity was tested using Levene's test ($\alpha = 0.05$). Differences of means of normally distributed and homoscedastic data were tested with ANOVA. All others were tested with the Kruskal-Wallis test and are reported as median with the corresponding interquartile range. Post hoc data analysis was done with Tukey's test. All tests were calculated with Minitab (Minitab, Version 16, London, UK).

Results

The average PAR (400–700 nm) in Weihenstephan during the month of May and October, the main cultivation periods for basil and borage, were 347 µmol m^{-2} s^{-1} and 235 µmol m^{-2} s^{-1}, respectively. Cultivation of basil under artificial light produced plants that showed no sign of abiotic stress (Figure 1). However, basil grown under artificial light had a significantly lower fresh weight compared to plants grown in a greenhouse (Table 2). Fresh weight of basil grown with artificial light was highest in G2 > AP673 > OF. Height of basil grown with LEDs emitting the spectrum G2 was comparable with plants grown in a greenhouse. Plants grown with light regimes AP673 and OF were significantly smaller (Table 2). Basil grown under G2 and OF had the highest internode distance and had the lowest quality rating (Table 2).

The concentration of CA was significantly higher in basil grown under artificial light compared to plants grown in the greenhouse (Table 2). There was, however, no significant difference in CA content between the light regimes G2, AP673 and OF. RA in basil was significantly higher in plants grown under G2 compared to all other light regimes. RA concentration in plants grown with AP673 was not significantly different from OF, but the content of both was significantly higher than in greenhouse plants. Regression analysis showed that RA contents of basil inversely correlated with the ratio of photons in the range of 620–680 nm (red) and 720–740 nm (far-red) (Figure 2). The correlation coefficient was highly significant ($p < 0.001$, $n_{total} = 60$).

The three lamps emit along with red and far-red additional blue light. To test the influence of the ratio of blue to red light without interference from far-red light new plants were grown under prototype LEDs. These LEDs emit only red and blue light. As shown in Table 3, there was no significant difference in RA contents of basil plants grown under different ratios of red to blue light.

Similar to basil, borage grown with artificial light showed no signs of abiotic stress. Fresh weight and height was highest in borage grown with G2 and AP673, followed by OF and

Table 2. Means ± SD of height, fresh weight, compactness (C), internode distance (ID), CA and RA (in % of the dry weight) of basil grown with artificial light and in the greenhouse. Compactness was rated from 1 = not compact to 5 = very compact. Internode distance is presented as median and inter quartile range. Values labeled with different letters are significantly different ($p = 0.05$, $n = 20$).

Light regime	FW (g)	Height (cm)	CA (%)	RA (%)	C	ID (cm)
Control	48.9 ± 2.5 a	21.4 ± 1.4 a	0.03 ± 0.02 b	1.4 ± 0.3 c	5 (1) a	5.0 (6.0) b
OF	20.7 ± 1.4 d	16.8 ± 1.2 c	0.05 ± 0.01 a	2.2 ± 0.2 b	3 (1) c	14.0 (3.5) a
AP673	24.6 ± 3.1 c	19.9 ± 1.1 b	0.05 ± 0.01 a	2.3 ± 0.3 b	4 (2) ba	11.0 (7.5) b
G2	29.7 ± 4.0 b	21.6 ± 1.6 a	0.04 ± 0.01 a	2.6 ± 0.3 a	3 (2) cb	16.9 (3.8) a

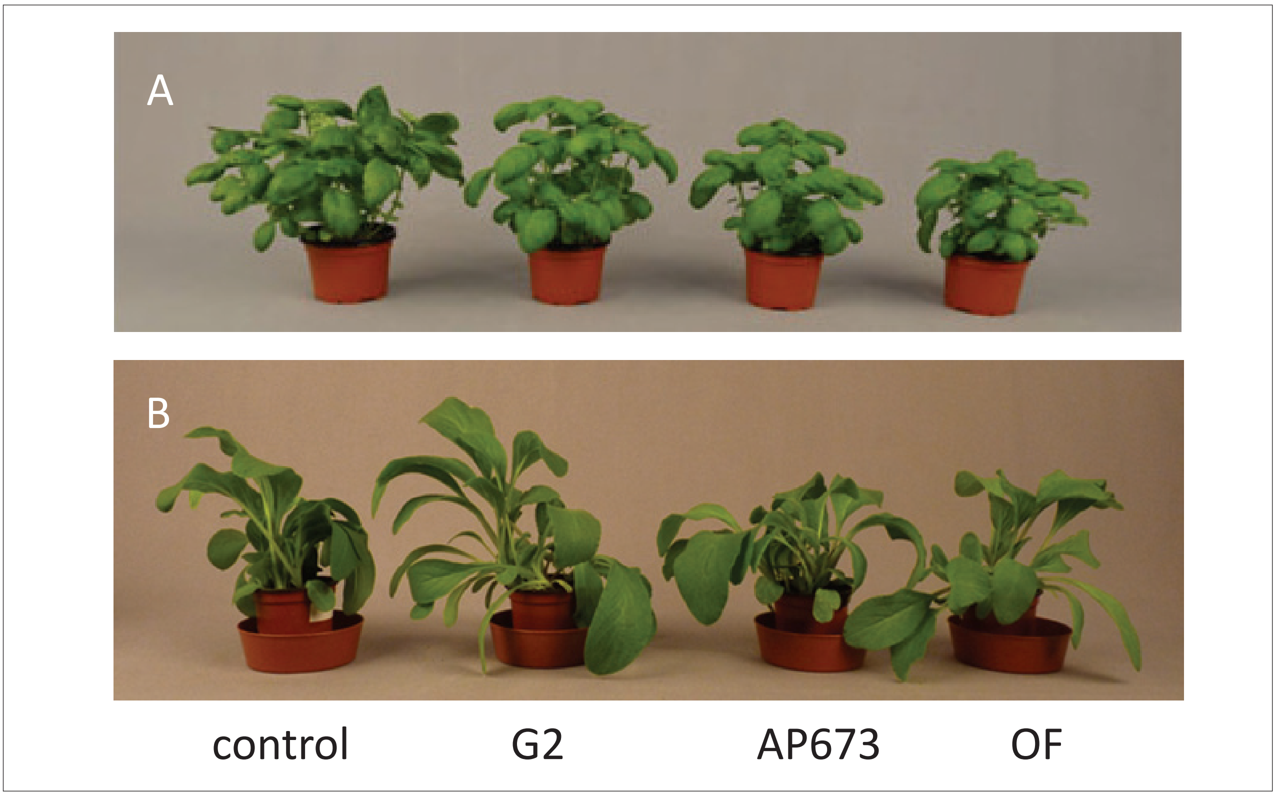

Figure 1. Representative specimen of basil (A) and borage (B) grown in the greenhouse (control) and under the light regimes G2, AP673 and OF.

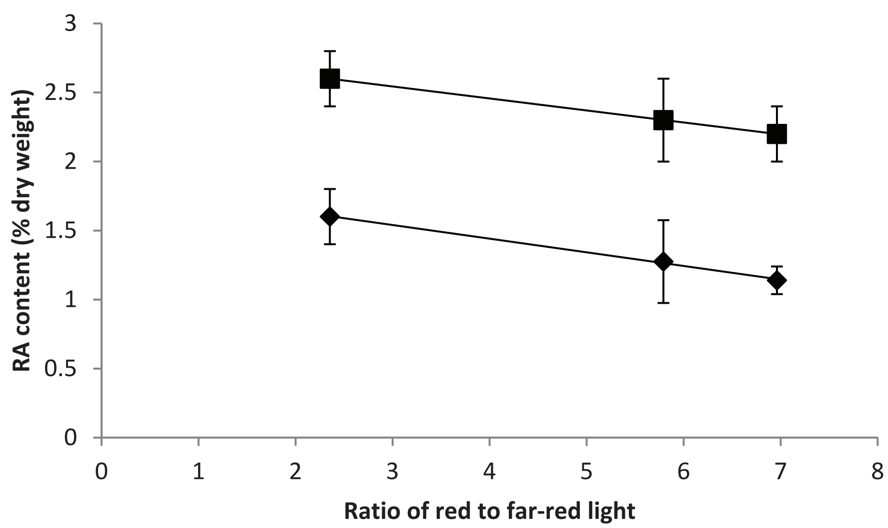

Figure 2. Regression analysis of RA content and the percentage ratio of red to far-red light in basil (■, $R^2 = 0.43$, $n = 60$, $p < 0.001$) and borage (♦, $R^2 = 0.53$, $n = 24$, $p < 0.001$).

Table 3. Height and weight after 38 days and RA content after 15 and 38 days of basil cultivated with different ratios of red to blue light. There were no statistically significant differences in weight (ANOVA, p = 0.665) and RA content (Kruskal-Wallis test; day 15 p = 0.065 and day 38 p = 0.154, respectively; *n* = 10).

% Red light	RA level after		Height	Weight
	15 days	38 days		
0	1.1 ± 0.3	3.0 ± 1.3	13.2 ± 3.0	17.0 ± 3.7
25	1.0 ± 0.2	2.5 ± 1.0	13.5 ± 2.7	16.6 ± 3.6
50	1.0 ± 0.2	2.5 ± 0.8	13.6 ± 3.7	16.7 ± 4.7
75	1.1 ± 0.1	3.4 ± 1.0	11.0 ± 1.5	17.7 ± 3.6
100	1.2 ± 0.2	3.6 ± 1.2	14.0 ± 3.0	19.4 ± 7.7

greenhouse plants (Table 4). In borage RA was also highest in plants grown under G2 followed by AP673 and OF (Table 4). Regression analysis showed the RA contents in borage decrease significantly with the ratio of red to far-red light, too (Figure 2).

Table 4. Means ± SD of height, fresh weight and RA content (% of dry weight) of borage grown with artificial light and in the greenhouse. Values labeled with different letters are significantly different (p = 0.05, *n* = 8).

	Fresh weight (g)	Height (cm)	RA content (%)
Control	21 ± 1.5 b	19.3 ± 1.5 b	–
Osram Fluora	29 ± 3.7 b	20.7 ± 1.7 b	1.1 ± 0.1 b
AP673	35 ± 2.5 a	21.4 ± 1.9 a	1.3 ± 0.3 b
G2	39 ± 3.7 a	26.0 ± 2.2 a	1.6 ± 0.2 a

Discussion

The data of this study confirm that basil and borage grown without sunlight, but under fluorescence lamps and LEDs, are healthy. There were no signs of abiotic stress that could provide an alternative explanation for the higher RA contents. The differences in weight and height of plants grown with artificial light and greenhouse plants can be attributed to the higher light intensity in the greenhouse during the month of May. For the same reason fresh weight of borage grown under artificial light in October (shorter days) is higher than in the greenhouse.

Despite a lower light intensity the content of RA and CA is higher in plants grown with artificial light. Moreover, the data show a significant correlation of the content of RA and the ratio of red to far-red light. It is well established that in plants phytochromes mediate the effect of red and far-red light. Thus, our data indicate that the RA content of basil and borage is regulated by phytochrome. The data from our second experiment (test of various ratios of red to blue light) rule out that the effect is mediated by blue or red light alone. However, for a final conclusion whether the effect is mediated by phytochrome one has to study RA levels in phytochrome mutants. We were not in the possession of a basil phytochrome mutant nor did we have the possibility to breed one. Hence, we consider our data as strong indication. Despite the fact that we cannot prove beyond doubt that RA is regulated by phytochrome, our data still confirm the hypothesis that RA levels are regulated by the ratio of red to far-red light.

The data from our study fit very well with the current knowledge of RA biosynthesis regulation in vitro. In cell culture the RA content correlates with PAL activity, indicating that the enzyme catalyses a rate limiting step (Razzaque, 1977). PAL activity also determines the rate of phenylpropanoid biosynthesis in tobacco (Bate, 1994). PAL activity on the other hand is regulated by phytochrome (Breggs, 1987; Brödenfeldt, 1987). Hence, it is reasonable to assume that phytochrome regulates the activity of PAL and subsequently the content of RA in basil and borage as well.

The LC-MS/MS analysis also revealed that the CA content, albeit deriving from cinnamic acid as well, did not correlate with the ratio of red to far-red light. CA is an intermediate product which is further transformed to ferulic acid. Thus, the level of CA depends on the activity of caffeate O-methyltransferase, the converting enzymes. As a consequence, the CA content does not necessarily correlate with the phytochrome photoequilibrium. In contrast, RA is not further converted and accumulates in trichomes (Gang, 2002). Hence, the level of RA correlates directly with the activity of the rate limiting enzyme of the biosynthesis pathway. We therefore speculate that the difference in the metabolic pathway of RA and CA account for the lack of correlations of CA with the ratio of red to far-red.

The RA biosynthesis pathway is evolutionary old and relatively widespread in the plant kingdom (Petersen and Simmonds, 2003). It is therefore likely that the mechanism of RA regulation is the same in distantly related species. To test this hypothesis we included borage in the study. *Boraginaceae* and *Lamiaceae* are distant relatives within the euasterids I. Phylogenetic dating showed that the branches of the two families had separated in the early cretaceous period, long before the order of *Lamiales* had split further into its distinct families (Bremer, 2004). Since the response of borage to different ratios of red to far-red light is the same as in basil we conclude that they share a common mechanism of regulation. If these two distant species share a common mechanism that it is reasonable to assume that all members of the *Lamiaceae* regulate RA biosynthesis in the same way. If this theory holds true it would be possible to create a lighting strategy which increases RA levels for all herbs of this family.

However, our data also show that a high level of far-red light has adverse effects on plant quality, in particular the internode distance. In many species internode elongation is promoted by far-red light. Therefore, it will be difficult to find a lighting strategy that guarantees compact plants and a high RA content. In mustard, exposure to short periods of far-red light is sufficient to induce anthocyanin biosynthesis. If this is also true for RA than alternating exposure to high far-red and longer periods with high red light could reconcile high quality and RA contents in basil. There is also evidence that blue light can reduce plant height (Cosgrove, 1981). However, in the second experiment, in which only blue and red light was given, there was no clear trend towards smaller plants with a higher level of blue light. This data indicates that a higher level of far-red light cannot be compensated with more blue light.

With the development of LEDs as a light source in horticulture the idea of growing herbs in multilayers gained momentum. Once the step towards an investment into a multilayer LED cultivation system is done, it is reasonable to gain the maximum benefit of it. In this scenario increasing the content of RA with optimized light regimes could be one way to add additional value to the crop.

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