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et al. 1992; CUVELIER et al. 1994; RICCHEIMER et al. 1996). Greece is an important centre for the production of *Salvia fruticosa*, which is mainly covered by the collection of plants directly from nature. The aforementioned activity may bring *Salvia fruticosa* populations at risk, and therefore, a new method for production of quality plants is critical.

One of the main environmental factors which are responsible for the production of secondary metabolites, and subsequently phenolic compounds, is light (KOPSELL, SAMS 2013; CARVALHO, FOLTA 2014). The application of radiation with different spectral output can activate physiological changes in plants (OUZOUNIS et al. 2014). Seed germination, shoot elongation and leaf expansion, among other plant characteristics, are partly controlled by light duration, intensity and quality (COOKSON, GRANIER 2006; BENTSINKA, KOORNNEEF 2008; DE CARBONNEL et al. 2010; CASAL 2013) which are perceived by plant photoreceptors (KAMI et al. 2010). Photoreceptors are proteins able to perceive, interpret and transduce light signals triggering changes at the metabolic, cell and whole organism level (LI et al. 2011). The photoreceptor proteins identified up to date are the phytochromes, that absorb mainly at red (R)/far-red (FR) part of the radiation spectra (CHEN, CHORY 2011), the cryptochromes and the phototropins, that absorb at the blue (B)/ultraviolet-A (UV-A) part of the radiation spectra (AHMAD, CASHMORE 1993; CHRISTIE 2007), and the UVR8 that absorb at the UV-B (280–315 nm) part of the radiation spectra (JENKINS 2014).

Red and far-red lights affect several plant characteristics including stem elongation, leaf development, and fresh and dry weight accumulation (LI, KUBOTA 2009; FAN et al. 2013; CHEN et al. 2016; DEMOTES-MAINARD et al. 2016; RABARA et al. 2017). It is commonly accepted that blue light supplementation to red light is essential for plant growth and development (YORIO et al. 1998; GOINS et al. 1998; SAMUOLIENE et al. 2010; HERNANDEZ, KUBOTA 2016; GUPTA 2017). Blue light suppresses stem elongation, but positively affects fresh and dry mass accumulation, and phenolics production (HUCHÉ-THÉLIER et al. 2016; BANTIS et al. 2016; HERNANDEZ, KUBOTA 2016; SNOWDEN et al. 2016). Moreover, green light responses have been tested over the last years, which revealed that it contributes to photosynthesis deeper in the canopy, especially under low light levels (WANG, FOLTA 2013; SMITH et al. 2017).

When natural light is not abundant, photoperiod and subsequently photosynthesis can be in-

creased with the application of artificial lighting. For this purpose, many lamp types have been used in closed systems (growth chambers) and greenhouses. Lamp types such as fluorescent (FL), high-pressure sodium (HPS), incandescent and metal halides have several disadvantages compared to the rather new technology of light-emitting diodes (LEDs). LEDs have a longer lifespan, are highly energetically efficient, offer the option of wavelength specificity and can dissipate excess heat away from plants through an external source (BOURGET 2008; MORROW 2008). However, their capital cost is still much higher than the lamp above types.

The research hypothesis was that pre-cultivation of *Salvia* seedlings under the effect of LED lights with different spectral output would variably affect their morphological and phytochemical properties. Robust seedlings with well-developed root system are desirable for transplantation, and root-to-shoot ratio is a valuable index of this trait. Irradiation with increased R light is expected to favour *Salvia's* vegetative growth (plant height, leaf size), while higher B and UV proportions are expected to enhance biomass production, and accumulation of phenolics. The study's objectives were: (i) to test if there is a considerable and more favourable potential in the use of LEDs for the pre-cultivation of *Salvia* seedlings, compared to FL lamps, (ii) to examine the effects of LED lights with broad spectra on the growth and total phenolic content of *Salvia* seedlings, and (iii) to determine the transplantation capacity of the seedlings after pre-cultivation under varying wavelengths.

## MATERIALS AND METHODS

**Plant material, growth conditions and light treatments.** The study was conducted from July to August 2015, at the Forest Research Institute, Thessaloniki provenance, Greece. *Salvia fruticosa* L. seeds were provided in June 2015 from Institute of Plant Breeding and Genetic Resources, Thessaloniki provenance. Seeds were hydrated for 24 h and then sowed in plastic mini-plug container trays (310 × 530 mm, 630 seedlings/m<sup>2</sup>; 27 cc; QP D 104 VW QuickPot<sup>®</sup>, Herkuplast-Kubern, Germany) filled with enriched peat (pH 6.0) which is suitable for growing young seedlings and as transplanting material. Fifty seeds per treatment were sowed and the mini-plug trays were immediately placed in a

Table 1. Spectral distribution and red : far-red (R : FR) ratio for the light treatments applied.

Light treatment	Lamp type	UV (%) < 400 nm	Blue (%) 400–500 nm	Green (%) 500–600 nm	Red (%) 600–700 nm	FR (%) 700–800 nm	R : FR
FL (control)	fluorescent	0	35.0	24.0	37.0	4.0	5.74
AP67	LED	0	13.8	15.1	53.0	18.1	2.77
L20AP67	LED	0	10.5	26.2	48.9	14.4	2.91
AP673L	LED	0	11.9	19.3	60.5	8.3	5.56
NS1	LED	1	20.2	38.9	35.7	5.2	8.16

FL – fluorescent; UV – ultraviolet light

growth chamber (each shelf had 0.6 m height, 1.2 m length and 0.55 m depth. The distance between the lamps and the mini-plug trays is 0.5 m) with controlled conditions. Light was provided by fluorescent tubes (FL, control treatment – Osram, Fluora, Munich, Germany) or 5 LEDs (Valoya Oy, Helsinki, Finland) emitting broad continuous spectra (Table 1). A brief description of the emission spectra of the five LEDs used is following: AP67 (moderate B, R and FR), L20AP67 [(moderate B, R and FR, high green (G)], AP673L (moderate B, high R), and NS1 (high B and G, low R, high R : FR, 1% UV). Conditions in the growth chamber were maintained at a photosynthetic photon flux density (PPFD) of  $200 \pm 10 \mu\text{mol}/(\text{m}^2 \cdot \text{s})$  with 14-h photoperiod, 22°C/18°C day/night temperature and  $80 \pm 10\%$  air relative humidity. The seedlings were daily irrigated with water sprinklers.

**Measurements.** Twenty-eight days after sowing 10 randomly selected seedlings per light treatment were sampled for morphological measurements. Specifically, the characteristics determined were leaf number, leaf area, shoot height, root length, and fresh and dry weight of overground (shoots and leaves) parts (FW and DW) and roots (FWR and DWR). Moreover, the dry-to-fresh weight ratio of overground parts (DW/FW) and roots (DWR/FWR), specific leaf area (SLA = leaf area/leaf dry weight), and root-to-shoot (R/S) dry weight ratio were calculated. Leaf area was measured on fresh leaves with a LI-3000C (LI-COR Biosciences, Lincoln, USA) leaf area meter. Dry weight was recorded after drying samples at 80°C in an oven, until constant weight.

**Total phenolic content.** Total phenolic content (TPC) was determined on five randomly selected *Salvia* seedlings after 28 days exposure to the different light treatments. Folin-Ciocalteu colorimetric assay (SINGLETON, ROSSI 1965) was used for the determination of TPC from plant extracts. For the

extraction process, seedlings (shoots and leaves) were submersed into liquid nitrogen for 5 min in order to perforate the waxy cuticle and rupture the cell membranes. Immediately they were placed in Falcon discs containing 3 ml of 6 M HCl : H<sub>2</sub>O : MeOH (7 : 23 : 70). The Falcon discs remained in the dark for 24 h, at 4°C. Afterwards, 2.5 ml of Folin-Ciocalteu reagent was added and the mixture was vortexed. This was followed by addition of 2 ml of 7.5% sodium carbonate solution after 1 min, and the mixture was vortexed again. Samples were then incubated for 5 min at 50°C. The absorbance of the coloured reaction product was measured at 760 nm versus a 500  $\mu\text{l}$  methanol, 2.5 ml Folin-Ciocalteu reagent and 2 ml of 7.5% aqueous sodium carbonate blank. The TPC in the extracts was calculated from a standard calibration curve obtained with different concentrations of gallic acid ( $R^2 = 0.998$ ). The absorbance was determined by a UV-VIS spectrophotometer (Shimadzu Scientific Instruments, Columbia, USA). Results were expressed as mg of gallic acid equivalents per g fresh weight (mg gallic acid/g FW).

**Root growth capacity evaluation.** Root growth capacity (RGC) is an index which has been developed for the evaluation of the seedling performance after transplanting. The index takes into consideration the root system expansion after transplantation, by which the plant successful establishment can be predicted (MATTSSON 1986, 1996). After 28 days of cultivation in the growth chamber, 10 randomly selected seedlings per light treatment were transplanted in steel boxes (35 × 26 × 8 cm) filled with a mixture of peat and sand (1 : 1). The steel boxes allow the root system to further expand in order to assess the RGC of the seedlings (MATTSSON 1986). The steel boxes were transferred in another growth chamber (20°C temperature;  $60 \pm 10\%$  air relative humidity; light provided by HPS and FL lamps with 14-h photoperiod and

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300  $\mu\text{mol}/(\text{m}^2\cdot\text{s})$  PPFD for all treatments at plant height), and placed on the surface of a water tank that serves to maintain a stable temperature for the root system ( $20 \pm 1^\circ\text{C}$ ). After 30 days of cultivation, the parameters measured were length of new roots (NRL) and dry weight of new roots (NRDW). The aforementioned characteristics are used to assess the RGC of the seedlings.

Shoot height, root length and NRL were measured with a digital caliper (Powerfix, Milomex, Pulloxhill, UK).

**Statistical analysis.** Statistical analysis was performed using SPSS (SPSS 15.0, SPSS Inc.). After 28 days of cultivation in the growth chamber, data were analysed by analysis of variance (ANOVA), while mean comparisons were conducted using a Tukey's test at  $\alpha < 0.05$ .

## RESULTS AND DISCUSSION

### Morphological characteristics

Manipulation of the light spectra, particularly the red and blue wavelengths, can help shape plant morphology as desired (HOENECKE et al. 1992; KOZAI et al. 2015; DAVIS, BURNS 2016; BANTIS et al. 2018). However, individual light sources induce different effects on plants, and therefore, their influence is highly species dependent (OUZOUNIS et al. 2015). Cultivation in closed systems with artificial light and heating will offer the species a chance to be produced throughout the year. Growth conditions during the experiment were appropriate which was confirmed by the regular development and morphology of the plants. After visual exami-

nation, seedlings of all treatments developed a typical green colour exhibiting no abnormalities.

A fast developing and extensive shoot growth is considered a shade-avoidance response and is controlled by phytochrome and cryptochrome photoreceptors, and possibly by UVR8 and phototropin photoreceptors (FRANKLIN 2008; CASAL 2012; RUBERTI et al. 2012; DEMOTES-MAINARD et al. 2016). A low R : FR ratio leads to reduced phytochrome B Pfr (the active state of phytochrome photoreceptor) levels which subsequently promotes the activity of Phytochrome Interacting Factors (PIFs). PIFs are able to induce shoot growth by binding and activating auxin-synthesis genes (CASAL 2013). FL and L20AP67 promoted the height increase of *Salvia fruticosa*, while NS1 and AP67 (the most B containing LEDs) light regimes exhibited the lowest values (Table 2). FRASZCZAK et al. (2014) found greater plant height under FL compared to the white (W) LED treatment, while internode inhibition has been reported under B light for several species (FOLTA et al. 2003; DOUGHER, BUGBEE 2004). Therefore, the relatively low B light proportion (10.5%) and R : FR ratio (2.91) of L20AP67 proved favourable in promoting *Salvia's* seedlings shoot growth. Regarding root length, no differences were observed during pre-cultivation in the growth chamber (Table 2), which was also reported for an oak species (*Quercus ithaburensis*) by SMIRNAKOU et al. (2017).

Apart from shoot growth mentioned above, R light acting through the phytochrome photoreceptors also affects other growth parameters including leaf area, and fresh and dry weight (SAGER, MCFARLANE 1997). In our case, seedlings grown under FL developed significantly more leaves (more

Table 2. Morphological and developmental parameters of *Salvia fruticosa* grown under five different light treatments described in Table 1

Parameters	Light treatments				
	FL (control)	AP67	L20AP67	AP673L	NS1
Shoot height (cm)	5.36 $\pm$ 0.65 <sup>a</sup>	2.57 $\pm$ 0.44 <sup>c</sup>	5.37 $\pm$ 0.52 <sup>a</sup>	4.73 $\pm$ 0.23 <sup>ab</sup>	3.29 $\pm$ 0.38 <sup>bc</sup>
Root length (cm)	12.64 $\pm$ 0.90 <sup>a</sup>	11.54 $\pm$ 1.00 <sup>a</sup>	13.37 $\pm$ 2.41 <sup>a</sup>	17.59 $\pm$ 3.78 <sup>a</sup>	16.37 $\pm$ 2.65 <sup>a</sup>
Specific leaf area ( $\text{m}^2/\text{kg}$ )	63.15 $\pm$ 7.99 <sup>a</sup>	38.09 $\pm$ 4.68 <sup>b</sup>	46.88 $\pm$ 6.72 <sup>ab</sup>	36.38 $\pm$ 2.96 <sup>b</sup>	32.12 $\pm$ 6.81 <sup>b</sup>
RGC : NRL (cm)	15.15 $\pm$ 1.77 <sup>a</sup>	17.59 $\pm$ 1.07 <sup>a</sup>	18.43 $\pm$ 2.65 <sup>a</sup>	15.69 $\pm$ 1.07 <sup>a</sup>	11.02 $\pm$ 1.14 <sup>a</sup>
RGC : NRDW (g)	0.0045 $\pm$ 0.0005 <sup>a</sup>	0.0042 $\pm$ 0.0013 <sup>a</sup>	0.0060 $\pm$ 0.0008 <sup>a</sup>	0.0055 $\pm$ 0.0006 <sup>a</sup>	0.0049 $\pm$ 0.0007 <sup>a</sup>
TPC (mg/g)	72.80 $\pm$ 6.26 <sup>a</sup>	101.44 $\pm$ 12.63 <sup>a</sup>	93.99 $\pm$ 5.50 <sup>a</sup>	89.92 $\pm$ 5.66 <sup>a</sup>	90.24 $\pm$ 5.02 <sup>a</sup>

RGC – root growth capacity; NRL – new root length; NRDW – new root dry weight; TPC – total phenolic content; average values ( $n = 10 \pm \text{SE}$ ; for TPC  $n = 5 \pm \text{SE}$ ) followed by different letters within a row differ significantly ( $\alpha < 0.05$ ) according to Tukey's criterion

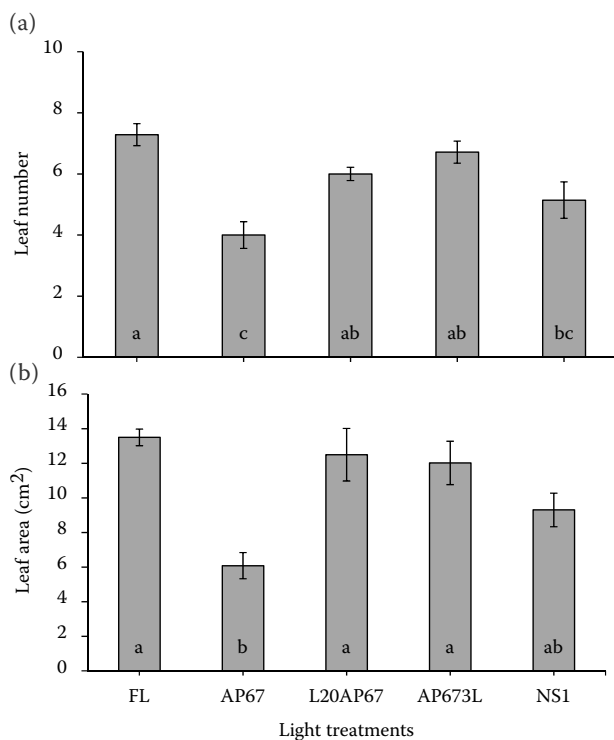


Fig. 1. (a) Leaf number, and (b) leaf area of *Salvia fruticosa* seedlings grown under five different light treatments. The spectral distribution of each light treatment is presented in Table 1

each data point is a mean value of 10 observations ( $n = 10$ )  $\pm$  SE; bars followed by a different letter within the same parameter differ significantly ( $\alpha < 0.05$ ) according to Tukey's criterion

than 7 leaves), as well as larger leaves along with L20AP67 and AP673L (the least B containing LEDs – 6–7 leaves) (Fig. 1a,b). Leaf area was increased under the influence of R light in cucumber (HOGEWONING et al. 2010). OUZOUNIS et al. (2016) found higher leaf number under R with additional B light compared to monochromatic R light, in eight out of nine tomato genotypes studied.

### Fresh and dry weights

The shoot height, leaf area and leaf number enhancement under FL, L20AP67, and AP673L naturally led to greater fresh mass accumulation. However, FWR was not significantly affected by the different light treatments (Fig. 2a). On the contrary, the different light treatments did not influence overground biomass production of Greek sage, while NS1 induced the production of significantly greater DWR compared to FL (Fig. 2b). Evidently, FW was

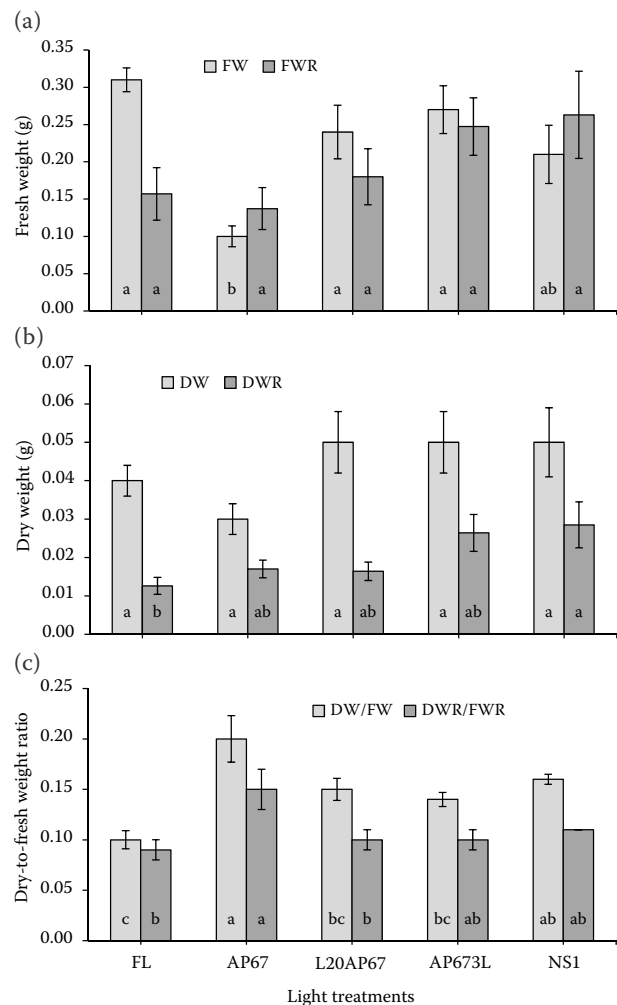


Fig. 2. (a) Fresh weight of overground parts (shoots and leaves – FW) and roots (FWR), (b) dry weight of overground parts (shoots and leaves – DW) and roots (DWR), and (c) DW-to-FW and DWR-to-FWR ratios of *Salvia fruticosa* seedlings grown under five different light treatments. The spectral distribution of each light treatment is presented in Table 1

each data point is a mean value of 10 observations ( $n = 10$ )  $\pm$  SE; bars followed by a different letter within the same parameter differ significantly ( $\alpha < 0.05$ ) according to Tukey's criterion

variably affected by the different light treatments but the same differences were not exhibited in the DW. Moreover, FWR was similar under all treatments but root dry weight was greater under NS1 (high B and G, low R, high R:FR, 1% UV). Since the different lights did not impose a significant effect on seedling root length, the root biomass increase under NS1 is probably a result of greater secondary root formation which was also reported for *Prunus avium* (BANTIS, RADOGLU 2017). The differences between fresh and dry weight results are depicted

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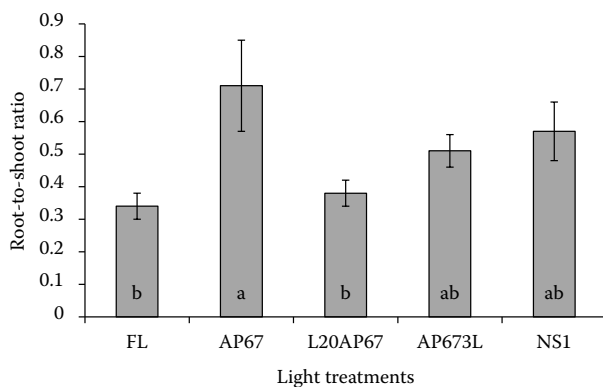


Fig. 3. Root-to-shoot dry weight ratio of *Salvia fruticosa* seedlings grown under five different light treatments. The spectral distribution of each light treatment is presented in Table 1

each data point is a mean value of 10 observations ( $n = 10$ )  $\pm$  SE. Bars followed by a different letter within the same parameter differ significantly ( $\alpha < 0.05$ ) according to Tukey's criterion

in DW/FW and DWR/FWR ratios, where AP67 (mainly) and NS1 (the most B containing LEDs) exhibited higher values (Fig. 2c). Similar effect of B light on dry mass accumulation was observed in strawberry (NADALINI et al. 2017) and lettuce (JOHKAN et al. 2010).

The production of high quality seedlings with focus on biomass allocation to the newly formed root system is essential for their ability to perform well after transplantation. FL and L20AP67 negatively affected R/S ratio of *Salvia fruticosa* (Fig. 3). Similar results were observed in wild cherry and common dogwood where L20AP67, and FL and L20AP67 respectively led to the production of seedlings with less R/S ratio (BANTIS, RADOGLU 2017). The results demonstrate that pre-cultivation under FL or L20AP67 leads to the production of a compact root system which provided the plant with limited ability to absorb water and nutrients, and therefore to inadequate supply the overground parts.

A positive effect on SLA was observed under FL (thinner leaves) (Table 2). The larger leaves developed under FL allowed greater interception of light and possibly higher photosynthetic rates. However, as mentioned above biomass was similar under all light treatments. Greater SLA was reported under W LED compared to FL for sweet basil after 21 days of cultivation, and for lemon balm until 21 days of cultivation (FRASZCZAK et al. 2014). SNOWDEN et al. (2016) reported a SLA decrease on radish, pep-

per and lettuce with increasing B light, and a SLA increase on pepper with increasing G light.

### Root growth capacity

In Mediterranean basin where extreme heat and drought incidents are typical even in spring and autumn, the production of quality seedlings with a vigorous root system and high transplanting success is challenging (RADOGLU et al. 2003; RAFTOYANNIS et al. 2006). After 31 days of cultivation in the growth chamber where RGC was determined, *Salvia fruticosa* developed the shortest roots when pre-cultivated under the influence of NS1 (high B and G, low R, high R:FR, 1% UV). However, the differences were not significant both for NRL and NRDW (Table 2). In two basil cultivars, shortest new roots and less new root biomass were developed under NS1 light treatment, but greater RGC was found under AP673L (moderate B, high R) (BANTIS et al. 2016). *Prunus avium* and *Cornus sanguinea* seedlings exhibited greater RGC after pre-cultivation under G2 and NS1 respectively (RADOGLU 2017). The aforementioned results prove that RGC parameters are species dependent agreeing with the report of KOSTOPOULOU et al. (2010).

### Total phenolic content

Secondary metabolite formation is controlled by genetic, environmental, physiological and biochemical factors (WINK 2010). Light is an essential parameter for secondary metabolite production (KOPSELL et al. 2004; KOPSELL, SAMS 2013), and different spectral wavelengths can regulate plant responses (SAMUOLIENE et al. 2013). Phenolic compounds act as blue and red pigments, protect plants from UV radiation and have antioxidant activity. In the case of *Salvia fruticosa*, seedlings grown under FL produced the least phenolic compounds compared to all LED treatments but the differences were not significant (Table 2). In baby lettuce, supplemental B light with HPS lamps imposed a negative effect on the phenolic compound production (SAMUOLIENE et al. 2013). PIOVENE et al. (2015) found greater TPC in sweet basil grown under RB and RBW LEDs compared to FL lamps, but no differences were reported for strawberry by the authors. In a more recent study with two basil cultivars, NS1

(high B and G, low R, high R:FR, 1% UV) positively affected the phenolic production (BANTIS et al. 2016). Greater TPC under NS1 was also expected in the case of *Salvia* since B light is linked with the production and accumulation of phenolics in plants. The contradiction with *Salvia's* results could be explained by species and variety dependency or cultivation conditions.

## CONCLUSION

The outcome of the present study demonstrates that a number of LEDs with broad spectra (L20AP67, AP673L) equally performed with FL conventional light on several developmental characteristics of *Salvia fruticosa*. The three aforementioned light treatments promoted seedling shoot height, leaf area, leaf number, fresh weight of overground parts, and specific leaf area compared to AP67 and NS1. The latter LEDs enhanced the seedling performance regarding the development of the root system, indicating that they guided biomass partition towards the underground parts. More research would be valuable in order to determine whether AP67 and NS1 are capable of assisting the production of compact seedlings. In addition, interesting responses occur with small interplays in the radiation wavelengths of different LEDs (L20AP67 versus AP67) and further investigation would contribute to our knowledge about light-plant interactions.

## References

- Ahmad M., Cashmore A.R. (1993): HY4 gene of *Arabidopsis thaliana* encodes a protein with the characteristics of a blue light photoreceptor. *Nature*, 366: 162–166.
- Aruoma O.I., Halliwell B., Aeschbach R., Loliger J. (1992): Antioxidant and pro-oxidant properties of active rosemary constituents: carnosol and carnosic acid. *Xenobiotica*, 22: 257–268.
- Bantis F., Ouzounis T., Radoglou K. (2016): Artificial LED lighting enhances growth characteristics and total phenolic content of *Ocimum basilicum*, but variably affects transplant success. *Scientia Horticulturae*, 198: 277–283.
- Bantis F., Radoglou K. (2017): Morphology, development, and transplant potential of *Prunus avium* and *Cornus sanguinea* seedlings growing under different LED lights. *Turkish Journal of Biology*, 41: 314–321.
- Bantis F., Smirnakou S., Ouzounis T., Koukounaras A., Ntagkas N., Radoglou K. (2018): Current status and recent achievements in the field of horticulture with the use of light-emitting diodes (LEDs). *Scientia Horticulturae*, 235: 437–451.
- Bentsinka L., Koornneef M. (2008): Seed Dormancy and Germination. *The Arabidopsis Book* 6: e0119.
- Bourget C.M. (2008): An introduction to light-emitting diodes. *HortScience*, 43: 1944–1946.
- Carvalho S.D., Folta K.M. (2014): Sequential light programs shape kale (*Brassica napus*) sprout appearance and alter metabolic and nutrient content. *Horticulture Research*, 1: 8.
- Casal J.J. (2012): Shade avoidance. *The Arabidopsis Book*. American Society of Plant Biologists 10, e0157.
- Casal J.J. (2013): Photoreceptor signalling networks in plant responses to shade. *Annual Review of Plant Biology*, 64: 403–427.
- Ceylan A. (1987): Medicinal Plant II. (Essential oil plants). Aegean University Agricultural Faculty publications, No: 481. (in Turkish)
- Chen M., Chory J. (2011): Phytochrome signaling mechanisms and the control of plant development. *Trends in Cell Biology*, 21: 664–671.
- Chen X., Xue X., Guo W., Wang L., Qiao X. (2016): Growth and nutritional properties of lettuce affected by mixed irradiation of white and supplemental light provided by light-emitting diode. *Scientia Horticulturae*, 200: 111–118. CrossRef
- Christie J.M. (2007): Phototropin blue-light receptors. *Annual Review of Plant Biology*, 58: 21–45.
- Cookson S.J., Granier C. (2006): A dynamic analysis of the shade-induced plasticity in *Arabidopsis thaliana* rosette leaf development reveals new components of the shade-adaptative response. *Annals of Botany*, 97: 443–452.
- Cuvelier M.-E., Berset C., Richard H. (1994): Antioxidant constituents in sage (*Salvia officinalis*). *Journal of Agriculture and Food Chemistry*, 42: 665–669.
- Das N.P., Pereira T.A. (1990): Effects of flavonoids on thermal autoxidation of palm oil: structure–activity relationships. *Journal of the American Oil Chemists Society*, 67: 255–258.
- Davis P.A., Burns C. (2016): Photobiology in protected horticulture. *Food and Energy Security*, 5: 223–238. CrossRef
- de Carbonnel M., Davis P., Roelfsema M.R.G., Inoue S.-I., Schepens I., Lariguet P., Geisler M., Shimazaki K.-I., Hangarter R., Fankhauser C. (2010): The Arabidopsis PHYTOCHROME KINASE SUBSTRATE2 protein is a phototropin signaling element that regulates leaf flattening and leaf positioning. *Plant Physiology*, 152: 1391–1405.
- Demotes-Mainard S., Péron T., Corot A., Bertheloot J., Le Gourrierc J., Pelleschi-Travier S., Crespel L., Morel P., Huché-Thélier L., Boumaza R., Vian A., Guérin V., Leduc N., Sakr S. (2016): Plant responses to red and far-red lights, applications in horticulture. *Environmental and Experimental Botany*, 121: 4–21. CrossRef
- Dougher T.A.O., Bugbee B. (2004): Long-term blue light effects on histology of lettuce and soybean leaves and stems.

<https://doi.org/10.17221/206/2017-HORTSCI>

- Journal of the American Society for Horticultural Science, 129: 467–472.
- Fan X., Zang J., Xu Z., Guo S., Jiao X., Liu X., Gao Y. (2013): Effects of different light quality on growth, chlorophyll concentration and chlorophyll biosynthesis precursors of non-heading Chinese cabbage (*Brassica campestris* L.). *Acta Physiologia Plantarum*, 35: 2721–2726. CrossRef
- Folta K.M., Lieg E.J., Durham T., Spalding E.P. (2003): Primary inhibition of hypocotyl growth and phototropism depend differently on phototropin-mediated increases in cytoplasmic calcium induced by blue light. *Plant Physiology*, 133: 1464–1470.
- Franklin K.A. (2008): Shade avoidance. *New Phytologist*, 179: 930–944. CrossRef
- Fraszczak B., Golcz A., Zawirska-Wojtasiak R., Janowska B. (2014): Growth rate of sweet basil and lemon balm plants grown under fluorescent lamps and LED modules. *Acta Scientiarum Polonorum*, 13: 3–13.
- Goins G.D., Yorio N.C., Sanwo-Lewandowski M.M., Brown C.S. (1998): Life Cycle experiments with *Arabidopsis* grown under red light-emitting diodes (LEDs). *Life Support and Biosphere Science*, 52: 143–149.
- Gupta D. (2017): *Light Emitting Diodes for Agriculture*. Springer, Singapore. CrossRef
- Hemphill J., Hemphill R. (1990): *Herbs: their cultivation and usage*. Blandford Press, London.
- Hernández R., Kubota C. (2016): Physiological responses of cucumber seedlings under different blue and red photon flux ratios using LEDs. *Environmental and Experimental Botany*, 121: 66–74. CrossRef
- Hogewoning S.W., Trouwborst G., Maljaars H., Poorter H., van Ieperen W., Harbinson J. (2010): Blue light dose-responses of leaf photosynthesis, morphology, and chemical composition of *Cucumis sativus* grown under different combinations of red and blue light. *Journal of Experimental Botany*, 61: 3107–3117.
- Hoenecke M.E., Bula R.J., Tibbitts T.W. (1992): Importance of 'blue' photon levels for lettuce seedlings grown under red-light-emitting diodes. *HortScience*, 27: 427–430.
- Huché-Théliér L., Crespel L., Gourrierc J., Le Morel P., Sakr S., Leduc N. (2016): Light signaling and plant responses to blue and UV radiations—Perspectives for applications in horticulture. *Environmental and Experimental Botany*, 121: 22–38. CrossRef
- Jenkins G.I. (2014): The UV-B photoreceptor UVR8: from structure to physiology. *Plant Cell*, 26: 21–37.
- Johkan M., Shoji K., Goto F., Hashida S., Yoshihara T. (2010): Blue light-emitting diode light irradiation of seedlings improves seedling quality and growth after transplanting in red leaf lettuce. *HortScience*, 45: 1809–1814.
- Kami C., Lorrain S., Hornitschek P., Fankhauser C. (2010): Light-regulated plant growth and development. *Current Topics in Developmental Biology*, 91: 29–66.
- Kopsell D.A., Sams C.E. (2013): Increases in shoot tissue pigments, glucosinolates, and mineral elements in sprouting broccoli after exposure to short-duration blue light from light emitting diodes. *Journal of the American Society for Horticultural Science*, 138: 31–37.
- Kopsell D.A., Kopsell D.E., Lefsrud M.G., Curran-Celentano J., Dukach L.E. (2004): Variation in lutein,  $\beta$ -carotene, and chlorophyll concentrations among *Brassica oleracea* cultivars and seasons. *HortScience*, 39: 361–4.
- Kostopoulou P., Dini-Papanastasi O., Radoglou K. (2010): Density and substrate effects on morphological and physiological parameters of plant stock material of four forest species grown in mini-plugs. *Scandinavian Journal of Forest Research*, 25: 10–17.
- Kozai, T. Niu G., Takagaki M. (2015): *Plant Factory: an Indoor vertical farming system for efficient quality food production*. Elsevier, Netherlands.
- Lattanzio V., Lattanzio V.M.T., Cardinali A. (2006): Role of phenolics in the resistance mechanisms of plants against fungal pathogens and insects. In: Imperato F. (ed.): *Phytochemistry: Advances in Research*, Research Signpost. Trivandrum, India: 23–67.
- Li Q., Kubota C. (2009): Effects of supplemental light quality on growth and phytochemicals of baby leaf lettuce. *Environmental and Experimental Botany*, 67: 59–64. CrossRef
- Li J., Li G., Wang H., Wang Deng X. (2011): *Phytochrome Signaling Mechanisms*. The *Arabidopsis Book* 9: e0148.
- Mattsson A. (1986): Seasonal variation in root growth capacity during cultivation of container grown *Pinus sylvestris* seedlings. *Scand Journal of Forest Research*, 1: 473–482.
- Mattsson A. (1996): Predicting field performance using seedling quality assessment. *New Forests*, 13: 223–48.
- Morrow R.C. (2008): LED lighting in horticulture. *HortScience*, 43: 1947–1950.
- Nadalini S., Zucchi P., Andreotti C. (2017): Effects of blue and red LED lights on soilless cultivated strawberry growth performances and fruit quality. *European Journal of Horticultural Science*, 82: 12–20.
- Ouzounis T., Frette X., Ottosen C.O., Rosenqvist E. (2014): Spectral effects of LEDs on chlorophyll fluorescence and pigmentation in *Phalaenopsis* 'Vivien' and 'Purple Star'. *Physiologia Plantarum*, 154: 314–327.
- Ouzounis T., Heuvelink E., Ji Y., Schouten H.J., Visser R.G.F., Marcelis L.F.M. (2016): Blue and red LED lighting effects on plant biomass, stomatal conductance, and metabolite content in nine tomato genotypes. *Acta Horticulturae (ISHS)*, 1134: 251–258.
- Ouzounis T., Rosenqvist E., Ottosen C.-O. (2015): Spectral effects of artificial light on plant physiology and secondary metabolism. *Hortscience*, 50: 1128–1135.
- Piovene C., Orsini F., Bosi S., Sanoubar R., Bregola V., Dinelli G., Gianquinto G. (2015): Optimal red:blue ratio in led



<https://doi.org/10.17221/206/2017-HORTSCI>

- lighting for nutraceutical indoor horticulture. *Scientia Horticulturae*, 193: 202–208.
- Pizzale L., Bortolomeazzi R., Vichi S., Uberegger E., Conte L.S. (2002): Antioxidant activity of sage (*Salvia officinalis* and *S. fruticosa*) and oregano (*Origanum onites* and *O. onites*) extracts related to their phenolic compound content. *Journal of the Science of Food and Agriculture*, 82: 1645–1651.
- Pokorny J. (1991): Natural antioxidants for food use. *Trends in Food Science and Technology*, 9: 223–227.
- Rabara R.C., Behrman G., Timbol T., Rushton P.J. (2017): Effect of spectral quality of monochromatic LED lights on the growth of artichoke seedlings. *Frontiers in Plant Science*, 8: 1–9. CrossRef
- Radoglou K., Raftoyannis Y., Halyvopoulos G. (2003): The effect of planting date and seedling quality on field performance of *Castanea sativa* Mill. and *Quercus frainetto* Ten. seedlings. *Forestry*, 76: 569–578.
- Raftoyannis Y., Radoglou K., Halyvopoulos G. (2006): Ecophysiology and survival of *Acer pseudoplatanus* L., *Castanea sativa* Miller. and *Quercus frainetto* Ten seedlings on a reforestation site in northern Greece. *New Forests*, 31: 151–163.
- Riccheimer S.L., Bernart M.W., King G.A., Kent M.C., Bailey D.T. (1996): Antioxidant activity of lipid-soluble phenolic diterpenes from rosemary. *Journal of the American Oil Chemists Society*, 73: 507–514.
- Ruberti I., Sessa G., Ciolfi A., Possenti M., Carabelli M., Morelli G. (2012): Plant adaptation to dynamically changing environment: the shade avoidance response. *Biotechnology Advances*, 30: 1047–1058. CrossRef
- Sager J.C., McFarlane J.C. (1997): Radiation. In: Langhans R.W., Tibbits T.W. (Eds.): *Plant Growth Chamber Handbook*. North Central Region Research Publication, Iowa State University Press: 1–29.
- Samuoliene G., Brazaityte A., Sirtautas R., Virsile A., Sakalauskaite J., Sakalauskiene S. (2013): LED illumination affects bioactive compounds in romaine baby leaf lettuce. *Journal of the Science of Food and Agriculture*, 93: 86–91.
- Samuoliene G., Brazaityte A., Urbonaviciute A., Šabajeviene G., Duchovskis P. (2010): The effect of red and blue light component on the growth and development of frigo strawberries. *Zemdirbyste-Agriculture*, 97: 99–104.
- Schwarz K., Ternes W. (1992): Antioxidative constituents of *Rosmarinus officinalis* and *Salvia officinalis*. II. Isolation of carnosic acid and formation of other phenolic diterpenes. *Zeitschrift für Lebensmittel-Untersuchung und-Forschung*, 195: 99–103.
- Seigler D. (1998): *Plant secondary metabolism*. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Singleton V.L., Rossi J.A. (1965): Colorimetry of total phenolics with phosphomolybdic-phosphotungstic acid reagents. *American Journal of Enology and Viticulture*, 16: 144–158.
- Smirnakou S., Ouzounis T., Radoglou K. (2017): Continuous spectrum LEDs promote seedling quality traits and performance of *Quercus ithaburensis* var. *macrolepis*. *Frontiers in Plant Science*, 8: 188.
- Smith H.L., Mcausland L., Murchie E.H. (2017): Don't ignore the green light: Exploring diverse roles in plant processes. *Journal of Experimental Botany*, 68: 2099–2110. CrossRef
- Snowden M.C., Cope K.R., Bugbee B. (2016): Sensitivity of seven diverse species to blue and green light: interactions with photon flux. *PLoS ONE*, 11: e0163121.
- Wang Y., Folta K.M. (2013): Contributions of green light to plant growth and development. *American Journal of Botany*, 100: 70–78. CrossRef
- Wink M. (2010): Functions and biotechnology of plant secondary metabolites. *Annals of Plant Reviews*, Vol. 3. Wiley-Blackwell, Oxford, UK.
- Yorio N.C., Goins G.D., Kagie H.R., Wheeler R.M., Sager J.C. (2001): Improving spinach, radish, and lettuce growth under red light-emitting diodes (LEDs) with blue light supplementation. *HortScience*, 36: 380–383.

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