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First observations of the microvine development under 100 % LED (light emitting diodes) illumination

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Summary

In order to reduce energy waste for artificial lights and subsequent air conditioning in plant growth chambers, the aim of this preliminary study was to evaluate the feasibility of growing the microvine under 100 % of LED illumination. Plant growth under two different LED lights was compared amongst each other and with plants maintained in greenhouse conditions. Regarding the impact on the reproductive and vegetative systems, the study showed that LED light is suitable to grow microvines in confined environments. Plants exposed to LED light exhibited similar leaf emergence rate but reduced vegetative and reproductive organ size compared to plants grown in the greenhouse. Photosynthesis for plants exposed to LED light was higher than what is usually observed on grapevine under natural conditions.

K e y w o r d s : grapevine development, growth chamber, rapid cycling vines, microvine, light emitting diodes (LED).

Introduction

The design of an experimental device yielding reproducible grapevine developmental patterns has become the bottleneck for post genomic studies since comparisons of high throughput transcriptomic or metabolomic data generated worldwide are impaired by the lack of a common reference. The grapevine actually suffers from several biological properties encountered in perennial plants yielding to the following major experimental limitations: i) adult plants require at least 1 m^2 to develop, ii) the juvenile period lasts 3 - 5 years and iii) inflorescences are produced only once a year. The delay resulting from such a reproductive feature considerably poises all approaches on flower and fruit development. Moreover, environmental conditions are heterogeneous and/or difficult to monitor in the field or even in greenhouses and it is almost impossible to fade out changing environment, which can bias the results notably.

To encounter these problems, new systems easier to handle for research purposes are needed. The microvine obtained through somatic embryogenesis from *Vitis vinfera* L. cv. 'Pinot Meunier' (Boss and Thomas 2002, Franks *et al.* 2002), was recently proposed as such a model (Chaïb *et al.* 2010). Its small size and the continuous fructification makes it well adapted for studies on fruit and plant development under controlled conditions in small-scale installations.

Up to now, the most common systems to ensure plant development and photosynthesis in culture rooms are based on HID (High Intensity Discharge) lights or fluorescent growth lights (when less powerful illumination is needed). These systems are quite efficient to convert power into visible light but their emission spectra may not fit the optimal wavelengths for angiosperms photosynthesis, which is mainly situated in the violet / blue regions and in the 640-680 nm band of the red light (Inada 1977, McCree 1972, Paradiso *et al.* 2011). In this respect, a 12 % increase in photosynthesis can be expected on green leaves upon optimizing light spectra with LED lamps (Paradiso *et al.* 2011). Several authors reported the successful use of LED light for plant growth but their impact on plants varied according to the species (Heo *et al.* 2006, Nhut 2002, Nhut and Nam 2010). Red and blue LED lights were found to increase vegetative dry matter and leaf photosynthesis in wheat (Goins *et al.* 1997). Successful use of LED light to grow lettuce has been reported several times (Bula *et al.* 1991, Goins *et al.* 1997, Kim *et al.* 2004). On cucumber, LEDs used as supplemental lighting source lead to higher leaf mass per area and dry mass allocation whereas leaf emergence rate decreased (Trouwborst *et al.* 2010). Using LED, several studies reported a reduction of organ size in particular when the fraction of blue light was high. It has been shown that the optimum ratio of blue to red light varies according to the species (Nhut and Nam 2010). The objective of this study was to investigate the response of grapevine exposed to 100 % LED light in growing chambers.

Material and Methods

The study was conducted with cuttings of microvines (3 x 6 plants) during four months. The genotype ML1 cl.7 was regenerated through somatic embryogenesis from cv. 'Pinot Meunier' clone 817 using the procedure described in (Torregrosa 1998). ML1 cl.7 exhibits a similar phenotype as the L1 Pinot Meunier mutant (VvGAI1/Vvgai1) previously described in (Chaïb *et al.* 2010). This line is charac-

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terized by a semi-dwarf stature, the continual production of hermaphroditic flowers and the development of black-skinned berries (Torregrosa, unpubl.). Potted cuttings, planted from lignified canes and presenting 5 to 7 unfolded leaves were used at the beginning of the study. Plants exposed to different LED treatments were maintained in the same growing chamber (Fig. 1). Control plants of the same lot were grown under ambient sunlight supplemented with HID lamps (Osram MT HIT HQI-BT 400W/D) in greenhouse conditions. The photoperiod was adjusted to 14 h·day^{-1}. Cumulative diurnal values of photosynthethetic photon flux density (PPFD) in the greenhouse were very variable and ranged from 2.52 to 31.32 mol·m^{-2}·d^{-1} with a mean daily cumulative PPFD of 16 mol·m^{-2}·d^{-1}. Mean diurnal temperature ranged from 17 to 24 °C in the greenhouse and from 26 to 29 °C in the growing chamber. All plants were daily watered with a standard nutrient solution (macro- and microelements from Murashige and Skoog 1962) to avoid nutrient or water deficit.

Two LED light panels with different emission spectra were compared. The first LED light panel was a SpectraPanel Pro 288 from FloraLED® (http://www.floraled.fr). According to the information provided by the supplier this panel was composed of 288 diodes with an operating power of 300 W. This panel is expected to emit a composite spectrum including all wavelengths in the visible light between 400 and 700 nm. The second panel (further called "Blue_Red LED") is expected to be optimized with respect to the absorption spectra of chlorophyll (Taiz and Zeiger 2010), *i.e.* with two main peaks of emission at 460 and 660 nm. This panel consisted of 300 diodes with the same operating power of 300 W, resulting in a luminous flux of 8000 Lm.

The emission spectra of the two LED panels were assessed with an Ocean Optics HR4000® spectrometer at a vertical distance of 0.65 m to the lamps. The distribution of PAR was determined using a standard PAR sensor (SDEC® Capteur de rayonnement photosynthetiquement actif – JYP 1000). The spatial PAR distribution of each panel was characterized over the illuminated surface at three different vertical distances from the lamps (1.0 m, 0.85 m and 0.65 m). Photosynthesis was measured in growth chamber at the stage, 21-23 unfolded leaves, following a 5 min irradiance period under LED light to stabilize photosynthesis and stomatal conductance. Four fully exposed leaves (three adult leaves which had finished their expansion and one young leaf) localized at different positions along the main proleptic axis were measured, using a Ciras – 2 Portable Photosynthesis System. Ambient conditions inside the module were maintained stable for each measurement (VPD at 1.5 kPa and CO_2 at 455 ppm, 5 min·meaurement[1]).

For the vegetative system the following parameters have been analyzed: leaf number (weekly), internode length of all phytomers (P0, P1 and P2) and length of main vein on fully expanded internodes and leaves which was used to calculate leaf surface using a previously determined relation (Pellegrino 2011, personal communication). Thermal time was calculated as the difference between mean T °C and the base temperature for grapevine (10 °C). The leaf emergence rate (LER) was calculated from the relationship between leaf number and cumulated TT (Lebon *et al.* 2006). Reproductive development variables were collected from clusters at the end of the first growth period (herbaceous plateau). Berry number and seed number per cluster were determined at ripe stage. Flowering rate was determined by counting floral buds before flowering and fecundated berries after fruit set on three clusters per plant.

Statistical analysis: Shapiro-Wilk normal distribution tests with subsequent standard two-sided student t-tests have been performed with R for MacOS X version 2.12.2.

Results and Discussion

Emission spectrum profiling and PAR (SDEC): The spectra obtained at 0.65 m distance from the LED panels in the central point beneath the lamps are

Fig. 1: Experimental set up. Left hand side operating FloraLED® panel, right hand side Blue_Red LED panel.

illustrated in Fig. 2. Each spectrum shows two main peaks, the less intense in the region of blue light at a wavelength of around 460 nm. The second and major peak was detected in the red light zone at a wavelength of around 660 nm. FloraLED® showed an additional minor peak in the zone of orange light at a wavelength of around 600 nm. Although displaying wider emissions peaks, no additional emission band could be detected, contrarily to the information provided by the manufacturer.

Fig. 3 illustrates the spatial repartition of PAR (photosynthetically active radiation) at 1.0 m vertical distance from lamps, showing maximum values of 78 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for FloraLED® and 63 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for Blue Red LED. Obviously, the PAR of both LED panels are far below values that have been reported necessary to saturate photosynthesis in grapevine which range between 500 and 700 $\mu mol \cdot m^{-2} \cdot s^{-1}$ when all other environmental parameters are set at optimum and temperature ranges between 20 to

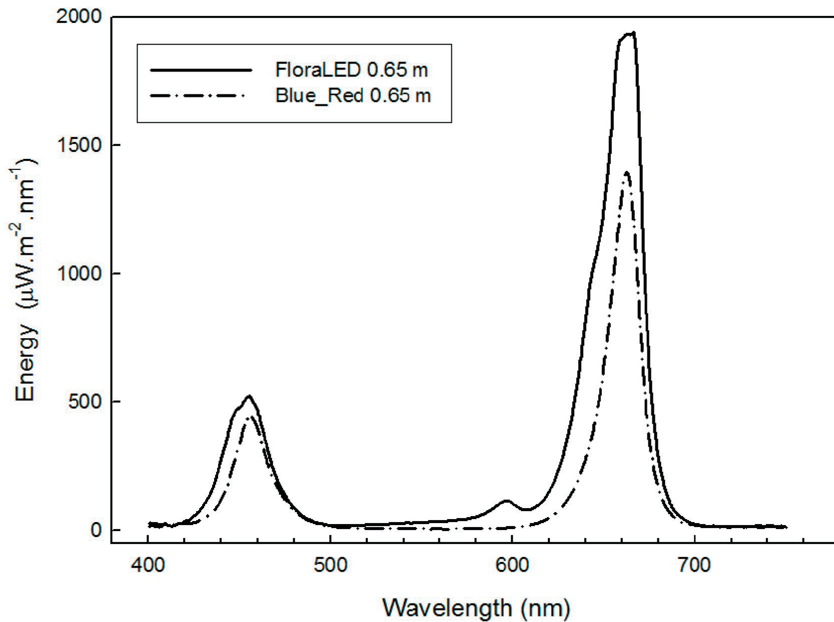

Fig. 2: Light spectra of the two LED panels at a distance of 0.65 m to the lamps. The dashed line shows the spectra of Blue_Red LED and the continuous line the spectra of FloraLED® panel.

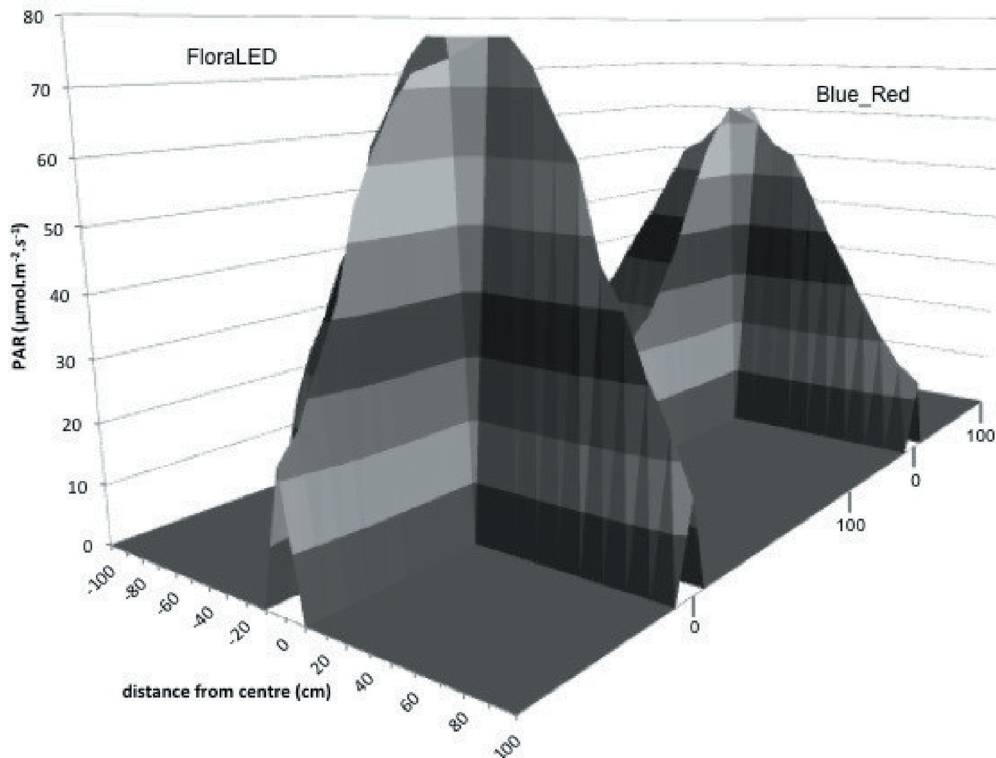

Fig. 3: Distribution of PAR for each LED panel. The PAR sensor was placed under the central point beneath each lamp. Consecutive measurements have been taken every 10 cm.

Table 1

Integrated PAR values for each LED panel at three distances. Average values and standard deviations of all height are illustrated at the bottom of the table

Distance (m)	FloraLED® (µmol·m⁻²)	Blue_Red LED (µmol·m⁻²)
1.00	198	164
0.85	252	185
0.65	236	195
avg	229	181
sd	28	16

30 °C (BAEZA *et al.* 1997, DÜRING 1988, ZUFFEREY *et al.* 2001). The spatial repartition of PAR was then characterized in order to calculate the global yield of each LED panel upon integrating light emitted on total illuminated surface. It was verified that 3 different vertical distances from the panels (1 m, 0.85 m and 0.65 m) yielded average values of 230 $\mu mol \cdot s^{-1}$ for FloraLED® and a 20 % lower value of 180 $\mu mol \cdot s^{-1}$ for the Blue_Red (Tab. 1). This yields conversion efficiencies of respectively 1.7 and 1.3 $W \cdot \mu mol^{-1}$ for FloraLED® and Blue_Red, provided that the same operating energy of 300 W documented by both manufacturers is valid. In the meantime, standard HID lights do have a fairly higher energy need of around 3 $W \cdot \mu mol^{-1}$.

Photosynthesis: Photosynthesis activities of the same leaves measured consecutively under FloraLED® and Blue_Red devices are illustrated in Fig. 4. Except for young leaves, photosynthesis was found up to 20 % higher ($p < 0.01$) with FloraLED®, which obviously results from its higher irradiance since a similar quantum yield of 0.14 $CO_2 \cdot photons^{-1}$ can be calculated for both panels (not shown). One should then reject that the narrow peak in the red wavelengths of Blue Red LED is supposed to result in an imbalance of photons available for photosystem I and II, leading to a decrease in net photosynthesis as reported in the literature (NHUT *et al.* 2010). Such a CO_2 quantum yield of adult leaves enlighted by LED panels is 1.7 fold higher than expected on a C3 plant under sunlight (SINGSAAS *et al.* 2001). Photosynthesis measurements on non water-stressed vines of 'Tempranillo' yielded values between 13.5 and 20.2 $\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$ according to canopy exposure and day time (CUEVAS *et al.* 2006). Consistantly with ESCALONA *et al.* (2003) on 'Manto Negro', GREER and WEEDON (2012) found 12 to 14 $\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$ on 'Semillon' leaves saturating above 500 $\mu mol\ photons \cdot m^{-2} \cdot s^{-1}$, whereas photosynthesis decreased to 4 $\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$ under the same solar irradiance of 50-70 $\mu mol\ photons \cdot m^{-2} \cdot s^{-1}$ emitted by LED lights. Although discussing the origin of excess CO_2 quantum yield observed with LED lights falls outside the scope of this preliminary work, present photosynthesis measurements clearly validate the use of dichromatic LED lights on grapevine.

Vegetative parameters: The plants exposed to the two different LED light panels did not show any difference in their leaf emergence rate throughout the whole experiment ($p > 0.05$). Moreover, the plants grown in the greenhouse showed the same leaf emergence rate as the both treatments from 20 °Cd to 80 °Cd before exhibiting a slight acceleration (Fig. 5) without being significantly different ($p > 0.05$). A similar effect was observed on cucumber (TROUWBORST *et al.* 2010) where plants which were additionally irradiated with red and blue LEDs (80 % red, 20 % blue) showed a slightly lower leaf emergence rate than the control.

As expected from the literature, plants grown under 100 % LEDs light showed an organ miniaturization. This is quantified in Figs 6 and 7 by means of internode length and leaf surface. Regarding the length of internodes (Fig. 6), no significant difference exists between FloraLED® and Blue_Red LED treatment but internodes of both, FloraLED and Blue_Red treatments are significantly shorter ($p < 0.001$) than those from greenhouse plants. Fig. 8 visualizes this miniaturization effect of organs for LED plants compared to plants maintained in the greenhouse. The shorter internodes for the LED grown plants ($p < 0.001$) can be an indication for a disturbed phytochromes photo-equilibrium due to a lack of far-red radiation in the spectra of both LEDs.

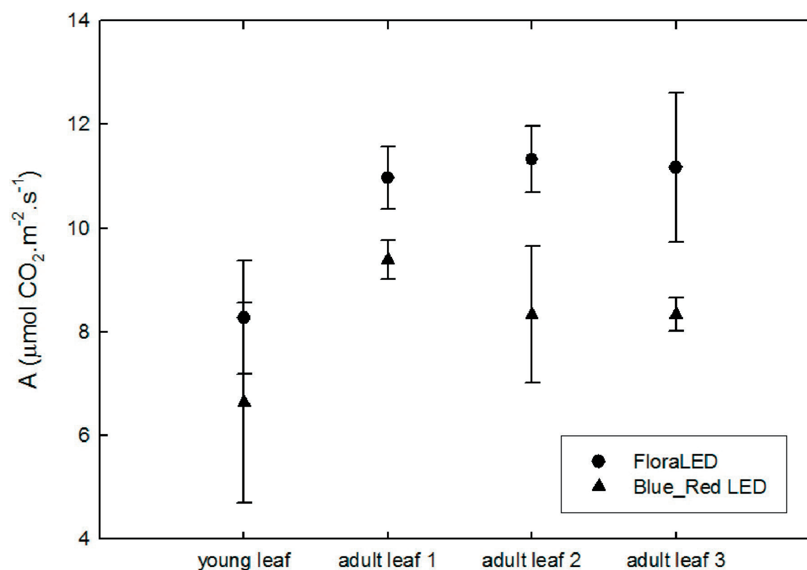

Fig. 4: Net photosynthesis of 4 leaves exposed to the LED panels. Similar level leaves of 3 plants have been measured (Vertical bars indicate SD). Circles show values of plants under FloraLED and triangles those of Blue_Red LED panels.

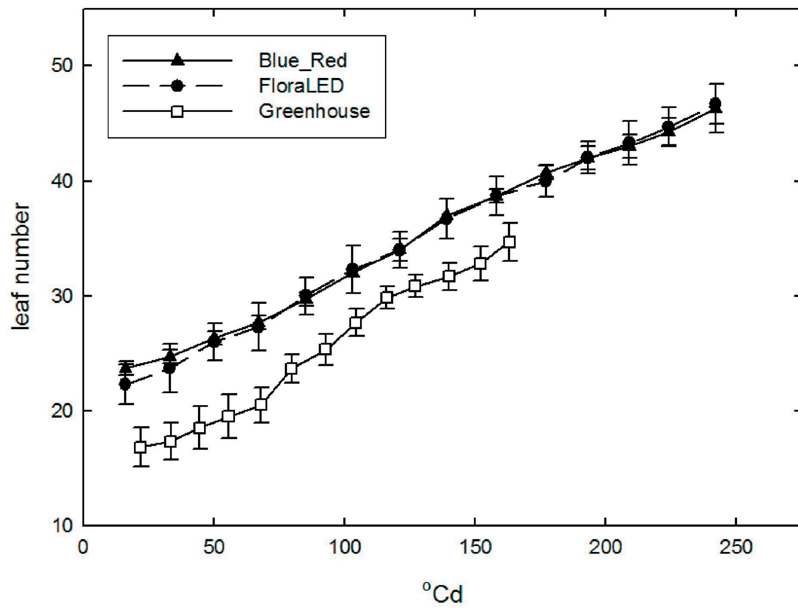

Fig. 5: Average leaf number of 6 plants exposed to LEDs and under greenhouse conditions (Vertical bars indicate SD).

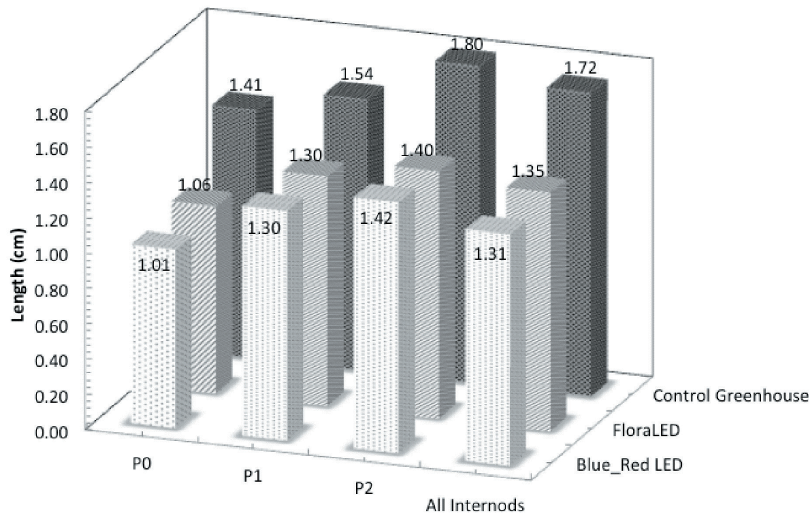

Fig. 6: Average internode lengths for each type of phytomer (P0, P1 and P0) as well as the average of all internodes are depicted for both LED treatment and for greenhouse plants. No significant difference exists between the FloraLED and Blue_Red treatment. Internodes of FloraLED and Blue_Red treatments are significantly shorter ($p < 0.001$) than those from greenhouse plants.

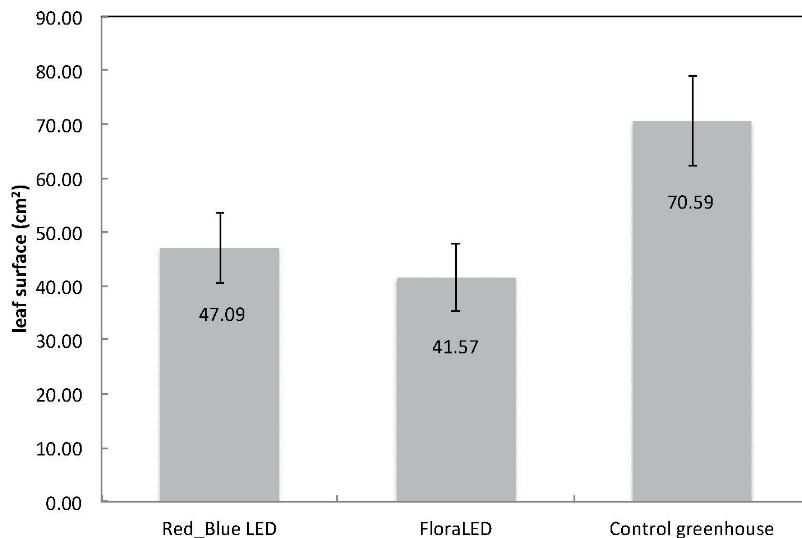

Fig. 7: Average leaf surface of single leaves at the end of expansion. (Vertical bars indicate SD). Greenhouse plants have significantly higher leaf surface ($p < 0.001$) than FloraLED and Blue_Red.

Fig. 8: Pictures of plants grown under greenhouse condition (left), FloraLED® (middle) and Blue_RED LED (right) devices. All plant do have the same age (15 weeks).

Table 2

Reproductive parameters of plants exposed to different light treatments (same letters in rows indicate no signifanct difference, different letters indicate significant difference ($p < 0.01$)

	Control greenhouse	Blue_Red LED	FloraLED
berries·cluster^{-1}	22 ± 9.8^a	20.8 ± 14.1^a	18.0 ± 10.5^a
seeds·berry^{-1}	1.35 ± 0.19^a	1.35 ± 0.21^a	1.25 ± 0.22^a
max berry weight before véraison (g)	1.1 ± 0.24^b	0.3 ± 0.04^a	0.3 ± 0.04^a
flowering rate (%)	70 ± 6.5^b	57 ± 3.4^a	58 ± 4.2^a

Particularly an alteration of the light spectra in the red/far-red wavelengths can trigger plant responses in plant height and flowering (Khattak *et al.* 2011). Similar effects were described on cucumber (*cucumis sativus*) (Trouwborst *et al.* 2010). In addition, studies on Arabidopsis seedlings showed a very strong inhibition of stem growth elongation when exposed to constant blue or red light (Folta *et al.* 2005). Several other authors confirmed a negative reciprocal relation of blue light transmission and plant height (McMahon and Kelly 1990, Mortensen 1990, Mortensen and Stromme 1987, Runkle and Heins 2002, Thomas and Dickinson 1979). Berry weight at the end of herbaceous phase was 3 fold lower for plants grown under LED compared to control plants (Tab. 2). A reduction in avocado fruit size induced by high irradiance was reported in the literature (Bertling and Cowan 1998), however, little information about negative or positive effects on fruit development due to specific light spectra or LED irradiation was published so far. All plants showed a continuous development of reproductive organs all along the main axis throughout the whole period of observation. Floral induction was slightly advanced under LED conditions when compared to the greenhouse (data not shown). No significant difference in seed number was observed ($p > 0.05$) (Tab. 2) leading to the assumption that fecundation was not altered by LED lights. Flowering rate was significantly lower for both LED treatments when compared to plants grown in the greenhouse (Tab. 2). The higher fruit set percentage for plants grown in the greenhouse can again be an indication for a shifted phytochromes photo-equilibrium that has an impact on flowering in plants (Khattak *et al.* 2011)

When comparing flowering rate percentages with values observed by Lebon *et al.* (2004) with 81.8 % for Gewürztraminer and 65.1 % for 'Pinot Noir' the obtained values for both LED treatments are still in a normal range for grapevine.

This is the first validation step of the use of 100 % LED irradiance on microvine. In our experimental conditions, it was possible to complete a full cycle of growth from shoot development to lignification (data not shown) and maintain the reproductive properties of the microvine, *i.e.* the continual production of inflorescences, flowers, berries and seeds during 4 months. The comparison of two different LED panels revealed significant differences in the PAR and, consequently, on photosynthesis but the slight differences in emission spectra did not prove critical for the microvine development in the conditions of the study. As for other plants, LED light led to a miniaturization of vegetative and reproductive organs but further work is needed to decipher which mechanisms underlay this response. This preliminary study paves the way for the design of a cost efficient reference system for growing grapevine in controlled and reproducible conditions.

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References

Baeza, P.; Ruiz, C.; Bartolome, M. C.; Lissarrague, J. R.; 1997: Differences in gas exchange in cv. Tempranillo (*Vitis vinifera* L.) as affected by training system, 391-397. Proc. 5th Int. Symp. Grapevine Physiol., Israel.

Bertling, I.; Cowan, A. K.; 1998: Effect of Photoinhibition on Fruit Growth and Development in Hass Avocado. S. Afr. Avocado Growers Assoc. Yearbook **21**, 36-38.

Boss, P. K.; Thomas, M. R.; 2002: Association of dwarfism and floral induction with a grape ‘green revolution’ mutation. Nature **416**, 847-850.

Bula, R. J.; Tennessen, D. J.; Morrow, R. C.; Tibbitts, T. W.; 1991: Light-emitting diodes as a radiation source for plants. HortScience **26**, 202-205.

Chaïb, J.; Torregrosa, L.; Mackenzie, D.; Corena, P.; Bouquet, A.; Thomas, M. R.; 2010: The grape microvine - a model system for rapid forward and reverse genetics of grapevines. Plant J. **62**, 1083-1092.

Cuevas, E.; Baeza, P.; Lissarrague, J. R.; 2006: Variation in stomatal behavior and gas exchange between mid-morning and mid-afternoon of north, south oriented grapevines (*Vitis vinifera* L. cv. Tempranillo) at different levels of soil water availability. Sci. Hortic. **108**, 173-180.

Düring, H.; 1988: CO_2 assimilation and photorespiration of grapevine leaves: responses to light and drought. Vitis **27**, 199-208.

Escalona, J. M.; J., F.; Bota, J.; Medrano, H.; 2003: Distribution of leaf photosynthesis and transpiration within grapevine canopies under different drought conditions. Vitis **42**, 57-64.

Folta, K.; Koss, L.; McMorrow, R.; Kim, H.- H.; Kenitz, J.; Wheeler, R.; Sager, J.; 2005: Design and fabrication of adjustable red-green-blue LED light arrays for plant research. BMC Plant Biol. **5**, 1-11.

Franks, T.; Botta, R.; Thomas, M. R.; Franks, J.; 2002: Chimerism in grapevines: implications for cultivar identity, ancestry and genetic improvement. Theor. Appl. Genet. **104**, 192-199.

Goins, G. D.; Yorio, N. C.; Sanwo, M. M.; Brown, C. S. 1997: Photomorphogenesis, photosynthesis, and seed yield of wheat plants grown under red light-emitting diodes (LEDs) with and without supplemental blue lighting. J. Exp. Bot. **48**, 1407-1413.

Greer, D. H.; Weedon, M. M.; 2012: Interactions between light and growing season temperatures on, growth and development and gas exchange of Semillon (*Vitis vinifera* L.) vines grown in an irrigated vineyard. Plant Physiol. Biochem. **54**, 59-69.

Heo, J.; Lee, C.; Paek, K.; 2006: Influence of mixed LED radiation on the growth of annual plants. J. Plant Biol. **49**, 286-290.

Inada, K.; 1977: Effects of leaf colour and the light quality applied to leaf-developing period on the photosynthetic response. Jpn. J. Crop Sci. **46**, 37-44.

Khattak, A. M.; S. Pearson, S.; Nawab, K.; Khan, M. A.; Marawat, K. B.; 2011: The effects of light quality and temperature on the growth and development of geraniums. Pak. J. Bot. **43**, 679-688.

Kim, H. H.; D., G.; Goins, R.; Wheeler, M.; Sager, J. C.; 2004: Stomatal conductance of Lettuce grown under or exposed to different light qualities. Ann. Bot. **94**, 691-697.

Lebon, E.; Pellegrino, A.; Louarn, G.; Lecoeur J.; 2006: Branch development controls leaf area dynamics in grapevine (*Vitis vinifera*) growing in drying soil. Ann. Bot. **98**, 175-185.

Lebon, G.; Duchêne, E.; Brun, O.; Magné, C.; Clément, C.; 2004: Flower abscission and inflorescence carbohydrates in sensitive and non-sensitive cultivars of grapevine. Sex Plant Reprod. **17**, 71-79.

McCree, K. J.; 1972: The action spectrum, absorbtance and quantum yield of photosynthesis in crop plants. Agric. Meteorol. **9**, 191-216.

McMahon, M. J.; Kelly, J. W.; 1990: Influence of spectral filters on height, leaf chlorophyll and flowering of *Rosa* x *hybrida* “Meirutral”. J. Environ. Hortic. **8**, 209-211.

Mortensen, L. M.; 1990: Effects of temperature and light quality on growth and flowering of *Begonia hiemalis* Fotsch. and *Campanula isophylla* Moretti. Sci. Hortic. **44**, 309-314.

Mortensen, L. M.; Stromme, E.; 1987: Effects of light quality on some greenhouse crops. Sci. Hortic. **33**, 27-36.

Murashige, T.; Skoog, F.; 1962: A Revised Medium for Rapid Growth and Bio Assays with Tobacco Tissue Cultures. Physiol. Plant. **15**, 473-497.

Nhut, D. T.; 2002: *In vitro* growth and physiological aspects of some horticultural plantlets cultured under red and blue light-emitting diodes (LEDs). Doctoral Thesis, Kagawa University.

Nhut, D. T.; Nam, N. B.; 2010: Light-emitting diodes (LEDs): An artificial lighting source for biological studies, 133-138. Proc. 3rd Int. Conf. Develop. BME, Vietnam.

Paradiso, R.; Meinen, E.; Snel, J. F. H.; De Visser, P.; Van Ieperen, W.; Hogewoning, S. W.; Marcelis, L. F. M.; 2011: Spectral dependence of photosynthesis and light absorbtance in single leaves and canopy in rose. Sci. Hortic. **127**, 548-554.

Runkle, E. S.; Heins, R. D.; 2002: Stem extension and subsequent flowering of seedlings grown under a film creating a far-red deficient environment. Sci. Hortic. **96**, 257 - 265.

Singsaas, E. L.; Donald, R. O.; DeLucia, E. H.; 2001: Variation in measured values of photosynthetic quantum yield in ecophysiological studies. Oecologia **128**, 15-23.

Taiz, T.; Zeiger, E.; 2010: Plant Physiology, 5th ed., Sinauer Associates Inc., Sunderland..

Thomas, B.; Dickinson, H. G.; 1979: Evidence for two photoreceptors controlling growth in deetiolated seedlings. Planta **146**, 545-550.

Torregrosa, L.; 1998: A simple and efficient method to obtain stable embryogenic cultures from anthers of *Vitis vinifera* L. Vitis **37**, 91-92.

Trouwborst, G.; Oosterkamp, J.; Hogewoning, S. W.; Harbinson, J.; Van Ieperen, W.; 2010: The responses of light interception, photosynthesis and fruit yield of cucumber to LED-lighting within the canopy. Physiol. Plant. **138**, 289-300.

Zufferey, V.; Murisier, F.; Schultz, H. R.; 2000: A model analysis of the photosynthetic response of *Vitis vinifera* L. cvs Riesling and Chasselas leaves in the field: I. Interaction of age, light and temperature. Vitis **39**, 19-26.

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