PLANT BIOSYSTEMS – AN INTERNATIONAL JOURNAL DEALING WITH ALL ASPECTS OF PLANT BIOLOGY, 2018
VOL. 152, NO. 3, 515–523
https://doi.org/10.1080/11263504.2018.1435583

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Tree seedling response to LED spectra: implications for forest restoration

Antonio Montagnoli[a], R. Kasten Dumroese[b], Mattia Terzaghi[a], Jeremiah R. Pinto[b], Nicoletta Fulgaro[a], Gabriella Stefania Scippa[c] and Donato Chiatante[a]

[a]Department of Biotechnology and Life Sciences, University of Insubria, Varese, Italy; [b]USDA Forest Service, Rocky Mountain Research Station, Moscow, ID, USA; [c]Department of Biosciences and Territory, University of Molise, Contrada Fonte Lappone, Pesche, Italy

ABSTRACT

We found that different spectra, provided by light-emitting diodes or a fluorescent lamp, caused different photomorphological responses depending on tree seedling type (coniferous or broad-leaved), species, seedling development stage, and seedling fraction (shoot or root). For two conifers (*Picea abies* and *Pinus sylvestris*) soon after germination (≤40 days), more seedling growth was related to a lower ratio of red-to-far-red (R:FR) light. As growth continued to 120 days, spectra with a greater complement of blue light yielded more growth. Roots showed more plasticity to light spectra than shoots. In general for the evergreen broad-leaved *Quercus ilex*, spectra with additional R:FR than for conifers yielded more growth in the first 57 days. Subsequently as seedlings grew, shoot growth appeared to be influenced less by light source than roots, with root length showing the greatest responses. Our results suggest that manipulating light spectra to foster desired seedling traits may be another tool for use in the production of high-quality seedlings as defined through the Target Plant Concept. Such seedlings are needed for restoration of the two billion hectares of degraded forestland, especially on harsh sites such as those found in the Mediterranean region, and to sequester carbon to mitigate climate change.

ARTICLE HISTORY
Received 27 November 2017
Accepted 11 January 2018

KEYWORDS
Photomorphological traits; high-quality seedling; Mediterranean region; environmental stresses; Target Plant Concept; *Picea abies*; *Pinus sylvestris*; *Quercus ilex*

1. Introduction

Changes in environmental conditions, mainly limited by light and water availability, are thought to directly affect plant growth and field performance (Niinemets 2010; Yamori et al. 2010; Montagnoli et al. 2012, 2014; Aronne et al. 2017). Plant growth and developmental processes are regulated by changes in light quality (color, wavelength), quantity (fluence rate), and photoperiod (duration of illumination) (Folta and Childers 2008; Zuchi and Astolfi 2012; Ouzounis et al. 2015). Seedlings might be affected more by light quality than older plants as they are more susceptible to environmental stresses (Chiatante et al. 2007, 2015; Di Iorio et al. 2011). Plants respond to irradiance changes through photomorphogenic responses leading to an adjustment of growth rate and traits (plant productivity, flowering, plant stature, growth habits) and conferring a fitness advantage allowing an individual to maximize the potential of the light environment for photosynthesis (Casal and Yanovsky 2005; Devlin et al. 2007; Folta and Childers 2008; Ariz et al. 2010).

Light sources such as fluorescent, metal halide, high-pressure sodium (HPS), and incandescent lamps are used as conventional light sources for growing plants in indoor cultivation (Jeong et al. 2012; Ouzounis et al. 2015). Although these light sources, especially HPS, are the most commonly used lighting system, their emissions, both spectrally and energetically, are far from optimal values for photosynthesis (Heuvelink et al. 2006). Indeed, the most efficient photosynthetic yield occurs in two distinct broad peaks in the blue (400–500 nm) and red (600–700 nm) ranges (McCree 1972). Moreover, photons in the 500–600 nm range are characterized as having low photosynthetic efficiency, while photons in the 700–800 nm range are considered far-red (FR), which is important for shoot elongation in woody plants modulated by the ratio of red-to-far-red (R:FR) (Apostol et al. 2015; Smirnakou et al. 2017).

During the last decades, solid-state lighting using light-emitting diode (LED) technology has arisen as an alternative source of light in greenhouse systems as they exhibit several advantages, such as: longer lifetime (about 100 000 h), smaller size and weight, solid-state construction, lower heat emission, and much less energy consumption than other sources (Bourget 2008; Landis et al. 2013). Additionally, specific wavelengths within a narrow spectral range can be set with LEDs with the aim of precisely tuning spectral quality and light intensity (Heuvelink et al. 2006; Ouzounis et al. 2015). Blue and red LEDs are usually used for plant growth because chlorophyll *a* and *b* absorbance maxima occur at 430, 663 nm and at 453 and 642 nm, respectively (Taiz and Zeiger 2010). In recent years, the use of LEDs as a radiation source for plants has attracted considerable interest because of its vast potential for developmental studies as well as for its commercial applications (Bian et al. 2015; Yeh et al. 2015). Thus, the selection of an optimal light source is an essential task in closed plant production systems, defined as a warehouse-like structure covered with opaque thermal insulators, in which ventilation is

CONTACT Antonio Montagnoli antonio.montagnoli@uninsubria.it

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Published online 11 Feb 2018

kept at a minimum, and fully reliant on artificial light sources (Kozai et al. 2006). Despite this importance, morphological effects of different light spectra have been focused solely on vegetables and commercially important flowering plants (Jeong et al. 2012 and references therein; Ouzounis et al. 2014). With respect to forest tree seedlings, few studies are completed (Astolfi et al. 2012; Jeong et al. 2012; Apostol et al. 2015; Smirnakou et al. 2017), highlighting the need for additional, detailed scientific works, particularly as the need for more seedlings for forest restoration continues to increase.

Worldwide, an estimated two billion ha of forests are degraded (Minnemayer et al. 2011). In addition to anthropogenic alterations of global ecosystems (Foley et al. 2005; Kareiva et al. 2007; Ellis et al. 2013), the anticipated effects of global climate change (Stanisci et al. 2016) suggest the future need for restoration will be even greater (Stanturf et al. 2014) and sites requiring restoration will become increasingly harsher (Oliet and Jacobs 2012). This is true for the Mediterranean region, where during the last century summers have become warmer (+0.8 °C) with less (5%) precipitation (Begni et al. 2001; Gonzalez et al. 2010), resulting in more drought stress (Piñol et al. 1998; De Luis et al. 2003). As a consequence, Mediterranean forests might undergo a decrease in tree productivity (Faria et al. 1998; Chaves et al. 2002; Pereira et al. 2004, 2007) because of increasing rates of tree mortality (Martínez-Vilalta and Piñol 2002; Lloret et al. 2004) and decreasing rates of regeneration because drought hampers reproductive development in mature trees (Moya et al. 2008; Ganatsas et al. 2017) and seedling establishment (Lloret et al. 2004) while increasing seedling mortality (Neilson and Wullstein 1985). Furthermore, hot and dry summers promote forest fires (Sanchez-Humanes and Espelta 2011), exacerbated in terms of frequency and severity by continuing changes to climate (Vilagrosa et al. 2003; Giorgi and Lionello 2008). *Pinus sylvestris*, in particular, shows no regeneration after crown fires (Pausas et al. 2007). Thus, international efforts and strategies are needed toward restoring degraded forest ecosystems (Chazdon 2008; Ciccarese et al. 2012; Stanturf et al. 2014).

Restoration strategies can be achieved by many techniques and tools (Stanturf et al. 2014) but restoration using container seedlings is a cost-effective alternative when the planting season is to be extended or adverse sites are to be planted (Brissette et al. 1991; Luoranen et al. 2005, 2006; Stanturf et al. 2014). For example, seedlings with more roots have a greater capability for water and nutrient absorption and transport and may have better survival potential and establishment after outplanting (Davis and Jacobs 2005; Tsakaldimi et al. 2009; Pinto et al. 2011, 2012, 2016). Moreover, container seedlings suffer less root disturbance during harvesting and shipping than bareroot stock, which often affords them an advantage (Mathers et al. 2007; Wilson et al. 2007), especially when outplanting conditions are more stressful (Barnett and McGilvray 1993). Within this framework, high-quality, container seedlings are produced to meet desired characteristics for outplanting under specified conditions (Brissette et al. 1991; Wang et al. 2007; Landis et al. 2010; Cole et al. 2011; Dumroese et al. 2016), which yields greater survival and growth after outplanting (Wilson and Jacobs 2006).

In container seedling production, artificial light sources are widely used in greenhouse to manipulate lighting and maximize crop response (Sysoeva et al. 2010; Apostol et al. 2015). Low light intensity for photoperiod extension is a common practice (Apostol et al. 2015), especially important for growing higher latitude seed sources and high-elevation ecotypes at lower latitudes (Landis et al. 1992; Omi and Eggleston 1993). Artificial lights are also used when ambient photosynthetically active radiation (PAR; wavelengths from 400 to 700 nm) is a limiting factor (Landis et al. 1992). Despite these uses, relatively little empirical work has been done with forest species. Thus, light quality and quantity remain an important challenge and area requiring more work, especially on the effect of different light properties on early seedling development. Some studies have demonstrated that at an early stage (i.e. 30 days after germination) endogenous factors, such as hormones and relative genes expression influence growth more than light because of species-specific growth habits (Pinfield and Stobart 1972; Lavender 1984; Bentsinka and Koornneef 2008; Chen et al. 2008; Baskin and Baskin 2014). In contrast, Smirnakou et al. (2017) showed that exposing *Quercus ithaburensis* var. *macrolepis* seedlings to LED radiation for just the first month after germination produced photomorphogenic traits that persisted for more than year.

Thus, our study objective was to test the effects of different light spectra provided by LEDs and a fluorescent reference (control) on the morphological traits of seedlings of three different tree species (*Picea abies* L. and *Pinus sylvestris* L. [coniferous], and *Quercus ilex* L. [broad-leaved]) at early and later growth stages. We chose these species because they have important ecological and economic values across a wide altitudinal and latitudinal range in the Mediterranean region, and in the case of *P. abies* and *P. sylvestris*, importance throughout Europe as well. *Picea abies* is the most important forest tree species throughout Central Europe (Schelhaas et al. 2003) with a natural range extending from montane to subalpine environments (Caudullo et al. 2016; Compostella and Caccianiga 2016). Favored by modern forestry because it grows fast and generates high volumes of valuable wood, *P. abies* is often cultivated in large-scale plantations (Caudullo et al. 2016). *Pinus sylvestris* has a wide distribution range encompassing a broad range of climatic conditions, from severe cold winters of northern Siberia to the Mediterranean climate of southern Spain (Matías and Jump 2012). This species constitutes approximately 20% of the commercial, timber-producing forest area in all member states of the European Union. *Quercus ilex* grows well on a wide variety of soils under different Mediterranean climates, from semi-arid to very humid, and from warm coastal areas to very cold high altitudes (de Rigo and Caudullo 2016). Often managed as coppices for the production of firewood and charcoal (Marignani et al. 2017), its more-structured, high forests provide recreational watershed and functions and, in the case of the Iberian Peninsula, are managed as savannas where the large, isolated trees emerging from the grassland provide fodder and shade for livestock, firewood, and refuge and breeding sites for a large number of vertebrates (de Rigo and Caudullo 2016).

2. Materials and methods

To meet our study objectives, we grew three species (*Picea abies, Pinus sylvestris, Quercus ilex*,) under five spectra (four LED, one fluorescent) and assessed seedling responses in the short- (40–57 days) and long- (120 days) term. A single growth room used to allow for strict control of environmental factors (uniform conditions across spectra) during seedling development.

2.1. Growth room characteristics

We used a single, 4-m wide, 3-m deep, and 2.2-m tall growth room at the University of Insubria, Varese, Italy. Using reflective white panels, we subdivided the room into five sections. Each section was illuminated with either fluorescent light (Fluora T8 (OSRAM); LEDVANCE GmbH; Garching, Germany) as reference (control) light, or one of four different, commercially available LED light spectra developed specifically for horticultural purposes (Valoya Oy; Helsinki, Finland): AP67, AP67-3L, G2, and NS1 (Table 1). Each section had a steel table with 50-mm tall edges. Light intensity yielded approximately 150 µmol m^{-2} s^{-1} (Light Meter HD2302.0; Delta Ohm; Caselle di Selvazzano, Italy) at 50 mm above the table surface.

2.2. Plant material and growing conditions

Seeds were provided by the National Forest Service (National Center for Study and Conservation of Forest Biodiversity–Peri, Italy). We sowed *P. abies* (Val di Fiemme, Trentino, 1200 m a.s.l) and *P. sylvestris* (Val Isarco, Trentino, 700 m a.s.l.) seeds without any treatment but *Q. ilex* (Torri del Benaco-Garda, Verona, m 300 a.s.l.) acorns were soaked 24 h in tap water to hydrate them before sowing. To ensure 100% occupancy after germination, we sowed multiple conifer seeds and removed all but one seedling in each cell soon after germination was complete. In the case of *Q. ilex* we sowed germinants. We used individual cells of mini-plug plastic container trays (QPD 104VW QuickPot; HerkuPlast-Kubern GmbH; Ering, Germany; 104 square cells 33 mm wide × 45 mm deep; 27 cc when filled to 40 mm), containing 100% sterile, stabilized peat growing medium (Preforma VECO3; Jiffy Products International; Moerdijk, Netherlands). A single tray of each species x spectra was sown. Trays of each species were randomly assigned to each spectra. The mini-plugs had basal drainage holes that allowed subirrigation every 3 days during germination and then every 2 days to maintain soil water content until harvest. Once transplanted into 3.5 L containers, irrigation frequency was determined gravimetrically: we watered the soil medium until saturation, measured an initial mass, and then irrigated back to saturation when container mass reached 60% of initial mass (Dumroese et al. 2015). Temperature and air humidity were kept at 22 °C and 60–70%, respectively. No fertilizer was added.

Table 1. Spectral distribution and red:far-red of the four LED light treatments and the fluorescent (control) light.

	Continuous spectrum wave length (nm)				
	400–500	500–600	600–700	700–800	
Light source	(%)				R:FR
LED					
AP67	13.8	15.1	53.0	18.1	2.7
AP67-3L	11.9	19.3	60.5	8.3	5.6
G2	7.7	2.4	64.4	25.5	2.5
NS1	20.2	38.9	35.7	5.2	8.2
Fluorescent					
Fluora T8	34.8	24.1	36.7	4.4	5.7

2.3. Seedling sampling

Seedlings were sampled for short-term effects either 40 (*P. abies* and *P. sylvestris*) or 57 (*Q. ilex*) days after germination. After randomly selecting eight seedlings per tray, we destructively sampled the remaining 96 plants for morphological traits described below. The eight seedlings in each species × spectra combination were then transplanted into 3.5 L pots (filled with 1:2:1 (v:v:v) mixture of peat, silica sand, and bark humus), returned to their respective spectra and grown until 120 days after germination, and then destructively sampled.

2.4. Morphological measurements

We measured seedling height (cm) from the base of the seedling to the highest leaf or needle. Leaf area for each seedling was measured by scanning and analysis using WinRHIZO software (Pro V. 2007d; Regent Instruments Inc.; Ville de Québec, Québec, Canada) and summed to obtain total leaf area (cm^2). After gently removing each seedling from the medium, roots were rinsed repeatedly with running tap water and scanned (400 dpi) with a calibrated flatbed scanner coupled to a lighting system for image acquisition (Expression 10000 XL; Epson America Inc.; Long Beach, California, USA). Root length (cm) was obtained measuring taproot and lateral roots by WinRhizo. In particular, very-fine root length (cm) included all roots with a diameter less than the largest diameter measured for the first-order later roots ($d < 0.35$ mm for *P. abies* and *P. sylvestris*; $d < 0.25$ mm for *Q. ilex*). Afterward, shoot (stem and leaves) and root (taproot and laterals) biomass (g) was calculated as dry mass after oven drying 52 h at 75 °C. Finally, we calculated the ratio of root-to-shoot biomass (R:S).

2.5. Statistical analysis

Morphological data were square-root or log-transformed to ensure normal distribution and equal variance for the use of parametric statistics. One-way ANOVA and the least significant difference (LSD) pairwise multiple comparison tests were performed among light sources, within each sampling time, and for each species. Statistical analysis was performed with SPSS software package version 17 (SPSS Inc.; Chicago, Illinois, USA).

3. Results

3.1. Picea abies

Seedlings grown under fluorescent lamps (control) had significantly more shoot biomass than all other spectra 40 days after germination (hereafter simply "40 days"); seedlings grown with NS1 were significantly smaller than those grown with AP67, AP67-3L, and G2, which were not significantly different among themselves (Figure 1a). When measured 120 days after germination (hereafter simply "120 days"), shoot biomass was greatest for AP67, G2, and the control, with AP67-3L being intermediate in response, and NS1 still yielding the smallest seedlings (Figure 1b). Seedlings grown with AP67, AP67-3L, and NS1 were tallest at 40 days, whereas control seedlings were shortest (Figure 1c). No differences in height were detected at 120 days (Figure 1d). For total leaf area, only G2 and NS1 were significantly different

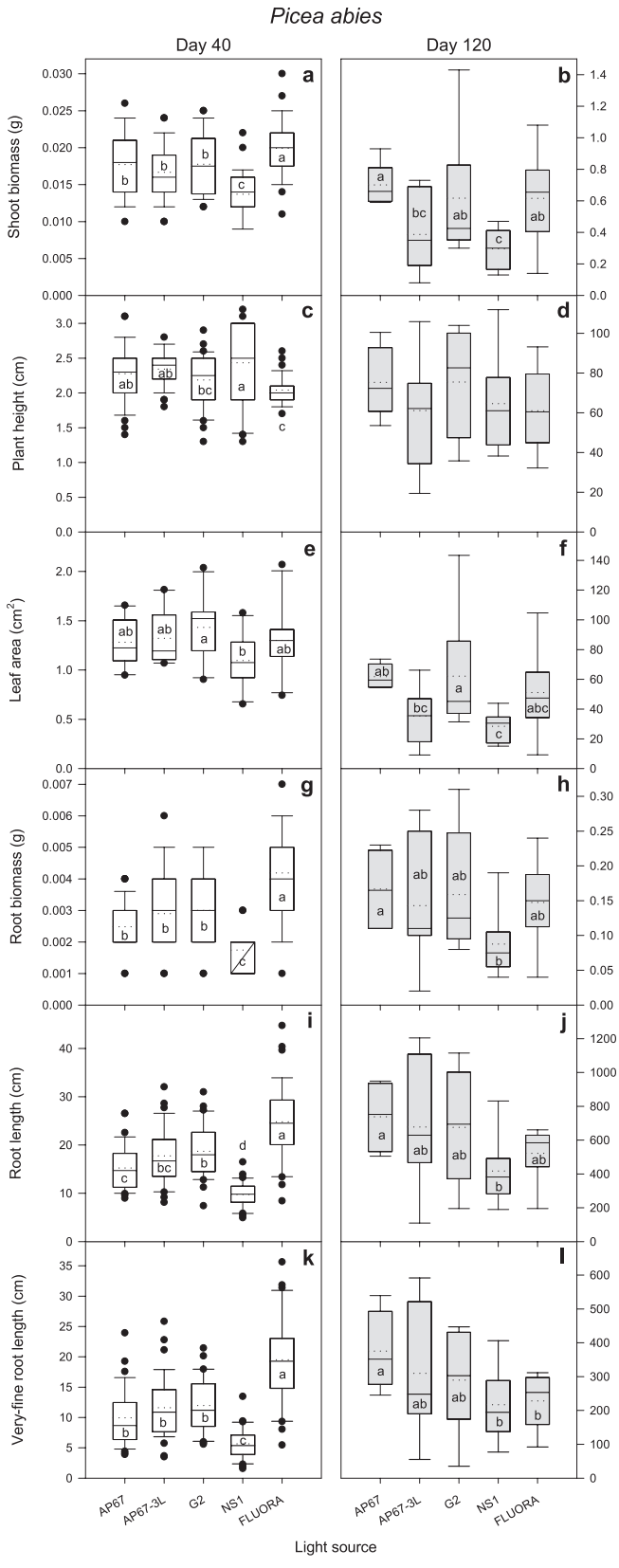

Figure 1. Short- (40 days after germination; $n = 96$) and long- (120 days after germination; $n = 8$) term morphological attributes of *Picea abies* seedlings grown under one fluorescent and four LED spectra.

Notes: Vertical boxes represent approximately 50% of the observations and lines extending from each box are the upper and lower 25% of the distribution. Outliers are represented as solid dots (•). The solid, horizontal line in the center of each box is the median value, whereas the dotted horizontal line is the mean. Data with different letters are statistically different ($p < 0.05$).

at 40 days (Figure 1e), and this was observed again at 120 days (Figure 1f).

Root biomass followed the same general trends as those observed for shoot biomass: at 40 days the control yielded significantly more biomass than NS1 with all other spectra intermediate (Figure 1g), and at 120 days, AP67 yielded more than NS1 with the other spectra intermediate in response (Figure 1h). Root length and very-fine root length measured at 40 days (Figure 1i and k) and 120 days (Figure 1j and l) followed the same pattern as that observed for root biomass. R:S measured at 40 days also followed the same pattern observed for shoot biomass and root biomass (Table 2), but at 120 days, AP67-3L had a significantly higher ratio than cohorts grown under AP67, G2, or control spectra.

3.2. *Pinus sylvestris*

When measured at 40 days, pine seedlings grown under G2 and control spectra had significantly more shoot biomass than those grown with AP67 and AP67-3L, which in turn had significantly more biomass than NS1 seedlings (Figure 2a). At 120 days, AP67 seedlings had significantly more biomass than AP67-3L, G2, and control seedlings, which had more biomass than the NS1 cohort (Figure 2b). Control seedlings were significantly shorter at 40 days than NS1 seedlings, which were significantly shorter than AP67-3L and G2 seedlings (Figure 2c). AP67 seedlings were similar in height to AP67, G2, and NS1 seedlings (Figure 2c). At 120 days, AP67 and AP67-3L seedlings were similar in height, and significantly taller than NS1 and control seedlings, which were also similar in height. The response of seedlings to G2 was intermediate (Figure 2d). We noted no differences among treatments for total leaf area at 40 days (Figure 2e), but at 120 days, AP67 had significantly more total leaf area than NS1; the other treatments were intermediate in their response (Figure 2f).

Control seedlings had significantly more root biomass at 40 days than did G2 seedlings, which had significantly more biomass than AP67 and AP67-3L seedlings, which were significantly heavier than NS1 seedlings (Figure 2g). At 120 days, AP67 seedlings had the most root biomass, significantly more than all other spectra. NS1 had the least root biomass. The control was intermediate between NS1 seedlings and AP67-3L and G2 seedlings (Figure 2h). Root length and very-fine root length measured at 40 days (Figure 2i and k) and 120 days (Figure 2j and l) followed the same pattern as that observed for root biomass. LEDs generated the same R:S values at 40 days, significantly smaller than the control, but this effect was not detected at 120 days (Table 2).

3.3. *Quercus ilex*

Seedlings grown under AP67 and AP67-3L had significantly more shoot biomass measured 57 days (Figure 3a) after germination (hereafter simply "57 days") than did seedlings grown with the other spectra, but this effect dissipated by 120 days (Figure 3b). Similarly, height measured at 57 days was significantly greater for seedlings grown under AP67 and AP67-3L than for control seedlings, with GS and NS1 being intermediate in response (Figure 3c). By 120 days, G2 seedlings were significantly taller than their AP67 cohorts. The other spectra were not significantly different among themselves or with the other

Table 2. Short- (40–57 days after germination; $n = 96$) and long- (120 days after germination; $n = 8$) term root-to-shoot ratios (means ± SE) of *Picea abies, Pinus sylvestris,* and *Quercus ilex* grown under one fluorescent (control) and four LED spectra.

	Picea abies		*Pinus sylvestris*		*Quercus ilex*	
	Sampling time (d)		Sampling time (d)		Sampling time (d)	
Light source	40	120	40	120	57	120
LED						
AP67	0.14 ± 0.007 cd	0.23 ± 0.02 b	0.18 ± 0.006 b	0.33 ± 0.04 a	0.44 ± 0.04 b	0.49 ± 0.05 a
AP67-3L	0.17 ± 0.009 b	0.37 ± 0.05 a	0.17 ± 0.005 b	0.30 ± 0.01 a	0.64 ± 0.03 ab	0.43 ± 0.06 a
G2	0.17 ± 0.010 bc	0.27 ± 0.02 b	0.18 ± 0.006 b	0.33 ± 0.05 a	0.67 ± 0.09 a	0.27 ± 0.04 b
NS1	0.13 ± 0.006 d	0.29 ± 0.02 ab	0.16 ± 0.009 b	0.29 ± 0.03 a	0.73 ± 0.09 a	0.39 ± 0.05 ab
Fluorescent						
Fluora T8	0.21 ± 0.010 a	0.25 ± 0.02 b	0.20 ± 0.008 a	0.30 ± 0.02 a	0.64 ± 0.07 a	0.37 ± 0.06 ab

Notes: Different letters within sampling time for each species indicate significant differences among light treatments at $p < 0.05$.

treatments (Figure 3d). At 57 days (Figure 3e), seedlings grown with AP67-3L had significantly more total leaf area than G2 seedlings; the other treatments were not significantly different than either AP67-3L or G2 and by 120 days (Figure 3f), we detected no significant differences.

Seedling grown under AP67-3L and NS1 had similar root biomass, but AP67-3L seedlings had significantly more root biomass than the other three spectra (Figure 3g). Similar to shoot biomass, this effect dissipated by 120 days (Figure 3h). At 57 days, seedlings grown with AP67-3L had significantly more total root length than G2 seedlings; the other treatments were not significantly different than either AP67-3L or G2 (Figure 3i). This same pattern was observed at 120 days (Figure 3j). The control spectra produced the greatest very-fine root length at 57 days, significantly more than NS1, which had significantly more than the remaining three spectra (Figure 3k). At 120 days, seedlings grown with AP67-3L had significantly more very-fine root length than G2 seedlings, but the other treatments were not significantly different than either AP67-3L or G2 (Figure 3l). Seedlings grown under AP67 had significantly less R:S measured at 57 days than did seedlings grown under G2, NS1, and the control. AP67-3L was intermediate in response (Table 2). By day 120, AP67 and AP67-3L had significantly greater R:S than G2; the other spectra were intermediate (Table 2).

4. Discussion

Our results show that plant response to light quality is related to plant type. Indeed, we noted differences between *P. abies* and *P. sylvestris*, as well as differences between these two conifers and the evergreen broad-leaved *Q. ilex*. Furthermore, the magnitude of these differences also changed with time.

For the conifers in the short-term, more growth, and especially root growth, was observed under the control light (fluorescent), having a medium R:FR value (5.7) among the spectra tested. Among the LED lights, the best growth, in general, was associated with an even lower R:FR (2.5–2.7), which is more than double that found in nature (1.15); G2 yielded the most growth.

This pattern changed, however, as growth continued in the long-term. At 120 days, the highest values were associated with AP67 that had the same R:FR ratio (2.7) but with nearly double the blue light of G2, especially for *P. sylvestris*. In nature, a low R:FR is an indication of shading by other plants and stimulates elongation growth as an adaptive advantage for competition (Franklin and Whitelam 2005). Thus, in response to low R:FR, more plant growth has been observed with several species regardless of their successional status (i.e. early or late) (Mølmann et al. 2006). Moreover, addition of blue light significantly delays bud set (allows continued shoot elongation) in *Picea abies* seedlings (Mølmann et al. 2006) but reductions in blue light, such as that caused by shade competition in dense community, can also stimulate growth (Franklin and Whitelam 2005). Because blue light amplifies responsiveness to phytochrome far-red (Pfr; Drumm-Herrel 1984), we hypothesize that the greater long-term growth of AP67 seedlings compared to G2 seedlings, both of which had similar R:FR, was because of higher efficiency of the Pfr in AP67 seedlings. The increased growth we observed with AP67 concurs with Smirnakou et al. (2015) for *Pinus sylvestris* and *Abies borisii-regis*.

Although total growth of *P. abies* measured at 120 days varied little among light sources, rate of growth was higher under LEDs than the control; that is, significant differences in growth observed at 40 days disappeared by 120 days. Roots responded more to differences in light spectra than did shoots, especially for *P. sylvestris*. Furthermore, because more root development occurred relative to shoots in the long-term, coniferous species seemed to invest carbohydrates toward the root system only at the long-term, thus privileging the early development of the above ground fraction. This finding is similar to that described by Kaakinen et al. (2004) for *Picea abies* seedlings. Moreover, although variation in the magnitude of R:S increment can be related to the soil nutrient concentration (Kaakinen et al. 2004), this pattern might also be attributable to the epigeal germination habit of the coniferous species. In this case, cotyledons are lifted above the soil by hypocotyl elongation, favoring shoot development (Ng 1978).

For *Quercus ilex*, in general, AP67-3L with a medium R:FR, yielded more growth in the short-term, and, unlike the conifers, had a reduced response to G2 and fluorescent light, similar to the results of Smirnakou et al. (2017) with *Q. ithaburensis* var. *macrolepis*. Furthermore, at the later developmental stage as seedling size became more variable, light source appeared less important for above ground portions, whereas LEDs with medium R:FR (AP67-3L), had a stronger effect on root morphology. In particular, root biomass remained unaffected while root length was higher for both fine and very-fine classes. This infers that AP67-3L seedlings had a longer and thinner root system than seedlings grown under the other light sources. Moreover, in our experiment, *Q. ilex* had a greater R:S in the short-term than in the

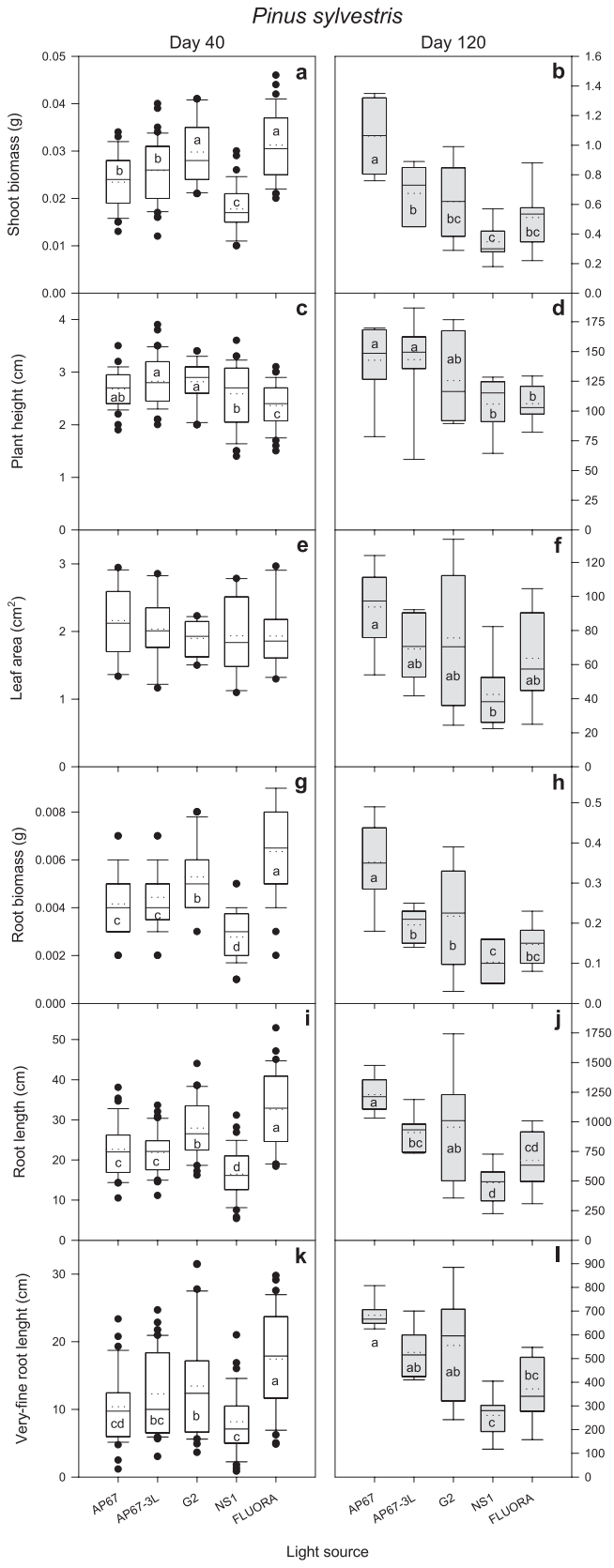

Figure 2. Short- (40 days after germination; n = 96) and long- (120 days after germination; n = 8) term morphological attributes of *Pinus sylvestris* seedlings grown under one fluorescent and four LED spectra.

Notes: Vertical boxes represent approximately 50% of the observations and lines extending from each box are the upper and lower 25% of the distribution. Outliers are represented as solid dots (•). The solid, horizontal line in the center of each box is the median value, whereas the dotted horizontal line is the mean. Data with different letters are statistically different ($p < 0.05$).

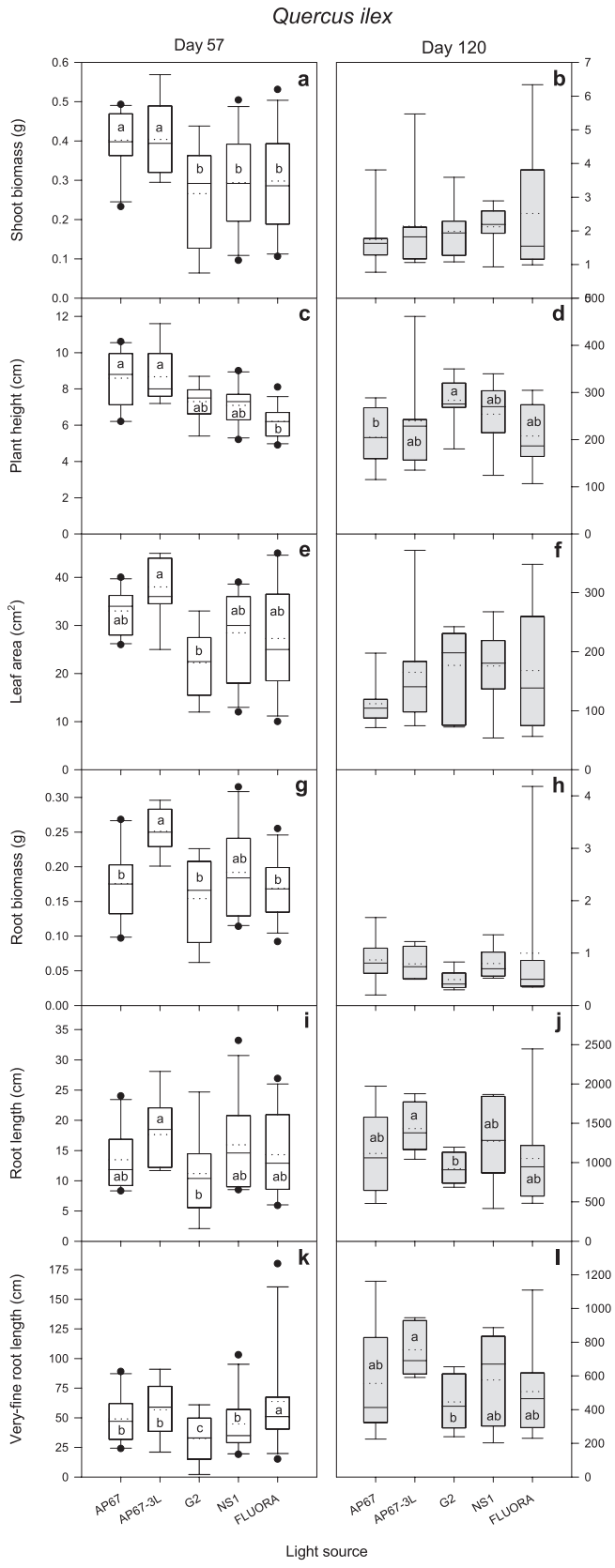

Figure 3. Short- (40 days after germination; n = 96) and long- (120 days after germination; n = 8) term morphological attributes of *Quercus ilex* seedlings grown under one fluorescent and four LED spectra.

Notes: Vertical boxes represent approximately 50% of the observations and lines extending from each box are the upper and lower 25% of the distribution. Outliers are represented as solid dots (•). The solid, horizontal line in the center of each box is the median value, whereas the dotted horizontal line is the mean. Data with different letters are statistically different ($p < 0.05$).

long-term, thus, shifting carbon allocation to the aboveground part only at the later developmental stage. As plant growth at this stage of seed development is still depending on endogenous factors (Bentsinka and Koornneef 2008; Baskin and Baskin 2014), the observed pattern is probably attributable to species-specific growth habits (Montagnoli et al. 2016b). Unlike coniferous species, *Quercus* is characterized by a hypogeal germination type where the hypocotyl does not expand, cotyledons remain in the seed at soil surface, and a robust taproot develops (Ng 1978). Thus, a rapid development of the taproot from the hypogeal cotyledons occurs in *Quercus* during germination (Crow 1988), with both organs having a storage function against a variety of stress factors, as well as a "risk avoidance strategy" against early predation (Kabeya and Sakai 2003). These reserves may also provide a greater potential for roots to utilize high light in gaps, particularly during seedling establishment (Paz 2003).

In the present work and in the short-term, *Q. ilex* seedlings showed 10-fold higher values for all morphological traits analyzed in comparison with conifers species. Modrzyński et al. (2015) also observed that seedlings arising from larger seeds have a greater biomass with a higher potential to survive compared to small-seeded species. In our study, this effect was dissipating in the long-term, highlighting the importance of investigating seedling development at different developmental stages for detecting early variation in development, which may give important insight into the moment when seedlings become independent of seed reserves (Modrzyński et al. 2015 and references therein).

Planting trees and/or encouraging natural regeneration of forests have large potential to sequester carbon (Sample 2017) and is considered the best natural solution to climate change (Griscom et al. 2017). Compared to traditional post-harvest reforestation efforts, these proposed planting efforts are more akin to forest restoration activities that pose greater challenges to success (Stanturf et al. 2014), particularly because harsher site conditions are involved (Oliet and Jacobs 2012). For many sites, outplanting nursery-grown seedlings will be necessary. To be successful, such planting stock must be produced in such a way as to overcome the limitations of the outplanting site; this process relies on the Target Plant Concept (Dumroese et al. 2016) through which nursery managers manipulate seedling growth to achieve desired morphological and physiological specifications. This is especially true in the Mediterranean region where harsh planting sites are common (Vallejo et al. 2000). For example, in a recent paper, Montagnoli et al. (2016a) highlighted how root morphology of different *Quercus* species, naturally coexisting in south Italy and undergoing drought stress, can provide important insight for implementing assisted migration, a useful restoration strategy to mitigate changes in climate (Williams and Dumroese 2013; Leverkus et al. 2015). Our data suggests that spectral manipulation may be another means to manipulate seedling growth to achieve desired plant characteristics identified through application of the Target Plant Concept.

A conundrum of nursery managers growing seedlings for reforestation to combat climate change and other environmental degradation is how to produce those seedlings, while minimizing the environmental impacts of production. Our work concurs with others that reforestation seedlings grown with LEDs have similar or greater amounts of growth compared to traditional light sources, such as fluorescent or HPS (Astolfi et al. 2012; Apostol et al. 2015; Smirnakou et al. 2017). Thus, LEDs can be employed and significantly reduce the carbon footprint associated with reforestation nurseries (Apostol et al. 2015), similar to the energy reductions noted in other crop production systems (e.g. Yeh and Chung 2009).

Acknowledgments

We are grateful to O. Argentino, B. Baesso, S. Bonacalza, A. Polzella, and R. Santamaria for assistance with seedling production, to the National Forest Service (National Centre for Study and Conservation of Forest Biodiversity–Peri, Italy) for providing seeds, and to Valoya Oy (Helsinki, Finland) for providing LED lights.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by The European Commission within the Seventh Framework Programme through Project ZEPHYR [grant number 308313]; Università degli Studi dell'Insubria [FAR].

References

Apostol KG, Dumroese RK, Pinto JR, Davis AS. 2015. Response of conifer species from three latitudinal populations to light spectra generated by light-emitting diodes and high-pressure sodium lamps. Can J Forest Res. 45(12): 1711–1719.

Ariz I, Esteban R, García-Plazaola JI, Becerril JM, Aparicio-Tejo PM, Moran JF. 2010. High irradiance induces photoprotective mechanisms and a positive effect on NH^+ stress in *Pisum sativum* L. J Plant Physiol. 167(13): 1038–1045.

Aronne PG, Arena C, De Micco V, Giovanetti M, Buonanno M. 2017. Full light and soil drought constrain plant growth in Mediterranean cliffs: the case of *Primula palinuri*. Plant Biosyst. DOI:10.1080/11263504.2017.1359211.

Astolfi S, Marianello C, Greco S, Bellarosa R. 2012. Preliminary investigation of LED lighting as growth light for seedlings from different tree species in growth chambers. Not Bot Horti Agrobo. 40(2): 31–38.

Barnett JP, McGilvray JM. 1993. Performance of container and bareroot loblolly pine seedlings on bottomlands in South Carolina. South J Appl For. 17(2): 80–83.

Baskin CC, Baskin JM. 2014. Seeds, ecology, biogeography and evolution of dormancy and germination. 2nd ed. San Diego (CA): Academic/Elsevier.

Begni G, Darras S, Hoepffner M, Pesin E, Tourre Y. 2001. The present status of knowledge on global climatic change; its regional aspects and impacts in the Mediterranean region. A scientific and strategic report to Blue Plan. Report MEDIAS/GB/db/2001-200. Toulouse (France): Medias France Groupement pour le développement de la recherche sur l'environnement global notamment dans le bassin Méditerranéen et l'Afrique subtropicale.

Bentsinka L, Koornneef M. 2008. Seed dormancy and germination. Arabidopsis Book. 6: e0119.

Bian Z, Yang QC, Liu WK. 2015. Effects of light quality on the accumulation of phytochemicals in vegetables produced in controlled environments: a review. J Sci Food Agric. 95(5): 869–7877.

Bourget CM. 2008. An introduction to light emitting diodes. HortScience. 43(7): 1944–1946.

Brissette JC, Barnett JP, Landis TD. 1991. Container seedlings. In: Duryea ML, Dougherty PM, editors. Forest regeneration manual. Forestry Sciences. Vol. 36. Dordrecht: Springer; p. 117–141.

Caudullo G, Tinner W, de Rigo D. 2016. *Picea abies* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, Houston Durrant T, Mauri A, editors. European atlas of forest tree species. Luxembourg: Publ. Off. EU; p. e012300+.

Casal JJ, Yanovsky MJ. 2005. Regulation of gene expression by light. Int J Dev Biol. 49(5-6): 501–511.

Chaves MM, Pereira JS, Maroco JP, Rodrigues ML, Ricardo CPP, Osório ML, Carvalho I, Faria T, Pinheiro C. 2002. How plants cope with water stress in the field. Photosynthesis Growth Ann Bot. 89(7): 907–916.

Chazdon RL. 2008. Beyond Deforestation: restoring forests and ecosystem services on degraded lands. Science. 320(5882): 1458–1460.

Chen H, Zhang J, Neff MM, Hong S-W, Zhang H, Deng X-W, Xiong L. 2008. Integration of light and abscisic acid signaling during seed germination and early seedling development. P Natl Acad Sci USA 105(11): 4495–4500.

Chiatante D, Scippa GS, Di Iorio A, De Micco V, Sarnataro M. 2007. Lateral root emission in woody taproots of *Fraxinus ornus* L. Plant Biosyst. 141(2): 204–213.

Chiatante D, Tognetti R, Scippa GS, Congiu T, Baesso B, Terzaghi M, et al. 2015. Interspecific variation in functional traits of oak seedlings (*Quercus ilex*, *Quercus trojana*, *Quercus virgiliana*) grown under artificial drought and fire conditions. J Plant Res. 128(4): 595–611.

Ciccarese L, Mattsson A, Pettenella D. 2012. Ecosystem services from forest restoration: thinking ahead. New Forest. 43(5-6): 543–560.

Cole RJ, Holl KD, Keene C, Zahawi RA. 2011. Direct seeding of late-successional trees to restore tropical montane forest. Forest Ecol Manag. 261(10): 1590–1597.

Compostella C, Caccianiga M. 2016. A comparison between different treeline types shows contrasting responses to climate fluctuations. Plant Biosyst. 151(3): 436–449.

Crow TR.1988. Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*) – a review. Forest Sci. 34(1): 19–40.

Davis AS, Jacobs DF. 2005. Quantifying root system quality of nursery seedlings and relationship to outplanting performance. New Forest. 30(2-3): 295–311.

Devlin PF, Christie JM, Terry MJ. 2007. Many hands make light work. J Exp Bot. 58(12): 3071–3077.

Drumm-Herrel H. 1984. Blue/UV light effect on anthocyanin synthesis. In: Senger H, editor. Blue light effects in biological systems. Berlin Heidelber: Springer-Verlag; p. 375–383.

Dumroese RK, Landis TD, Pinto JR, Haase DL, Wilkinson KM, Davis AS. 2016. Meeting forest restoration challenges: using the target plant concept. Reforesta. 1: 37–52.

Dumroese RK, Montville ME, Pinto JR. 2015. Using container weights to determine irrigation needs: a simple method. Native Plants J. 16(1): 67–71.

Ellis EC, Kaplan JO, Fuller DQ, Vavrus S, Klein Goldewijk K, Verburg PH. 2013. Used planet: a global history. P Natl Acad Sci USA 110(20): 7978–7985.

Faria T, Silvério D, Breia E, Cabral R, Abadia A, Abadia J, Pereira JS, Chaves MM. 1998. Differences in the response of carbon assimilation to summer stress (water deficits, high light and temperature) in four Mediterranean tree species. Physiol Plant. 102(3): 419–428.

Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK, et al. 2005. Global consequences of land use. Science. 309(5734): 570–574.

Folta KM, Childers KS. 2008. Light as a growth regulator: controlling plant biology with narrow-bandwidth solid-state lighting systems. HortScience. 43(7): 1957–1964.

Franklin KA, Whitelam GC. 2005. Phytochromes and shade-avoidance responses in plants. Ann Bot. 96(2): 169–175.

Ganatsas P, Tsakaldimi M, Zarkadi P, Stergiou D. 2017. Intraspecific differences in the response to drying of *Quercus ithaburensis* acorns. Plant Biosyst. 151(5): 878–886.

Giorgi F, Lionello P. 2008. Climate change projections for the Mediterranean region. Global Planet Change. 63(2): 90–104.

Gonzalez P, Neilson RP, Lenihan JM, Drapek RJ. 2010. Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change. Global Ecol Biogeog. 19(6): 755–768.

Griscom BW, Adams J, Ellis PW, Houghton RA, Lomax G, Miteva DA, Schlesinger WH, Shoch D, Siikamäki JV, Smith P, et al. 2017. Natural climate solutions. P Natl Acad Sci USA. [accessed 2017 Oct 10]:[6 p.]. http://www.pnas.org/content/early/2017/10/11/1710465114.full.pdf. DOI:10.1073/pnas.1710465114.

Heuvelink E, Bakker MJ, Hogendonk L, Janse J, Kaarsemaker R, Maaswinkel R. 2006. Horticultural lighting in the Netherlands: new developments. Acta Horticulturae. 711: 25–33.

Di Iorio A, Montagnoli A, Scippa GS, Chiatante D. 2011. Fine root growth of *Quercus pubescens* seedlings after drought stress and fire disturbance. Environ Exp Bot. 74: 272–279.

Jeong SW, Park S, Jin JS, Seo ON, Kim G-S, Kim Y-H, Bae H, Lee G, Kim ST, Lee WS, et al. 2012. Influences of four different light-emitting diode lights on flowering and polyphenol variations in the leaves of chrysanthemum (*Chrysanthemum morifolium*). J Agric Food Chem. 60(39): 9793–9800.

Kaakinen S, Jolkkonen A, Iivonen S, Vapaavuori E. 2004. Growth, allocation and tissue chemistry of *Picea abies* seedlings affected by nutrient supply during the second growing season. Tree Physiol. 24(6): 707–719.

Kabeya D, Sakai S. 2003. The role of roots and cotyledons as storage organs in early stages of establishment in *Quercus crispula*: a quantitative analysis of the nonstructural carbohydrate in cotyledons and roots. Ann Bot. 92(4): 537–545.

Kareiva P, Watts S, McDonald R, Boucher T. 2007. Domesticated nature: shaping landscapes and ecosystems for human welfare. Science. 316(5833): 1866–1869.

Kozai T, Ohyama K, Chun C. 2006. Commercialized closed systems with artificial lighting for plant production. Acta Horticulturae 711(711): 61–70.

Landis TD, Dumroese RK, Haase DL. 2010. The container tree nursery manual. Vol. 7, Seedling processing, storage, and outplanting. Agriculture Handbook 674. Washington (DC): USDA Forest Service.

Landis TD, Pinto JR, Dumroese RK. 2013. Light emitting diodes (LED): applications in forest and native plant nurseries. Forest Nursery Notes. 33(2): 5–13.

Landis TD, Tinus RW, McDonald SE, Barnett JP. 1992. The container tree nursery manual. Vol. 3, Atmospheric environment. Agriculture Handbook 674. Washington (DC): USDA Forest Service.

Lavender DP. 1984. Plant physiology and nursery environment: interactions affecting seedling growth. In: Duryea ML, Landis TD, editors. Forest nursery manual: production of bareroot seedlings. Corvallis: Martinus Niihoff/Dr. W Iunk Publishers, The Hague/Boston/Lancaster for Forest Research Laboratory, Oregon State University; p. 133–141.

Leverkus AB, Castro J, Delgado-Capel MJ, Molinas-González C, Pulgar M, Marañón-Jiménez S, Delgado-Huertas A, Querejet JI. 2015. Restoring for the present or restoring for the future: enhanced performance of two sympatric oaks (*Quercus ilex* and *Quercus pyrenaica*) above the current forest limit. Restor Ecol. 23(6): 936–946.

Lloret F, Peñuelas J, Ogaya R. 2004. Establishment of co-existing Mediterranean tree species under a varying soil moisture regime. J Veg Sci. 15(2): 237–244.

Luoranen J, Rikala R, Konttinen K, Smolander H. 2005. Extending the planting period of dormant and growing Norway spruce container seedlings to early summer. Silva Fenn. 39(4): 481–496.

Luoranen J, Rikala R, Konttinen K, Smolander H. 2006. Summer planting of *Picea abies* container-grown seedlings: Effects of planting date on survival, height growth and root egress. Forest Ecol Manag. 237(1-3): 534–544.

De Luis M, Gonzalez-Hidalgo JC, Raventos J. 2003. Effects of fire and torrential rainfall on erosion in a Mediterranean gorse community. Land Degrad Dev. 14(2): 203–213.

Marignani M, Chiarucci A, Sadori L, Mercuri AM. 2017. Natural and human impact in Mediterranean landscapes: An intriguing puzzle or only a question of time? Plant Biosyst. 151(5): 900–905.

Martínez-Vilalta J, Piñol J. 2002. Drought-induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. Forest Ecol Manag. 161(1-3): 247–256.

Mathers HM, Lowe SB, Scagel C, Struve DK, Case LT. 2007. Abiotic factors influencing root growth of woody nursery plants in containers. HortTechnol. 17(2): 151–162.

Matías L, Jump AJ. 2012. Interactions between growth, demography and biotic interactions in determining species range limits in a warming world: The case of Pinus sylvestris. Forest Ecol Manag. 282(15): 10–22.

McCree kJ. 1972. Action spectrum, absorptance and quantum yield of photosynthesis in crop plants. Agric Meteorol. 9: 191–216.

Minnemayer S, Laestadius L, Sizer N. 2011. A world of opportunity. Washington (DC): World Resource Institute.

Modrzyński J, Chmura DJ, Tjoelker MG. 2015. Seedling growth and biomass allocation in relation to leaf habit and shade tolerance among 10 temperate tree species. Tree Physiol. 35(8): 879–893.

Mølmann JA, Junttila O, Johnsen Ø. 2006. Effects of red, far-red and blue light in maintaining growth in latitudinal populations of Norway spruce (*Picea abies*). Plant Cell Environ. 29(2): 166–172.

Montagnoli A, Di Iorio A, Terzaghi M, Trupiano D, Scippa GS, Chiatante D. 2014. Influence of soil temperature and water content on fine root seasonal growth of European beech natural forest in southern Alps, Italy. Eur J Forest Res. 133(5): 957–968.

Montagnoli A, Terzaghi M, Baesso B, Santamaria R, Scippa GS, Chiatante D. 2016a. Drought and fire stress influence seedling competition in oak forests: fine-root dynamics as indicator of adaptation strategies to climate change. Reforesta. 1: 86–105.

Montagnoli A, Terzaghi M, Di Iorio A, Scippa GS, Chiatante D. 2012. Fine-root morphological and growth traits in a Turkey oak stand in relation to seasonal changes in soil moisture in the southern Apennines, Italy. Ecol Restor. 27(4): 725–733.

Montagnoli A, Terzaghi M, Fulgaro N, Stoew B, Wipenmyr J, Ilver D, Rusu C, Scippa GS, Chiatante D. 2016b. Non-destructive phenotypic analysis of early stage tree seedling growth using an automated stereovision imaging method. Front Plant Sci. 7: 1644.

Moya D, Espelta JM, Lopez-Serrano FR, Eugenio M, De Las Heras J. 2008. Natural post-fire dynamics and serotiny in 10-year-old *Pinus halepensis* Mill. Stands along a geographic gradient. Int J Wildland Fire. 17(2):287–292.

Neilson RP, Wullstein LH. 1985. Comparative drought physiology and biogeography of *Quercus gambelii* and *Quercus turbinella* in relation to seedling drought response and atmospheric flow structure. Am Midl Nat. 114: 259–271.

Ng FSP. 1978. Stategies of establishment in Malayan forest trees. In: Tomlinson PB, Zimmermann MH, editors. Tropical trees as living systems. Cambridge: Cambridge University Press; p. 129–162.

Niinemets Ü. 2010. Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: past stress history, stress interactions, tolerance and acclimation. Forest Ecol Manag. 260(10): 1623–1639.

Oliet JA, Jacobs DF. 2012. Restoring forests: advances in techniques and theory. New Forest. 43(5-6): 535–541.

Omi SK, Eggleston KL. 1993. Photoperiod extension with two types of light sources: effects on growth and development of conifer species. Tree Planters' Notes. 44(3): 105–112.

Ouzounis T, Fretté X, Rosenqvist E, Ottosen C-O. 2014. Spectral effects of supplementary lighting on the secondary metabolites in roses, chrysanthemums, and campanulas. J Plant Physiol. 171(16): 1491–1499.

Ouzounis T, Rosenqvist E, Ottosen C-O. 2015. Spectral effects of artificial light on plant physiology and secondary metabolism: a review. HortScience. 50(8): 1128–1135.

Pausas JG, Llovet J, Rodrigo A, Vallejo R. 2007. Are wildfires a disaster in the Mediterranean basin? – A review. Int J Wildland Fire. 17(6): 713–723.

Paz H. 2003. Root/shoot allocation and root architecture in seedlings: variation among forest sites, microhabitats, and ecological groups. Biotropica. 35(3): 318–332.

Pereira JS, David JS, David TS, Caldeira MC, Chaves MM. 2004. Carbon and water fluxes in Mediterranean-type ecosystems: constraints and adaptations. Prog Bot. 65: 467–498.

Pereira JS, Mateus JA, Aires LM. 2007. Net ecosystem carbon exchange in three contrasting Mediterranean ecosystems. The effect of drought. Biogeosciences. 4(5): 791–802.

Pinfield NJ, Stobart AK. 1972. Hormonal regulation of germination and early seedling development in *Acer pseudoplatanus* (L.). Planta. 104(2): 134–145.

Piñol J, Terradas J, Lloret F. 1998. Climate warming, wildfire hazard, and wildfire occurrence in coastal eastern Spain. Clim Change. 38(3): 345–357.

Pinto JR, Marshall JD, Dumroese RK, Davis AS, Cobos DR. 2011. Establishment and growth of container seedlings for reforestation: a function of stocktype and edaphic conditions. Forest Ecol Manag. 261(11): 1876–1884.

Pinto JR, Marshall JD, Dumroese RK, Davis AS, Cobos DR. 2012. Photosynthetic response, carbon isotopic composition, survival, and growth of three stocktypes under water stress enhanced by vegetative competition. Can J Forest Res. 42(2): 333–344.

Pinto JR, Marshall JD, Dumroese RK, Davis AS, Cobos DR. 2016. Seedling establishment and physiological responses to temporal and spatial soil moisture changes. New Forest. 47: 223–241.

de Rigo D, Caudullo G. 2016. *Quercus ilex* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, Houston Durrant T, Mauri A, editors. European atlas of forest tree species. Luxembourg: Publ. Off.; p. e014bcd.

Sample VA. 2017. Potential for additional carbon sequestration through regeneration of nonstocked forest land in the United States. J Forest. 115(4): 309–318.

Sanchez-Humanes B, Espelta JM. 2011. Increased drought reduces acorn production in *Quercus ilex* coppices: thinning mitigates this effect but only in the short term. Forestry. 84(1): 73–82.

Schelhaas M-J, Nabuurs G-J, Schuck A. 2003. Natural disturbances in the European forests in the 19th and 20th centuries. Glob Change Biol. 9(11): 1620–1633.

Smirnakou S, Ouzounis T, Radoglou K. 2015. Effects of continuous spectrum LEDs used in indoor cultivation of two coniferous species *Pinus sylvestris* L. and *Abies borisii-regis* Mattf. Scand J Forest Res. 32(2):115–122.

Smirnakou S, Ouzounis T, Radoglou K. 2017. Continuous spectrum LEDs promote seedling quality traits and performance of *Quercus ithaburensis* var. *macrolepis*. Front Plant Sci. 8: 188.

Stanisci A, Frate L, Morra Di Cella U, Pelino G, Petey M, Siniscalco C, Carranza ML. 2016. Short-term signals of climate change in Italian summit vegetation: observations at two GLORIA sites. Plant Biosyst. 150(2): 227–235.

Stanturf JA, Palik BJ, Dumroese RK. 2014. Contemporary forest restoration: a review emphasizing function. For Ecol Manag. 331: 292–323.

Sysoeva MI, Markovskaya EF, Shibaeva TG. 2010. Plants under continuous light: a review. Plant Stress. 4(1): 5–17.

Taiz L, Zeiger E. 2010. Plant physiology. 5th ed. Sunderland (MA): Sinauer Associates.

Tsakaldimi M, Tsitsoni T, Ganatsas G, Zagas T. 2009. A comparison of root architecture and shoot morphology between natural regenerated and container seedlings of *Quercus ilex* L. Plant Soil. 324(1–2): 103–113.

Vallejo VR, Serrasolses I, Cortina J, Seva JP, Valdecantos A, Vilagrosa A. 2000. Restoration strategies and actions in Mediterranean degraded lands. In: Enne G, Zanolla C, Peter D, editors. Desertification in Europe: mitigation strategies, land use planning. Luxembourg: Office for Official Publications of the European Communities; p. 221–223.

Vilagrosa A, Bellot J, Vallejo VR, Gil-Pelegrin E. 2003. Cavitation, stomatal conductance, and leaf dieback in seedlings of two co-occurring Mediterranean shrubs during an intense drought. J Exp Bot. 54(390): 2015–2024.

Wang FX, Wang ZY, Leeb JHW. 2007. Acceleration of vegetation succession on eroded land by reforestation in a sub- tropical zone. Ecol Engine. 31(4): 232–241.

Wilson BC, Jacobs DF. 2006. Quality assessment of temperate zone deciduous hardwood seedlings. New Forest. 31(3): 417–433.

Wilson ER, Vitols KC, Park A. 2007. Root characteristics and growth potential of container and bare-root seedlings of red oak (*Quercus rubra* L.) in Ontario, Canada. New. Forest. 34(2): 163–176.

Williams MI, Dumroese RK. 2013. Preparing for climate change: forestry and assisted migration. J Forest. 111(4): 287–297.

Yamori W, Evans JR, Von Caemmerer S. 2010. Effects of growth and measurement light intensities on temperature dependence of CO_2 assimilation rate in tobacco leaves. Plant Cell Environ. 33(3): 332–343.

Yeh N, Chung J-P. 2009. High-brightness LEDs – Energy efficient lighting sources and their potential in indoor plant cultivation. Renew Sust Energ Rev. 13(8): 2175–2180.

Yeh N, Ding TJ, Yeh P. 2015. Light-emitting diodes' light qualities and their corresponding scientific applications. Renew Sustain Energ Rev. 51: 55–61.

Zuchi S, Astolfi S. 2012. Changes in growth irradiance are reflected on H^+ATPase activity of plasma membrane enriched vesicles from maize (*Zea mays* L.) root. J Plant Physiol. 169(1): 50–54.