NRC Research Press

ARTICLE

Response of conifer species from three latitudinal populations to light spectra generated by light-emitting diodes and high-pressure sodium lamps

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Abstract: Light-emitting diode (LED) technology shows promise for supplementing photosynthetically active radiation (PAR) in forest nurseries because of the potential reduction in energy consumption and an ability to supply discrete wavelengths to optimize seedling growth. Our objective was to examine the effects of light spectra supplied by LED and traditional high-pressure sodium (HPS) lamps on growth and physiology of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) seedlings. We used three latitudinal sources for each species: British Columbia (BC), Idaho (ID), and New Mexico (NM). Container seedlings were grown for 17 weeks in the greenhouse under an 18 h photoperiod of ambient solar light supplemented with light delivered from HPS or LED. In general, seedlings grown under LED had significantly greater growth, gas exchange rates, and chlorophyll contents than those seedlings grown under HPS. The growth and physiological responses to supplemental lighting varied greatly among species and seed sources. Generally, LED-grown seedlings from BC had the greatest growth and tissue dry mass followed by ID and NM populations. Compared with HPS, the significant increase in seedling growth and concomitant energy savings with LED (29% energy consumption relative to HPS) demonstrates the promise of using LED as PAR supplemental lighting for container seedling production.

Key words: PAR supplemental lighting, energy savings, gas exchange, light response curve, chlorophyll, container nursery.

Résumé : La technologie des diodes électroluminescentes (DEL) est prometteuse comme complément au rayonnement photosynthétiquement actif (PAR) dans les pépinières forestières à cause de la réduction potentielle de consommation d'énergie et de sa capacité à fournir des longueurs d'onde discrètes pour optimiser la croissance des semis. Notre objectif consistait à étudier les effets des spectres optiques fournis par les DEL et les lampes traditionnelles à vapeur de sodium à haute pression (HPS) sur la croissance et la physiologie des semis de douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) et d'épicéa d'Engelmann (*Picea engelmannii* Parry ex Engelm.). Pour chaque espèce, nous avons utilisé trois provenances le long d'un gradient latitudinal : Colombie-Britannique (CB), Idaho (ID) et Nouveau-Mexique (NM). Les semis en conteneur ont été cultivés pendant 17 semaines en serre avec une photopériode de 18 h de lumière solaire ambiante et une lumière d'appoint produite par des DEL ou des HPS. En général, les semis éclairés avec les DEL avaient une croissance, un taux d'échange gazeux et un contenu en chlorophylle significativement plus élevés que les semis éclairés avec les HPS. La croissance et les réactions physiologiques à l'éclairage d'appoint variaient grandement selon l'espèce et la provenance. Généralement, les semis de la CB éclairés avec les DEL avaient la croissance et la matière sèche des tissus les plus élevées suivis par les populations de l'ID et du NM. Comparativement aux HPS, l'augmentation significative de la croissance des semis et les économies d'énergie concomitantes engendrées par les DEL (29 % de consommation d'énergie par rapport aux HPS) démontrent qu'il est avantageux d'utiliser les DEL comme éclairage PAR d'appoint pour la production de semis en conteneur. [Traduit par la Rédaction]

Mots-clés : éclairage PAR d'appoint, économies d'énergie, échange gazeux, courbe de réponse à la lumière.

Introduction

Supplemental lighting (SL) can be an energy-intensive necessity for nursery production of high-quality native plants and forestry crops when ambient photosynthetically active radiation (PAR; wavelengths from 400 to 700 nm) is limiting. In forest nurseries used to produce container seedlings, SL is generally used two ways: (*i*) at low intensity to extend photoperiod (maintain seedlings in an active growth phase) and (*ii*) at high intensity to accelerate growth rate (Landis et al. 1992). SL to extend photoperiod is commonly used to maintain phytochrome activity, thus preventing early terminal bud formation and failure of seedlings to reach target height (Landis et al. 1992). This is especially critical for photoperiod-sensitive species (long critical daylength requirements) native to high latitudes such as blue spruce (*Picea pungens* Englm.), white spruce (*Picea glauca* (Moench) Voss), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Håbjørg 1972; Arnott 1974; Arnott and Simmons 1985; Tinus 1995). McCreary et al. (1978) reported that a 22 h photoperiod was optimal for preventing early terminal bud formation in Douglas-fir seedlings, but the degree of response varies greatly among species and among seed origins within species. For example, Vaartaja (1959) and Clapham et al. (1998) reported that seeds from lower latitude sources respond less strongly to photoperiod than seeds from higher latitude sources. Although less common in forest nurseries, SL can be used at high intensities for

Received 15 March 2015. Accepted 22 June 2015.

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Can. J. For. Res. **45**: 1711–1719 (2015) dx.doi.org/10.1139/cjfr-2015-0106

long daily durations to increase the daily light integral. Supplement daytime PAR aids seedling production during naturally short or dark days (Arnott and Simmons 1985; Landis et al. 1992; Lascoux et al. 1993; Torres and Lopez 2010).

A wide variety of SL types are used in nurseries to control plant development and manipulate plant quality (Tinus 1995; Bourget 2008). Many forest nurseries use high-intensity discharge lamps such as high-pressure sodium (HPS), because they more efficiently produce light than other traditional lamps (see Landis et al. (1992)). Despite this, the use of HPS requires a huge amount of electrical energy that is, for most forest nurseries, economically impractical. More importantly, however, is that HPS and other high-intensity discharge lamps fail to provide the spectrum that is most efficient for photosynthesis (Bourget 2008; Massa et al. 2008). Although all photons between 400 and 700 nm (PAR) are capable of driving photosynthesis, they vary in their effectiveness. The most efficient photosynthetic yield occurs in two distinct broad peaks in the blue (400 to 500 nm) and red (600 to 700 nm) ranges (McCree 1972); photons in the 500 to 600 nm range are characterized as having low photosynthetic efficiency. Optimally, a lamp that provides the most efficient wavelengths for photosynthesis with less energy consumption would have the potential to improve seedling quality and reduce production costs.

Light-emitting diodes (LEDs) are solid state, robust, very long-lived, energy efficient, and can be manufactured to produce an exact light quality. Thus, LEDs can supply plants with optimum wavelengths for photosynthesis while requiring only a fraction of the electricity used by HPS, the current industry standard (Bourget 2008; Landis et al. 2013). Blue and red LEDs are usually used for plant growth because chlorophyll *a* and *b* (chl *a* and chl *b*, respectively) efficiently absorb blue and red wavelengths; absorbance maxima for chl *a* are 430 and 663 nm whereas those of chl *b* are 453 and 642 nm (Taiz and Zeiger 2010). Shoot elongation in woody plants is also modulated by the ratio of red to far-red (R:FR; FR wavelength, 700 to 800 nm) wavelengths (Gilbert et al. 1995). For example, a mixture of R and FR appeared to be more effective in maintaining growth of Norway spruce (*Picea abies* (L.) Karst.) seedlings than either of the light qualities alone (Mølmann et al. 2006). The narrow spectra of supplemental LEDs have potential implications on seedling growth, development, and physiology. Therefore, it is possible that any variation in relative quantum efficiency in the spectra of a SL type may affect the efficacy of the light source on photoreceptors affecting chlorophyll concentrations (chl *a* and *b*, total chl, and primary pigments responsible for photosynthesis) and other light-regulated processes.

Any new lighting technology that significantly reduces electricity consumption while producing high-quality seedlings should be of value in forest nurseries. Although knowledge about the influence of light conditions (spectra, photoperiod, and intensity) on plant growth and commercial applications of LEDs have been described for horticulture (Currey and Lopez 2013; Gomez et al. 2013; Randall and Lopez 2014), the impact and science underlying the use of LEDs as a PAR supplement light source in forestry crops is less understood. To our knowledge, no published study has examined the potential of using LEDs on forestry crops to produce similar or better quality seedlings compared with HPS and whether this can be done at reduced energy cost.

Our objective was to compare the effect of PAR SL provided by LEDs (a customized, narrow red and blue spectrum) with that of HPS (broad spectrum) on growth, gas exchange, and chlorophyll concentrations of Douglas-fir and Engelmann spruce seedlings from British Columbia, Idaho, and New Mexico (high, middle, and low latitudinal populations, respectively). We hypothesized that exposure to the light spectra produced by LEDs for PAR SL would yield seedlings of equal or better morphology and physiological status than seedlings exposed to HPS light and that the effect of the light spectra would be pronounced with increasing latitude of seed origin. We used Douglas-fir and Engelmann spruce due to their wide latitudinal distributions (Little 1971; Hermann and Lavender 1990) and their importance in the forest regeneration programs in western North America.

Materials and methods

Our study employed a 2 species × 3 seed sources × 2 supplemental light sources × 4 replications experimental design. The greenhouse was a fully automated, double-walled, polycarbonate structure at the USDA Forest Service Rocky Mountain Research Station in Moscow, Idaho, USA (46.723179, –117.002753).

Lighting, plant materials, and growing conditions

A light map was developed for four greenhouse tables (2.4 m × 1.0 m), each randomly located and fitted with two 400 W HPS lamps (29 cm wide × 53 cm long; Sunlight Supply, Inc., Vancouver, Washington, USA). Spectral measurements with a quantum sensor (QSO-S PAR, Decagon Devices, Inc., Pullman, Washington, USA) taken below the HPS lamps and at regular intervals across the greenhouse tables revealed a mean photosynthetic photon flux density (PPFD) of 70–80 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at anticipated plant canopy height (76 cm below the lights). This height was chosen to reduce effects such as influence on water status and thermal damage, caused by heat conductance from the HPS lamps (bulb surface temperature, ∼450 °C) (Spaargaren 2001). Subsequently, we added four LED fixtures (each fixture comprised eight modules and each module was 4 cm wide × 123 cm long with 87 bulbs) emitting 85:10:5 red:blue:green (DR/W LED 120-110V, Philips, Texas, USA) to each of the remaining four tables to match the PPFD supplied by HPS. Our SL types inherently occluded incoming solar radiation. The HPS system was larger and bulkier than the LED system. To mitigate shading effects between treatments, a mock shade of identical size to the HPS fixtures was installed at the corresponding location above the LED fixtures. The spectral quality and distribution of the SL types (Fig. 1) were taken using a spectroradiometer (StellarNet Inc., Tampa, Florida, USA).

Stratified seeds of Douglas-fir and Engelmann spruce from three latitudinal sources (∼50°, British Columbia (BC); ∼46°, Idaho (ID); ∼34°, New Mexico (NM); Table 1) were sown on 28 January 2014 into Ray Leach Cone-tainers (2.5 cm diameter and 16 cm deep, 66 mL, 1076 $seedlings \cdot m^{-2}$, 200 $containers \cdot tray^{-1}$; Stuewe and Sons Inc., Tangent, Oregon, USA) at a rate to ensure one seedling per cell after thinning. The growing medium was a 45:45:10 peat: vermiculite:bark (*v*:*v*:*v*) "professional growers mix" (Sun Gro Horticulture, Ltd., Bellevue, Washington, USA) amended with Osmocote controlled-release fertilizer (15N:9P_2O_5:12K_2O; 5–6 months; The Scotts Company, Marysville, Ohio, USA) to provide 76 mg of nitrogen (N) per seedling. Filled containers were placed onto greenhouse tables. Greenhouse conditions were set for 28/24 °C day/night air temperatures and a relative humidity of 55%–60%. Once germination was complete (about 10 days after sowing with SL delivered from HPS), one tray (200 seedlings) of each species × seed source combination was randomly assigned to each of the eight tables, half of which had been fitted with LEDs and the remaining had been fitted with HPS as described previously.

To avoid light pollution between light sources, each table was isolated by a three-layer plastic curtain hung from the greenhouse framework. The middle layer, 6 mm thick black polyethylene plastic, was encased with white plastic. Seedlings were grown with an 18 h photoperiod (0600 to 2400); LEDs and HPS supplemented ambient sunlight. Irrigation scheduling was determined gravimetrically for each tray. Seedlings were irrigated when an average of 25% of the water (by mass) available at field capacity had been depleted (Dumroese et al. 2015). On each table, trays were randomly distributed, redistributed weekly, and centered under the HPS and LED fixtures.

Fig. 1. Spectral distribution of high-pressure sodium (HPS) and light-emitting diodes (LEDs), each delivering a photosynthetic photon flux (PPF) of 70–80 μmol·m^{-2}·s^{-1}.

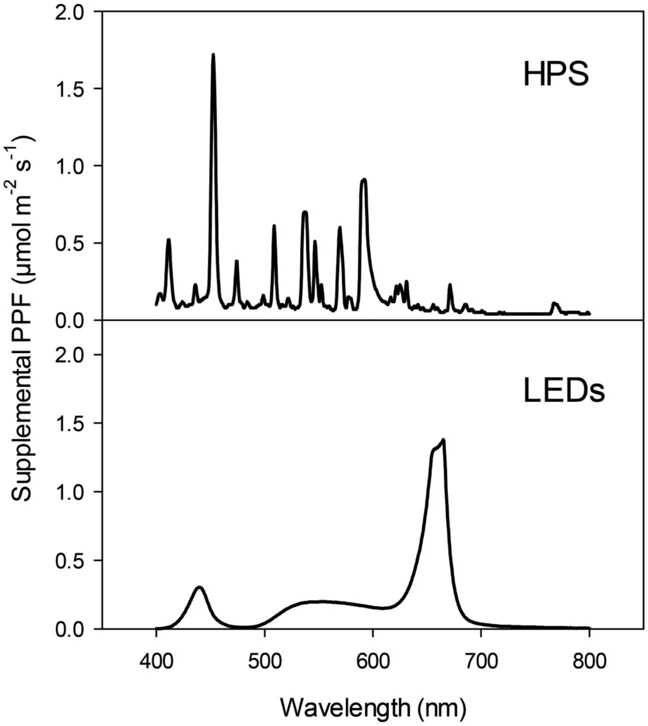


Table 1. Douglas-fir and Engelmann spruce seed origins.

Seed source	Collection site	Latitude	Longitude
Douglas-fir			
British Columbia	Cartwright Lake	50.4844	–116.2556
Idaho	Nez Perce National Forest	45.8512	–115.5556
New Mexico	Lincoln National Forest	32.8340	–105.6970
Engelmann spruce			
British Columbia	Newington Creek	49.1223	–116.4308
Idaho	University of Idaho, Experimental Forest	46.7982	–116.8126
New Mexico	Chicoma Mountain	36.0073	–106.3846

Measurements

SL types

Mean energy use for HPS and LEDs was measured in the hours from 0600 to 2400 using plug power meters (P440 Kill A Watt, P3 International, New York, New York, USA) at three sampling dates: beginning (7 February), middle (25 April), and end (13 June) of the experiment. To ensure the distance between fixtures and the crop canopy was sufficient, air temperature and relative humidity data under each lighting source were measured in the hours between 0600 and 2400 on four sampling dates (15 March, 5 April, 9 May, 6 June) using ECH$_2$O RHT sensors positioned at canopy height and recorded on Em50 data loggers (Decagon Devices, Inc.).

Seedling parameters

To characterize SL treatment effects on seedling growth and physiology, we measured nine seedling parameters: height, root collar diameter (RCD), shoot dry mass, root dry mass, chlorophyll fluorescence, light response curves, needle chlorophyll content, relative water content (RWC), and gas exchange. For each of these, except light response curves, we measured three randomly selected seedlings within each species × seed source × light type × replicate combination (n = 12).

Seedling growth (height and RCD), tissue dry mass, and gas exchange were measured 5, 9, 13, and 17 weeks after SL was initiated. After measuring height and RCD, roots were washed free of soil, and tissue dry mass was obtained after oven drying for 72 h at 70 °C. Chlorophyll fluorescence, light response curves, needle chlorophyll contents, and shoot RWC were measured at the end of the experiment (week 17). All gas exchange measurements (net photosynthesis and stomatal conductance) were made in the hours between 1000 and 1300 using a LI-6400 Portable Photosynthesis System and 6400-22 Opaque Conifer Chamber (LI-6400XT, Lincoln, Nebraska, USA). The conifer chamber was clamped around the entire shoot, and measurements were made at 26 °C and at 1100 μmol·m^{-2}·s^{-1} (PPFD determined by light response curves and set above light saturation for both species) equipped with an artificial light source 6400-18A RGB Light Source (15% blue light). Cuvette CO$_2$ concentration was set at 400 μmol·m^{-2}·s^{-1}, relative humidity was set at 60%–65%, and flow rate kept at 500 μmol·s^{-1}. Following enclosure of needles in the cuvette, data was logged when foliage reached a steady-state value (CV of CO$_2$ and H$_2$O within the chamber was <0.25%). Only needles were then scanned using Image J (Bethesda, Maryland, USA; available from http://rsb.info.nih.gov/ij/).

At the end of the experiment (week 17), needle photochemical efficiency was expressed as leaf chlorophyll fluorescence (ratio of F_v to F_m (F_v/F_m)). Chlorophyll fluorescence was measured on the upper 3 cm portion of the shoots using an integrated fluorescence chamber, 6400-40 Leaf Chamber Fluorometer (LI-6400XT, Lincoln, Nebraska, USA). Prior to chlorophyll fluorescence measurements, terminal shoots were subjected to required dark period by covering them with aluminum foil for 20 min as described in Islam et al. (2008). F_v/F_m estimates maximal quantum yield of photosystem II photochemistry in dark needles.

Photosynthetic light response curve measurements were performed on six randomly selected seedlings within each species × seed source × lighting type combination using similar cuvette conditions described for gas exchange measurements except for the varying PPFD (Q) of 0, 60, 120, 250, 500, 1000, 1500, and 2000 μmol·m^{-2}·s^{-1}; the PPFD was changed in the order of high to low. Measurements were organized by sample across replication and time to reduce time-of-day effects. The nonlinear model described by Whitehead and Gower (2000) was fitted to the data using the SAS software package version 9.1 (SAS Institute Inc., Cary, North Carolina, USA). The fitting was done on data from individual seedlings and seedling groups pooled for each combination of SL type, species, and seed sources. Light-saturated net photosynthesis rates (A_{max}), light compensation point (LCP), light saturation point (LSP), dark respiration (R_d), quantum yield (Φ), and convexity factor (th) were determined from the light response curves of individual seedlings as in Dubois et al. (2007).

Needle chl *a* and chl *b* contents were measured using the method of Arnon (1949), as modified to use dimethyl sulfoxide (DMSO) (Hiscox and Israelstam 1979) because DMSO is as reliable as acetone for chlorophyll extraction (Tait and Hik 2003) but does not require maceration. Chlorophyll content was analyzed according to the methods developed by Hiscox and Israelstam (1979) and Tait and Hik (2003), as adapted by Islam et al. (2008). Absorbance readings were determined with GENESYS20 Visible Spectrophotometer (Thermo Fisher Scientific Inc., Waltham, Massachusetts, USA), and chlorophyll concentrations were calculated on a dry mass basis.

Shoot RWC was determined as follows: RWC = [(fresh mass – dry mass) ÷ (turgid mass – dry mass)] × 100. Turgid mass was determined by placing each shoot in a 50 mL conical centrifuge tube filled with distilled water and maintained at 4 °C in darkness to minimize respiration losses until it reached a constant mass, typically after 12 h. Dry mass was obtained after placing the samples in a 70 °C oven for 72 h.

Data analyses

Tests for normality and constant variance to ensure validity of the assumptions of analysis of variance (ANOVA) revealed that no transformations were necessary. ANOVA (SAS PROC Mixed (α = 0.05); SAS Institute Inc.) was used to examine the effects of independent variables (species, seed source, and supplemental light source) and their interactions on the dependent variables (height, RCD, shoot and root dry mass, chlorophyll concentrations, chlorophyll fluorescence, gas exchange, RWC, and light response curve parameters). Growth and gas exchange variables were analyzed for each sampling date. Means were compared for significant differences at $P < 0.05$ using Tukey's test. Tukey honestly significance difference test was used to analyze for multiple mean comparisons for which seedling parameters were significantly different following ANOVA. Values of light response curve parameters were determined for each seedling measured, and the statistical significance of the treatment effects was determined for each variable by ANOVA. Differences in energy consumption between SL types were also determined.

Results

Energy use, greenhouse conditions, and spectral quality

For one table, the mean daily energy consumption for the LED fixture was 4.4 kWh·day^{-1}, i.e., 29% of the 15.0 kWh·day^{-1} consumed by the pair of HPS lamps. In general, air temperature and relative humidity at plant height were similar between LEDs and HPS (Table 2). Figure 1 shows the variation in spectral composition between HPS (broad spectrum) and LEDs (red, green, and blue spectrum).

Table 2. Mean (± standard error) daily greenhouse air temperature, relative humidity, and ambient photosynthetic photon flux density (PPFD) at seedling height during sampling dates of Douglas-fir and Engelmann spruce seedlings grown with supplemental lighting (in the hours from 0600 to 2400) delivered from high-pressure sodium lamps (HPS) or light-emitting diodes (LED).

Sampling date	Ambient PPFD	Supplemental lighting	Air temperature (°C)	Relative humidity (%)
Week 5, 15 March	228	HPS	27.0±0.3	58±7
		LED	26.8±0.3	60±7
Week 9, 5 April	400	HPS	24.7±0.4	47±6
		LED	23.4±0.4	50±8
Week 13, 9 May	344	HPS	26.1±0.5	44±1
		LED	25.7±0.4	46±1
Week 17, 6 June	386	HPS	26.1±0.3	42±4
		LED	26.0±0.3	43±4

Note: The ambient PPFD values are the sums of the supplemental lighting and incoming sunlight.

Seedling height, RCD, dry mass, and RWC

SL types, species, seed sources, and their interactions differed significantly ($P \leq 0.0048$) across growth measures. In general, seedlings grown under LEDs had significantly greater height, RCD, and biomass compared with seedlings grown under HPS (Table 3). SL type significantly ($P < 0.0001$) affected seedling height, RCD, and shoot and root dry mass (DM), and these treatment effects were observed at 5 weeks after exposure to SL (Table 3), with mean values increasing as the weeks progressed. For growth (height, RCD, and shoot and root DMs), we detected a significant ($P = 0.0250$) interaction between SL types and seed sources, suggesting a clear clinal growth response to SL associated with the latitudinal origin of seeds. Of the studied seed sources, LED-grown seedlings from BC (highest latitude) generally had the greatest growth and tissue DM, followed by ID (mid-latitude) and NM (lowest latitude) populations (Table 3). Multiple comparisons revealed significant differences in growth between BC and NM populations based on SL type, and the differences were more pronounced in Engelmann spruce than in Douglas-fir. For example, for height growth in the 17th week of exposure to SL, LEDs caused an 18%, 17%, and 3% increase in Douglas-fir and a 47%, 55%, and 18% increase in Engelmann spruce for BC, ID, and NM sources, respectively, compared with HPS-grown seedlings. SL types had no effect on shoot RWC (88%–89%) but seed source did ($P < 0.0002$), with values increasing as latitude decreased (86%, 88%, and 90% for BC, ID, and NM, respectively).

Gas exchange and chlorophyll (*a*, *b*, total, and fluorescence) measures

Similar to growth parameters, SL types, species, seed sources, and their interactions differed significantly ($P < 0.001$) across gas exchange measures. In addition, both net photosynthesis (A) and stomatal conductance (g_s) were significantly different among SL types and seed sources ($P \leq 0.005$) after 9 weeks of treatment exposure (A of Engelmann spruce was significantly ($P = 0.0384$) affected by SL types as early as 5 weeks of treatment exposure). Although the effects of SL type on gas exchange rates were not as consistent as the growth rates throughout the sampling dates, Engelmann spruce from the highest latitude (BC) showed significantly greater mean A and g_s values than those from the lowest latitude (NM) (Table 4). Douglas-fir from NM populations were significantly ($P = 0.0181$) influenced by LEDs only 9 weeks after lighting, where we noted a 21% increase in A for seedlings grown under LEDs than HPS, whereas those from BC and ID were unaffected. Also, both species from ID were largely unaffected by SL except after 5 weeks, where LED-grown Engelmann spruce seedlings had 56% greater A ($P = 0.0056$) compared with those seedlings grown under HPS (Table 4).

By the end of the experimental period (week 17), chl *a*, chl *b*, and total chl were significantly affected by SL types and species but not by their interaction (Table 5). LED-grown Douglas-fir seedlings from NM had a 40% and 50% increase in total chl and chl *a*, respectively, compared with seedlings grown under HPS (Fig. 2). Mean values across SL type and seed source for chl *a*, chl *b*, and total chl for Douglas-fir and Engelmann spruce were 6.05, 1.73, and 8.36 mg·g^{-1} DM and 6.96, 2.31, and 8.70 mg·g^{-1} DM, respectively.

SL types had no effect on F_v/F_m (from 0.76 to 0.77); however, species and seed sources interacted to significantly affect F_v/F_m ($P = 0.0251$). Mean F_v/F_m values were 0.83 and 0.85 for Douglas-fir and Engelmann spruce, respectively.

Light response curve parameters

Except for R_d ($P = 0.0334$), neither of the light response curve parameters measured at the end of experiment were significantly affected by two-way (SL type × species) or three-way (SL type × seed sources × species) interactions (Table 5). We observed that SL type significantly altered A_{max}, R_d, and Φ. Species and seed sources interacted to significantly affect A_{max} and R_d. For HPS and LEDs across species and seed sources, mean A_{max} values were 4.96 and 5.25 μmol·m^{-2}·s^{-1}, respectively; mean R_d values were 0.28 and 0.35 μmol·m^{-2}·s^{-1}, respectively; and mean Φ values were 0.01 and 0.03, respectively. SL types had no effect, however, on LSP (1177–1357 μmol·m^{-2}·s^{-1}) or LCP (27.1–27.2 μmol·m^{-2}·s^{-1}) across species and seed sources. In addition, R_d, Φ, LSP, LCP, and F_v/F_m were not significantly influenced by seed source but A_{max} was. A_{max} was significantly affected by species (Table 5), with mean values of 4.66 and 4.84 μmol·m^{-2}·s^{-1} for Douglas-fir and Engelmann spruce, respectively.

Discussion

SL, energy usage, and nursery practices

SL is commonly used to compensate for low light levels, especially at latitudes where solar radiation inputs for crops are limited (Tinus and McDonald 1979; Arnott 1989; Hao and Papadopoulos 1999; Hemming et al. 2008). SL for vegetable and floriculture production

Table 3. Mean values of growth and tissue dry mass of Douglas-fir and Engelmann spruce seedlings from three latitudinal seed sources (British Columbia (BC), Idaho (ID), New Mexico (NM)) grown with supplemental lighting (SL; high-pressure sodium (HPS) or light-emitting diodes (LED)) from 0600 to 2400 daily (n = 12).

		Douglas-fir				Engelmann spruce			
SL	Seed sources	Week 5	Week 9	Week 13	Week 17	Week 5	Week 9	Week 13	Week 17
Shoot height (cm)									
HPS	BC	4.44a	7.67a	10.97a	15.04a	2.37a	4.38a	7.52a	9.51a
	ID	4.03a	6.61b	8.05b	13.23b	2.88b	4.77a	6.57ab	10.01a
	NM	5.00b	7.40ab	9.26b	14.11ab	3.02b	3.60a	5.94b	8.50a
LED	BC	5.08*a	7.23ab	9.94a	17.78*a	2.78a	4.84a	9.08*a	13.95*a
	ID	4.03b	6.66a	10.61*a	15.52*a	2.82a	5.99*b	8.61*a	15.53*a
	NM	4.92a	7.57b	10.98*a	14.58b	3.11a	4.72*a	5.75b	10.00b
Root collar diameter (mm)									
HPS	BC	0.78a	0.92a	1.18a	1.44a	0.47a	0.77a	1.03a	1.61a
	ID	0.78a	1.00a	1.13a	1.54a	0.52a	0.84a	1.23a	1.63a
	NM	0.77a	0.92a	1.13a	1.50a	0.58b	0.76a	1.20a	1.69a
LED	BC	0.83a	0.95a	1.25a	1.94*a	0.58*a	0.95*a	1.48*a	2.10*a
	ID	0.82a	1.06b	1.28*a	1.92*a	0.59*a	0.98*a	1.43*a	1.98*ab
	NM	0.78a	0.92a	1.18a	1.44a	0.61a	0.94*a	1.28b	1.87b
Shoot dry mass (g)									
HPS	BC	0.05a	0.13a	0.22ab	0.38a	0.02a	0.09a	0.17a	0.30a
	ID	0.04b	0.13a	0.19a	0.33a	0.03a	0.10a	0.17a	0.37a
	NM	0.07c	0.19b	0.26b	0.43a	0.03a	0.10a	0.18a	0.39a
LED	BC	0.07*a	0.15a	0.28*a	0.61*a	0.04*a	0.11a	0.29*a	0.54*a
	ID	0.05b	0.14a	0.31*a	0.55*a	0.04*a	0.13a	0.26*a	0.57*a
	NM	0.05a	0.13a	0.22ab	0.38a	0.04*a	0.13*a	0.25*a	0.53*a
Root dry mass (g)									
HPS	BC	0.02a	0.04a	0.09a	0.15a	0.01a	0.02a	0.03a	0.09a
	ID	0.01b	0.05a	0.07a	0.22b	0.01a	0.03a	0.04a	0.10a
	NM	0.02a	0.04a	0.05b	0.12a	0.01a	0.02a	0.03a	0.09a
LED	BC	0.02*a	0.05a	0.10a	0.23*ab	0.01a	0.03a	0.08*a	0.19*a
	ID	0.01b	0.05a	0.10*a	0.25a	0.01a	0.03a	0.06b	0.15*a
	NM	0.02a	0.05a	0.11*a	0.19*b	0.02*a	0.03*a	0.05b	0.15*a

Note: For each parameter under LED SL, pairs of means (HPS and LED) within each species and seed source at each sampling date that are marked with an asterisk indicate a significant difference from the HPS at $P < 0.05$. Different lowercase letters indicate significant differences after Tukey's adjustment for multiple comparisons across seed sources within SL types for each sampling date.

Table 4. Mean values of net photosynthesis (A) and stomatal conductance (g_s) of Douglas-fir and Engelmann spruce seedlings from three latitudinal seed sources (British Columbia (BC), Idaho (ID), New Mexico (NM)) grown with supplemental lighting (SL; high-pressure sodium (HPS) or light-emitting diodes (LED)) from 0600 to 2400 daily.

		Douglas-fir				Engelmann spruce			
SL	Seed sources	Week 5	Week 9	Week 13	Week 17	Week 5	Week 9	Week 13	Week 17
A (μmol CO_2·m^{-2}·s^{-1})									
HPS	BC	2.73a	2.89a	3.47a	3.79ab	1.06a	1.46ab	3.07ab	4.64a
	ID	1.64b	1.86b	2.42b	2.90a	1.06a	1.87a	3.40a	4.46a
	NM	3.29c	3.17a	4.26c	4.55b	1.09a	1.23b	2.62b	3.90a
LED	BC	2.60a	2.60a	3.23ab	4.65a	1.27a	2.52*a	4.27*a	5.72a
	ID	1.80b	1.98b	2.75a	3.79a	1.65*b	2.25a	4.12ab	5.10ab
	NM	3.23c	3.84*c	3.90b	4.81a	1.63*b	2.18*a	3.39*b	4.02b
g_s (mmol H_2O·m^{-2}·s^{-1})									
HPS	BC	0.03a	0.05a	0.04a	0.05a	0.02a	0.03ab	0.05a	0.09a
	ID	0.02b	0.02b	0.03b	0.04a	0.02a	0.04a	0.05a	0.09a
	NM	0.06c	0.06a	0.06a	0.07b	0.02a	0.02b	0.04a	0.09a
LED	BC	0.04a	0.04a	0.04ab	0.07a	0.02a	0.06*a	0.07*a	0.11a
	ID	0.02b	0.03a	0.03a	0.06a	0.02a	0.04a	0.06a	0.08ab
	NM	0.05c	0.07*b	0.05b	0.08a	0.02a	0.05*a	0.05a	0.05b

Note: For each parameter under LED SL, pairs of means (HPS and LED) within each species and seed source at each sampling date that are marked with an asterisk indicate a significant difference from HPS at $P < 0.05$. Different lowercase letters indicate significant differences after Tukey's adjustment for multiple comparisons across seed sources within SL types for each sampling date.

is known to improve plant morphology and development and increase plant growth (Dorais et al. 1991; Grimstad 1987; McCall 1992; Hernandez and Kubota 2012; Currey and Lopez 2013). In forest nurseries growing container stock, provision of light during natural short photoperiods is a common practice to prevent seedling dormancy and maintain growth rates to meet target size specifications for outplanting (Arnott and Simmons 1985; Landis et al. 1992; Lascoux et al. 1993; Tinus 1995).

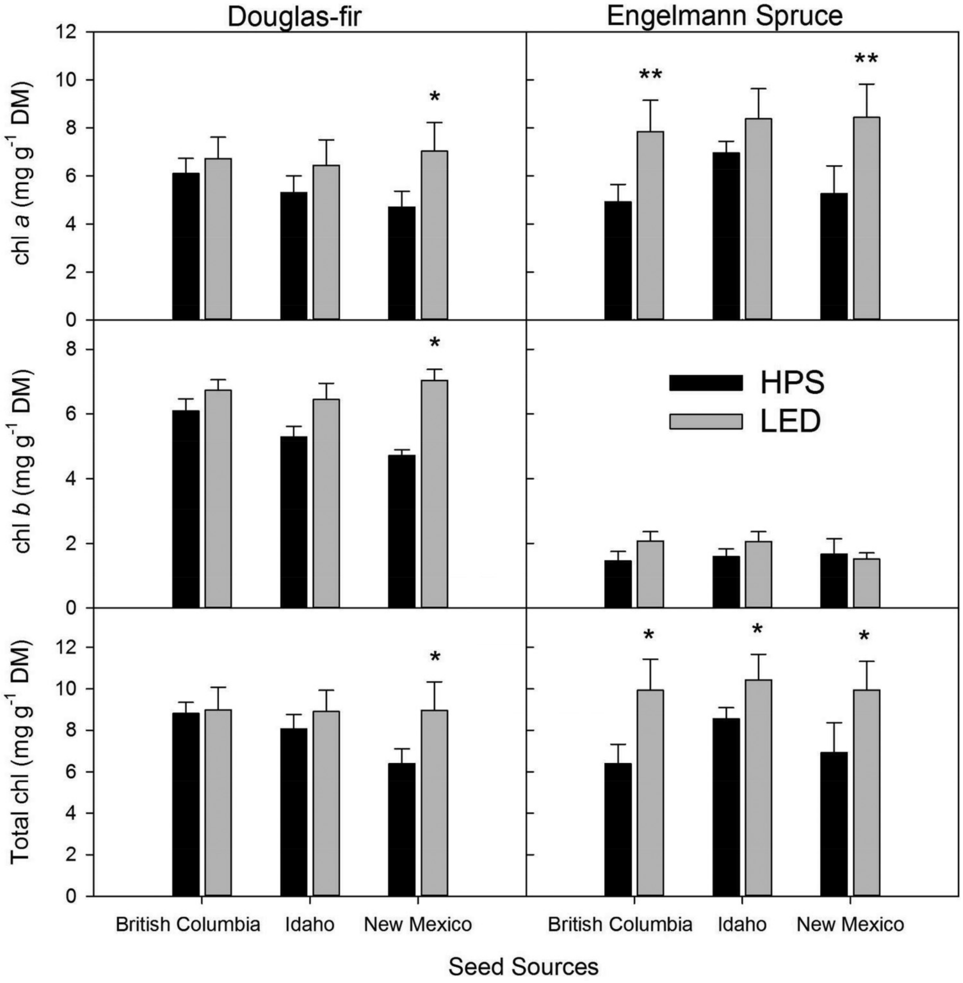
Claims of 50% energy savings when using LEDs compared with HPS while yielding similar biomass are now common in the marketplace (Craford 2005). In our study, SL provided by LEDs was achieved with only 29% of the energy required by HPS, more than

Table 5. P values for the effects of independent variables (supplemental lighting types, species, and seed sources) and their two- and three-way interactions on the response variables assessed using analysis of variance at $P < 0.05$ ($n = 6$).

	Source of variation							
Response variable	Supplemental lighting (SL)	Species (Sp)	Seed sources (SS)	Replication	SL × Sp	Sp × SS	SL × SS	SL × Sp × SS
F_v/F_m	0.5195	**0.0048**	0.3339	0.0119	0.6588	**0.0251**	**0.0059**	0.0590
chl *a*	**<0.0001**	**0.0339**	0.6836	0.0782	0.1849	0.2227	0.3639	0.6064
chl *b*	**0.0469**	**0.0009**	**0.0286**	0.0951	0.1554	0.3066	0.9967	0.1768
total chl	**<0.0001**	**0.0407**	0.1755	0.5871	**0.0499**	0.1726	0.3482	0.3069
Shoot RWC	0.3347	0.2007	**0.0002**	0.1201	0.7865	0.3070	0.2503	0.1043
A_{max}	**0.0028**	**0.0080**	**0.0432**	0.3638	0.0589	**0.0027**	0.1214	0.2598
LCP	0.6638	0.6721	0.9305	0.5674	0.0603	0.8317	0.7295	0.8320
LSP	0.3056	0.2314	0.7231	0.0759	0.9966	0.1354	0.6573	0.3915
R_d	**0.0295**	0.6308	0.8911	0.2260	**0.0334**	**0.0351**	0.3882	0.4727
Φ	**0.0006**	0.9385	0.5102	0.1788	0.3796	0.6321	0.0719	0.4932
th	0.4972	0.4183	0.5968	0.0721	0.2506	0.0680	0.2677	0.0946

Note: F_v/F_m, chlorophyll fluorescence; chl *a*, chlorophyll *a*; chl *b*, chlorophyll *b*; total chl, total chlorophyll; shoot RWC, shoot relative water content; A_{max}, maximum rate of photosynthesis at saturating irradiance; LCP, light compensation point; LSP, light saturation point; R_d, dark respiration; Φ, quantum yield; and th, convexity factor. Significant ($P < 0.05$) treatment effects are given in boldface.

Fig. 2. Chlorophyll contents (chl *a*, chl *b*, and total chl; mg·g^{-1} dry mass (DM)) of Douglas-fir and Engelmann spruce seedlings from three latitudinal sources grown under supplemental lighting types (light-emitting diodes (LEDs) and high-pressure sodium (HPS)). Each data point represents mean ($n = 12$) ± standard error. LED bars marked with an asterisk above indicate a significant difference from HPS at $P < 0.05$ (*) and $P < 0.01$ (**). Only pairs of means (HPS and LED) at each source are being compared.



the 35%–40% reduction observed for annual bedding plants (Currey and Lopez 2013) but similar to the 75% reduction for tomato crops (Gomez et al. 2013). These results suggest that the energy savings from using LEDs should be of value in container seedling production.

Seedling growth, physiology, and spectral quality

Our study confirmed our hypotheses regarding seedling growth and physiological differences between SL types. We observed significant increases in height growth and tissue DM in Douglas-fir and Engelmann spruce seedlings exposed to LEDs compared with similar PPFD from HPS (Table 3). Several studies have shown the benefit of LED SL on growth and development in ornamental and vegetable crops (Massa et al. 2008; Hernandez and Kubota 2012; Currey and Lopez 2013). For example, after 28 days of treatment, plug quality (e.g., high root mass, compact crown, and short time to flower after transplant) of several annual bedding plants exposed to 100 μmol·m^{-2}·s^{-1} for a 16 h photoperiod under LEDs (85:15 red:blue) was significantly higher compared with plugs grown under HPS (Randall and Lopez 2014). In our study, the greater growth measures and DM production of the LED-grown Douglas-fir and Engelmann spruce seedlings compared with those grown under HPS correlates with enhanced gas exchange measures and chl *a* and total chl contents (Tables 3 and 4; Fig. 2), which concurs with the long-established finding that chlorophyll content is positively associated with photosynthetic ability (Emerson 1929; Buttery and Buzzell 1977; McCree 1972; Lin and Jolliffe 1996). This peak LED spectral output (with two broad peaks in the red and blue regions) is an important advantage over HPS.

Our study illustrated that although the overall PAR output delivered by HPS and LEDs was similar, the variation in spectral composition between HPS (broad spectrum) and LEDs (red and blue spectrum) resulted in differences in growth and seedling function. On one hand, red light is known to have the highest relative quantum yield from the PAR spectrum (single leaf measurements) (McCree 1972), matching well with chlorophyll absorption peaks (Kriedemann 2010; Sager and McFarlane 1997). Blue light, on the other hand, is a key wavelength for chloroplast development, chlorophyll formation, stem elongation, and stomatal opening (Cosgrove 1981; Hogewoning et al. 2010; Schwartz and Zeiger 1984; Assmann 1993; Briggs et al. 2006). Our results agree with the findings of Currey and Lopez (2013) whereby LEDs containing 85:15 red:blue (similar to the spectral ratio we used) led to a significantly higher accumulation of DM in *Petunia* spp. (annual bedding plant) compared with HPS.

The application of photoperiodic lighting with very low light levels is more common than high-intensity PAR SL in container forest nurseries. Arnott and Macey (1985) concluded that ambient daylight supplemented with a PPFD of 2 μmol·m^{-2}·s^{-1} from HPS for 19 h was sufficient to optimize first-year growth of white spruce, Engelmann spruce, and mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) seedlings. McCreary et al. (1978) reported that a 22 h photoperiod using HPS was optimal for preventing early terminal bud formation in Douglas-fir. Tinus and McDonald (1979) and Landis et al. (1992) suggested that a minimum between 5 and 8 μmol·m^{-2}·s^{-1} was effective for triggering phytochrome, the photoreceptor that absorbs specific wavelengths and mediates physiological processes (Briggs et al. 2006; Cashmore 2006; Sharrock and Matthews 2006), keeping crops actively growing in many operational nurseries. Lower irradiance levels, however, were effective for preventing terminal bud formation in blue spruce (0.5 μmol·m^{-2}·s^{-1}) (Tinus 1995) and Engelmann spruce (0.4–1.6 μmol·m^{-2}·s^{-1}) (Arnott 1979).

Gas exchange and light response are variable processes that are influenced by seedling developmental stages and spectral quality (Taiz and Zeiger 2010). Currey and Lopez (2013) reported that LED-grown *Petunia* spp. showed an increase in DM accumulation but gas exchange and light response curves parameters were similar between LED- and HPS-grown plants. Our lack of observing consistent significant differences between SL type for growth and gas exchange throughout the sampling dates (Table 4) suggests that, although the measured response variables were significantly increased by LEDs overall, these effects may be transient in nature.

F_v/F_m reflects potential quantum efficiency of photosystem II and, therefore, provides a sensitive indicator of plant photosynthetic performance (Bjorkman and Demmig 1987) and plant stress. A healthy seedling is reported to have F_v/F_m close to 0.8, and a decrease from this value indicates stress (Fracheboud et al. 1999; Maxwell and Johnson 2000). The lack of significant differences in F_v/F_m between SL types suggested that the narrow blue and red spectra supplied by LEDs did not affect the maximal photochemical efficiency of photosystem II and early photomorphogenesis (Table 5). Although F_v/F_m was significantly different between Engelmann spruce and Douglas-fir, this has little impact from a production standpoint because our observed values are within those reported for healthy, unstressed seedlings (Fracheboud et al. 1999; Maxwell and Johnson 2000).

HPS lamps, which emit long-wave (heat) radiation, are characterized by having a high surface temperature (maximum, 450 °C). Consequently, nursery managers install them at a sufficient distance above the crop canopy to avoid thermal damage (Spaargaren 2001) and altered plant water status. Our temperature and relative humidity data (Table 2) combined with a lack of significant differences in shoot RWC of seedlings grown under HPS and LEDs (Table 5) indicate that similar environmental conditions existed beneath both SL types and that water was not a limiting factor under our irrigation regime.

Currey and Lopez (2013) did not observe a growth increase for annual bedding plants (*Impatiens* spp. and *Pelargonium* spp.) grown under LEDs compared with HPS. The reason why the growth and physiological responses of Engelmann spruce to LEDs were greater than Douglas-fir in our study is unclear, but it may be associated with differences in growth patterns (e.g., shade tolerance), requirements for R:FR, light response curve parameters ($A_{\max}$ and Φ), and main photosynthetic pigments (higher mean values in Engelmann spruce than Douglas-fir) or other light absorption characteristics that we did not measure. Because light capturing by plants is such a complex process that is dynamically influenced at multiple integration levels (cell to crop), spectral differences can cause complex interactions in plants that are difficult to explain (Zhu et al. 2010; Dougher and Bugbee 2001).

Researchers report that growth response to SL varies greatly among seed sources (Håbjørg 1972; Arnott and Macey 1985; Arnott and Simmons 1985; Clapham et al. 1998). Our findings showed that seedling growth and tissue DM decreased latitudinally from BC (high), through ID (middle), to NM (low) seed sources in Douglas-fir and Engelmann spruce (Table 3). Similar to our findings, a clinal response to SL has been reported for trees (Håbjørg 1972; Junttila and Kaurin 1985; Sullivan and Teramura 1992), where species originating from higher latitudes have a longer critical photoperiod (i.e., shorter night) than those from lower latitudes (Arnott and Macey 1985; Arnott and Simmons 1985). This variation in growth response to SL as influenced by seed sources could be interpreted as an adaptive response to the length of the growing season (Clapham et al. 1998). Norway spruce and downy birch (*Betula pubescens* Ehrh.) seedlings from populations at higher latitudes have been shown to require SL to prevent dormancy and maintain growth compared with populations originating from lower latitudes (Vaartaja 1959; Håbjørg 1972; Clapham et al. 1998; Mølmann et al. 2006).

We conclude that LEDs significantly improved growth and function of Douglas-fir and Engelmann spruce seedlings compared with HPS but the magnitude was species specific. Seed sources from the highest latitude (BC) showed the greatest growth and physiological measures, with reductions as latitude decreased (i.e., moving to ID and then to NM populations). The amount of growth and electrical efficiency gained on an individual species basis should be carefully considered with different light sources. In our study, LEDs with the same PPFD as HPS produced similar or larger seedlings while using only 29% of the energy needed by HPS, suggesting that LEDs are a viable alternative for container seedling production. Given the growth response we observed with LEDs, the potential benefit of incorporating technology into the production of slow-growing species warrants expanded research and implementation. In addition, as LED technology continues to increase in energy efficiency concomitant with decreases in production cost, its adoption for supplemental PAR lighting at high light intensity (rather than just for photoperiod control) could lead to reduced culturing time, improved growth rates, and year-round production.

Acknowledgements

This study was funded by the USDA Forest Service Rocky Mountain Research Station and the National Center for Reforestation, Nurseries, and Genetic Resources and the University of Idaho, College of Natural Resources Center for Forest Nursery and Seedling Research. We thank Don Regan, Brian Meyers, Craig Kingsbury, Lori Mackey, Jesse Paul, Garrett Hanson, Rebecca Sheridan, Layla Dunlap, and Kenneth Pete for filling containers and sowing and Katherine McBurney for greenhouse and technical support. We also thank Dr. Owen Burney and the USDA Forest Service Coeur d'Alene Nursery for providing seeds and David St. Germain for assistance in data collection.

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