Forest Ecology and Management 390 (2017) 8–14

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Content of far-red light in supplemental light modified characteristics related to drought tolerance and post-planting growth in Scots pine seedlings

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ARTICLE INFO

Article history:
Received 28 November 2016
Received in revised form 13 January 2017
Accepted 16 January 2017
Available online 25 January 2017

Keywords:
Field performance
Gas exchange
Morphology
Pinus sylvestris
Red-to-far-red ratio
Spectral composition

ABSTRACT

Light quality affects the morphological development of a plant. The aim of the experiment was to examine the effect of far-red radiation (FR, 700–800 nm) on growth, morphology, and root growth capacity (RGC) in Scots pine seedlings originating from latitudes 61°N and 67°N, and on gas exchange and subsequent field growth in seedlings originating from 61°N. The seedlings were grown in a greenhouse under natural daylight, receiving either FR-rich (+FR) or FR-deficient (−FR) supplemental light for 20 h per day, provided using light-emitting diodes (LEDs). The seedlings were outplanted and grown in the field for two growing seasons. Growth under +FR hastened terminal bud formation in seedings originating from 61°N, and delayed it in seedlings from 67°N. At the end of the growth period under the LEDs, +FR seedlings were dominated by secondary needles and had a higher needle mass than −FR seedlings, whose foliage comprised mainly primary needles. −FR improved root growth capacity in the seedlings originating from 61°N, but not in seedlings originating from 67°N. In seedlings from 61°N, photosynthesis (P_n) at the needle area level was higher and stomatal conductance lower under −FR, resulting in higher water use efficiency than under +FR. Due to the greater amount of photosynthetic tissue under +FR, the whole-seedling-level P_n was higher under +FR. Height and diameter growth were greater in −FR seedlings than in +FR seedlings during the second growing season. Growth habit and growth rate of Scots pine seedlings can be manipulated by controlling the FR content in the supplemental light, enabling production of seedlings targeted for outplanting on sites with specific characteristics.

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1. Introduction

Scots pine (*Pinus sylvestris*) is the dominant and economically one of the most important tree species in Northern Europe (Mattsson, 2016; Anon., 2016). As a shade-intolerant species, Scots pine strongly responds to alterations in light spectral composition (Clapham et al., 2002). In shade conditions, indicated by low red-to-far-red ratio (R:FR), Scots pine seedlings have shown increases in stem elongation and shoot dry mass accumulation to optimize light capture (Clapham et al., 2002; de la Rosa et al., 1998; Sarala et al., 2011; Riikonen et al., 2016). The R:FR is sensed through phytochrome photoreceptors, which exist in a biologically inactive R-absorbing Pr form and a biologically active FR-absorbing Pfr form. The equilibrium between these forms changes with the spectral composition of light, and results in a series of developmental responses in different plant species (Pierik and Wit, 2014).

In the Northern latitudes with short nights and long twilights, characterized by low R:FR, Scots pine communities use the length of the light period as a cue for controlling growth because dark timekeeping may be imprecise (Clapham et al., 2002). Clapham et al. (2002) showed that in Scots pine, the requirement for FR for maintaining the development of secondary needles increases with increasing latitude of origin, and that the change in the requirement for FR occurs at latitudes of about 64°N.

The morphology of first- and second-year Scots pine seedlings is different. Under natural conditions the growth during the first year is free growth: After seed germination and hypocotyl elongation, the apical meristem produces stem units for shoot elongation. Shoot elongation ceases when all stem units have stopped elongating and no new ones start to elongate. A bud is enclosed in a rosette of primary needles, with no or only a few axillary secondary needles (primary needle seedling). During the second year, the stem units within the rosette of primary needles start to elongate (free growth) before actual bud break (fixed growth, i.e. the growth that

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http://dx.doi.org/10.1016/j.foreco.2017.01.015
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consists of structures initiated in the bud the year before). In the second growing season, the primary needles are replaced by secondary needles (secondary needle seedling), and at the end of the growing season a terminal bud with a whorl of lateral buds will be formed. In the third growing season growth is solely fixed growth (Lanner, 1976).

If primary needle seedlings are grown under favorable growth conditions the shoot will continue elongating after bud set. These seedlings produce axillary secondary needles, and form a terminal resting bud already in the first growing season (Thompson, 1982). Pine seedlings with secondary needles are believed to be more tolerant to drought and frost (Climent et al., 2006, 2009), and have a higher root growth capacity (RGC, Nyström, 1991) than the primary needle seedlings after outplanting. However, when Luoranen and Rikala (2012) grew two-year-old-like seedlings with secondary needles in a single growing season by applying an early-season short-day treatment, they found that survival and height growth was similar in the treated secondary needle seedlings and untreated primary needle seedlings in a three-year field trial. Overall, the research results on the subject are scarce, species-dependent and inconsistent (Climent et al., 2006, 2009; Mustard et al., 1997).

In our earlier experiment with the same experimental set-up as was used in the study reported here, we grew Scots pine seedlings originating from 62°N by using LED lights containing different proportions of R, B and FR as sole sources of radiation (Riikonen et al., 2016). We found that most of the seedlings grown without FR were dominated by primary needles, which was associated with some characteristics related to drought tolerance, such as higher water-use efficiency, root-to-shoot ratio, and root growth capacity when compared with seedlings grown under FR-rich treatment. These seedlings, in turn, had predominantly secondary needles, and had higher height growth and larger needle dry mass (Riikonen et al., 2016). Our results thus confirmed the stimulating effect of FR on height growth and leaf mass found in earlier studies with different plant species, but conflicted with the assumed superiority of the secondary needle pines in drought resistance, although the seedlings were not tested under field conditions.

In this experiment, Scots pine seedlings originating from two latitudinal populations (61°N and 67°N) were grown under natural daylight, and in addition, the seedlings received either FR-rich or FR-deficient supplemental light. Based on the existing research and our previous study (Riikonen et al., 2016), our hypotheses were as follows: (1) Supplemental light, deficient in FR, may enhance seedling attributes that are related to drought resistance; (2) Presence of FR in the supplemental light is required for production of secondary needles, especially in seedlings originating from 67°N; (3) Field performance of primary and secondary needle seedlings may differ.

2. Materials and methods

2.1. Plant material

The experiment was performed in a glass greenhouse in Suonenjoki, Finland (62°39′N, 27°03′E, 142 m above sea level). On 22 January 2015, Scots pine seeds of local (61°N) and northern (67°N) origins (collected from three forest stands for each origin) were sown into plastic containers (Plantek PL121F, BCC, iso-Vimma, Finland; 121 seedlings per tray, 50 cm^3 cell volume, 820 seedlings m^{-2}). The trays were filled with pre-fertilized and pre-limed medium-coarse sphagnum peat (Kekkilä XL white 420F6, Kekkilä Oy, Tuusula, Finland) and covered with a layer of sand (1–2 mm), and kept at an optimum moisture level of 35–50% (Lilja et al., 2010). From mid-February until the outplanting, the seedlings were fertilized weekly with 0.1% Taimi-Superex (19% nitrogen [N], 5% phosphorus, 20% potassium + micronutrients; Kekkilä Inc., Eurajoki, Finland), resulting in a total of 11.9 g N m^{-2}.

2.2. Light treatments

The light treatments were organized on six greenhouse tables (1.2 × 3 m). In addition to the natural daylight coming through the roof and walls of the glasshouse, the seedlings were provided supplemental light by LED tubes (60 W; Kasvua Oy, Hämeenlinna, Finland); Five tubes were installed side by side above the seedling trays in each table. White plastic walls were installed between the tables to prevent the LED treatments from interfering each other. Two different light spectra were used (three tables of each spectrum): 25% blue (400–500 nm) + 70% red (600–700 nm) + 5% far-red (700–800 nm) (+FR) and 25% blue + 75% red (−FR) (Riikonen et al., 2016). The intensity of the supplemental light was 150 μmol photosynthetically active radiation (PAR) m^{-2} s^{-1} in both treatments, and it was adjusted by shifting the LED tubes vertically. The supplemental light was provided for the seedlings for 20 h per day (04:00–00:00), and the PAR was regularly measured with a quantum sensor (LI-COR LI-190 SB, LI-COR Inc., Lincoln, USA). The trays were rotated twice weekly to ensure even light conditions under the treatments. Spectral distribution of light in the greenhouse was measured at mid-day on 25 April 2015, during partly cloudy weather using a spectroradiometer (AvaSpec-ULS2048 Starline, Avantes BV, Apeldoorn, The Netherlands) (Table 1). The greenhouse roof transmitted about 50% of PAR in the sun light, and the total amount of PAR coming inside the greenhouse was around 90 μmol at the time of the measurements. The R:FR was estimated from spectral irradiance data, according to Smith (1982), using R (R Core Team, 2016) and the packages "photobiology" and "photobiologyPlants" (Aphalo, 2015). R:FR is constant during the day time, but it is reduced during twilight (Nilsen, 1985). The natural day length during the growth period under the LEDs was 6 h 30 min at the beginning (26 January 2015) and 18 h 50 min at the end of the LED treatments (25 May 2015). This means that the supplemental light treatments had greatest impact at the beginning of the experiment and when the sun elevation was low. The treatments were replicated three times, and there was one seedling tray from both seed origins in each treatment and replication (total of three trays per seed origin, 363 seedlings). Air temperature was maintained at 20/18 °C day/night, and RH at 60%.

2.3. Outplanting in the nursery field

The −FR seedlings originating from 67°N remained very small (average height at the end of the growth period in the glass house was below 4 cm), and thus, only the seedlings originating from 61°N were outplanted in the nursery field. On 25 May 2015, the seedlings were transferred to a plastic house and on 4 June outside to acclimate before outplanting on 10 June 2015 in a former nursery field prepared for test use (fine sandy soil with a layer of silt-clay-peat mixture on the surface). The seedlings were planted in a split-plot design composed of six blocks (n = 6 after planting in the field), which consisted of six parallel rows of seedlings representing each of the glass house tables and the forest stand within the table, i.e. each row consisted of 18 seedlings (1 m between the seedlings). All seedlings had a visible terminal bud at the time of planting. The average temperature after the outplanting was 12.4 °C (±2.3), 14.4 °C (±2.1) and 16.0 °C (±1.9) in June, July and August 2015, respectively.

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