

Light-Use Efficiency and Photosynthetic Capacity of Northern White-Cedar (*Thuja occidentalis* L.) Cuttings Originated from Layering and Seed

Rongzhou Man, Pengxin Lu, William C. Parker, Gordon J. Kayahara, and Qing-Lai Dang

ABSTRACT

Northern white-cedar (*Thuja occidentalis* L.) regeneration originating from layering is generally considered to be more shade tolerant than that of seed origin. In this study, we examined photosynthetic light-use efficiency, an important component of shade tolerance, of these two forms of regeneration using light-response curves of 1-year-old rooted cuttings of layers and seedlings grown under low (20% of full sun) and high (>90% of full sun) light conditions. Northern white-cedar showed a strong potential for photosynthetic acclimation to light availability, as indicated by significant differences in the light compensation point (LCP), dark respiration (R_d), apparent quantum efficiency (PE), and light saturation point (Q_{sat}) but not light-saturated rate of net photosynthesis (A_{max}) between cuttings grown under high and low light. Values of R_d , LCP, and PE did not differ between layers and seedlings grown under high and low light, but layers had higher A_{max} and Q_{sat} than seedlings when grown under high light. This result may reflect a comparatively lower capacity for photosynthetic acclimation of seedlings to high light conditions, perhaps because of their younger physiological age. A lower capacity for photosynthetic acclimation to light in seedlings could limit the repair and recovery of their photosynthetic systems from damage associated with the more extreme microenvironments of open, recently disturbed sites.

Keywords: light-response curves, shade tolerance, layers, seedlings

Northern white-cedar (*Thuja occidentalis* L.) is a commercially important, ecologically valuable tree species, providing both a variety of wood products and critical wildlife habitats in eastern Canada and the northeastern United States (Johnston 1990). It is a long-lived, slow-growing tree species that exhibits a bimodal site distribution, occupying both poorly drained lowland and mesic, upland sites (Johnston 1990). On wet, lowland sites with organic soils, white-cedar occurs in pure stands or in association with black spruce (*Picea mariana* [Mill.] BSP), tamarack (*Larix laricina* [Du Roi] K. Koch), and black ash (*Fraxinus nigra* Marsh.; Sims et al. 1990). It also occurs in pure stands on upland, mineral soil sites, but most commonly grows in mixtures with balsam fir (*Abies balsamea* [L.] Mill.), white spruce (*Picea glauca* [Mill.] Voss), yellow birch (*Betula alleghaniensis* Britton), paper birch (*Betula papyrifera* Marsh.), quaking aspen (*Populus tremuloides* Michx.), bigtooth aspen (*Populus grandidentata* Michx.), balsam poplar (*Populus balsamifera* L.), eastern hemlock (*Tsuga canadensis* [L.] Carr.), and eastern white pine (*Pinus strobus* L.).

Northern white-cedar regenerates both sexually via seed and vegetatively by layering (Johnston 1990). On wet sites, layering is the most prevalent form of natural regeneration (Nelson 1951) and occurs when low-hanging branches of standing or windthrown trees come in contact with moist substrates and form adventitious roots

(Curtis 1946, Johnston 1990). The growth and survival of young layers in the forest understory are thought to be enhanced by a temporary vascular connection with the parent tree root system that provides access to a stable supply of soil moisture, decreasing the potential negative effects of periodic, summer drought (Johnston 1990).

In contrast, on upland sites, northern white-cedar regenerates primarily from seed, with mineral soil, burned organic surfaces, rotten wood, decayed litter, or humus as the preferred seedbeds (Johnston 1990, Simard et al. 2003). After canopy disturbance, prolific natural regeneration may establish, but very few germinants survive for more than 3–4 years (Larouche et al. 2011). High seedling attrition is probably associated with northern white-cedar's poor initial root development and subsequent moisture stress-induced mortality in more open microsites of recently disturbed areas, such as skid trails (Johnston 1977). As a consequence of this initial sensitivity to moisture stress, partial shade during early establishment is required to reduce cedar seedling mortality from drought, especially in areas with warm, dry summers (Johnston 1990).

From an ecological perspective, shade tolerance can be viewed as the genetic capacity of a plant to tolerate or adapt to shade (Boardman 1977). Shade tolerance has been studied extensively in forests

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This article uses metric units; the applicable conversion factors are: centimeters (cm): 1 cm = 0.39 in.; meters (m): 1 m = 3.3 ft; kilometers (km): 1 km = 0.6 mi.

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and shown to be a complex property of plant species resulting from the interaction of a specific suite of physiological, morphological, and anatomical traits that confer some capacity to tolerate low light (Valladares and Niinemets 2008). These traits are expressed at the leaf, crown, and whole plant level and may be influenced by abiotic, biotic, and ontogenetic factors, such that shade tolerance of a given species may vary with site and plant age (Valladares and Niinemets 2008). Because of its two reproductive strategies and the variety of successional niches in which it occurs, shade tolerance classification of northern white-cedar has proven problematic, with the species being classified from very shade tolerant to intermediate in tolerance (Bakuzis and Hansen 1959, Johnston 1990, Humbert et al. 2007). Curtis (1946) suggested that northern white-cedar trees that establish from layering may be more shade tolerant than those established from seed. This conclusion was based on field observations that abundant cedar regeneration formed by layering persists under dense forest canopies, whereas seedlings do not survive and were generally absent in old fields and forest openings, despite initially high densities. Johnston (1990) and Hofmeyer et al. (2009) also suggested differential shade tolerance between regeneration of seed and vegetative origin, citing high tolerance for layers and intermediate tolerance for seedlings. Although these conclusions are often incorporated into silvicultural guides used by forest managers (Boulfroy et al. 2012), relatively little information is available on the ecophysiological basis for shade tolerance of this species and how it may differ with site factors.

Photosynthetic light-use efficiency is a leaf-level physiological trait that plays an important role in shade tolerance and enables plants to maximize net carbon gain in low-light habitats. Information on light-use efficiency of northern white-cedar is limited to southern Ontario populations (Matthes-Sears and Larson 1991), and no physiological evidence is available on comparative differences in light-use efficiency between white-cedar grown from layering or seed. Comparatively little research has been conducted on the ecology and silviculture of northern white-cedar, and a better understanding of the physiological basis for growth responses to light availability should improve our ability to select appropriate silvicultural systems for management of northern white-cedar.

The two objectives of this study were to examine the photosynthetic light-response characteristics of northern white-cedar cultivated under high- (>90% of full sun) and low- (20% of full sun) light conditions and to compare light-use efficiency and photosynthetic capacity of cedar regeneration of layer and seed origin grown under high and low light. Our hypothesis was that northern white-cedar regeneration grown under low light would exhibit more efficient light use and that cedar regeneration of similar genotype does not differ in photosynthetic light-use efficiency, regardless of whether it originated from layering or seed.

Methods

Propagation of Rooted Cuttings

Four mesic, upland sites dominated by natural northern white-cedar with abundant understory layers were selected as a source of layer and seed origin white-cedar regeneration. These sites were at least 20 km apart and located near Chapleau (47°50' N, 83°24' W) in the boreal forest region of northern Ontario. In late June 2009, at each site, 30 lateral shoots were collected from the top main stem of layers that were 0.5–1.0 m in height and separated by a distance of 10 m. A single cutting (15 cm long) was taken from each layer. Similarly, 30 seedlings of 10–15 cm in height growing in nearby

openings (within 100 m of collected layers) were excavated. Both cuttings and seedlings were covered with ice and transported to the laboratory, where stems of seedlings were prepared as cuttings. Cuttings from layers and seedling stems were treated with rooting powder (Stim-Root No. 1; Spectrum Brands IP Inc., Madison, WI) to promote initiation of adventitious roots. The cuttings were then inserted into moisture-saturated growth medium of a 2:1 (v/v) commercial peat moss-vermiculite mixture (pH 4.0) in 164 cm³ volume (3.8 cm × 21 cm) SC-10 Super Cell tubes. Rooting was conducted under a fogging system supplemented with regular misting using a computer-controlled water-walker to maintain relative humidity greater than 90%, along with a 26° C (day)/18° C (night) diurnal temperature regime and 16-hour photoperiod of low-light intensity (7.4% of full sun). In early September, the rooted cuttings were moved to a greenhouse with light levels at approximately 20% of full sun. Air temperature in the greenhouse was 2–5° C higher than ambient temperature until the fall and winter when temperature was maintained slightly above freezing.

Conditioning of Rooted Cuttings

In late April of the following year, after rooted cuttings were fully flushed, half of the cuttings from the layers and seedlings were moved to another greenhouse and grown under high-light intensity (90% of full sun; referred to as “high light cuttings”) with a temperature regime of 26° C (day)/18° C (night) with a 16-hour photoperiod. The other half of the rooted cuttings remained in the greenhouse under low light (20% of full sun; referred to as “low light cuttings”). In early June, all rooted cuttings were moved outdoors where high light cuttings were exposed to full sun, and low light cuttings were grown at 20% sunlight beneath double-layered shade screens. All rooted cuttings were watered and received maintenance fertilization. Groups of plants from each cutting type and site combination were randomly located in the greenhouses and under the shade screens and were relocated monthly until mid-August when photosynthetic measurements were initiated.

Measurements of Photosynthetic Light-Response Curves

The photosynthetic response to photosynthetic photon flux density (PPFD) was measured on a single upper branch of the current year's growth using a portable, open gas exchange system (LI-6400; LI-COR, Lincoln, NE) equipped with a 2-cm × 3-cm leaf cuvette and an artificial light source (6400-02B LED; LI-COR). The gas exchange system was programmed to provide PPFD, from high to low, of 800, 500, 300, 150, 100, 60, 40, 20, and 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$, with each PPFD level maintained for 4–6 minutes. Photosynthetic light response was measured under a carbon dioxide (CO₂) concentration of 400 $\mu\text{mol mol}^{-1}$, air temperature of 23° C, air flow of 300 $\mu\text{mol s}^{-1}$, and relative humidity of 40–50%.

The nonlinear monomolecular model, $y = a(1 - e^{b-cx})$, described by Causton and Dale (1990), was fitted to data from individual cuttings using the nonlinear regression procedure (PROC NLIN) of SAS 9.2 (SAS Institute, Cary, NC). With use of these model coefficients, a is the light-saturated rate of net photosynthesis (A_{max} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$), b/c is the light compensation point (LCP; $\mu\text{mol m}^{-2} \text{s}^{-1}$), $a(1 - e^b)$ is the dark respiration rate (R_d ; $\mu\text{mol m}^{-2} \text{s}^{-1}$), and ace^b is the initial slope of the curve indicating the quantum efficiency of photosynthesis (PE; $\text{mmol CO}_2 \text{mol}^{-1}$). The light saturation point (Q_{sat} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) for each individual cutting was determined from the fitted light-response curve at the PPFD when the rate of net photosynthesis attained 95% of A_{max} .

Table 1. Light-response parameters of northern white-cedar cuttings of layering and seed origin grown under high- (90% full sunlight) and low- (20% full sunlight) light conditions.

Light treatment	Origin	Sample size	R_d ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	LCP	PE ($\text{mmol CO}_2 \text{ mol}^{-1}$)	A_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Q_{sat}
High	Layering	12	1.40 (0.12)	22 (1.90)	71 (3.16)	6.21 (0.24)	344 (13.18)
	Seed	18	1.23 (0.10)	18 (1.69)	75 (2.58)	5.44 (0.20)	290 (10.68)
Low	Layering	24	0.91 (0.09)	11 (1.57)	91 (2.23)	5.62 (0.18)	230 (9.25)
	Seed	24	0.82 (0.09)	10 (1.57)	89 (2.23)	5.50 (0.18)	225 (9.25)

Data are least-square means (SE).

Experimental Design

The study used a randomized complete block design with factorial combinations of two light levels (high versus low) and two cutting types (layering versus seed origin) in six blocks (individual cuttings used on six sampling dates). The sampling dates were used as blocks to account for differences of cutting growth and environment that occurred during the measurement period. An experimental unit was the treatment combination of light (two levels) and cutting type (two levels), which consisted of one cutting from each of the four field sites. Because the objective of this study was to detect differences between cutting types in their response to light availability, sites where cuttings were collected were treated as random subsamples within the experimental units. In total, 78 cuttings were measured (Table 1), less than the maximum of 96 (6 blocks \times 2 light levels \times 2 cutting types \times 4 sites), because of the poor rooting success of layer cuttings from some sites.

Data Analysis

Analysis of variance of photosynthetic light-response characteristics was performed using the Proc Mixed procedure in SAS 9.2. The analytical model was

$$Y_{ijkp} = \mu + B_i + L_j + C_k + LC_{jk} + e_{ijk} + w_{ijkp}$$

where B is the effect of block (measurement date), L is the fixed effect of the light environment, C is the fixed effect of the cutting type, e_{ijk} is the experimental error, and w_{ijkp} is the residual effect, representing the subsampling error. When significant treatment interactions ($L \times C$) were suggested ($\alpha = 0.10$), multiple contrasts were conducted.

Results

Photosynthetic light-response characteristics of northern white-cedar differed significantly with light treatment, with R_d , LCP, and Q_{sat} being higher and PE lower in cuttings grown under high-light conditions (Figure 1 and Tables 1 and 2). Mean A_{max} was slightly higher, but not significantly so, for cuttings grown under high light. Cutting type had comparatively less influence on light-response characteristics, having a significant effect only on A_{max} and Q_{sat} , dependent on light treatment. For cuttings grown under high light, A_{max} and Q_{sat} were significantly higher for plants of layer than seed origin (Tables 1 and 2).

Discussion

Northern white-cedar cuttings showed strong photosynthetic acclimation in response to growth under high and low light. Light-use efficiency was higher in cuttings grown under 20% of full sunlight, as evidenced by lower LCP, R_d , and Q_{sat} and higher PE. Mean values of light-response parameters documented in our study are very sim-

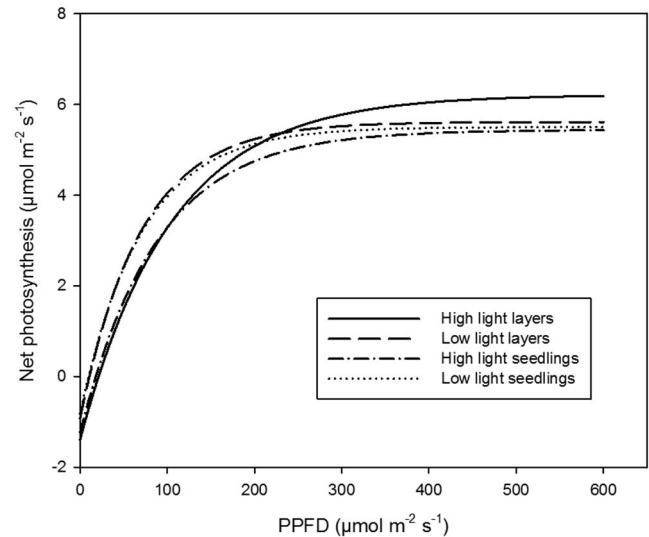


Figure 1. Light-response curves of northern white-cedar cuttings from layering and seed origin grown under high- ($\geq 90\%$ of full sun) and low- (20% of full sun) light conditions. Shown are the mean relationships between net photosynthesis and PPFD for four cutting and light treatment combinations.

Table 2. Results of analysis of variance and summary of $P > F$ values for light and cutting effects on light-response parameters of northern white-cedar.

Source of variation ^a	R_d	LCP	PE	A_{max}	Q_{sat}
L	<0.001	<0.001	<0.001	0.147	<0.001
C	0.159	0.177	0.838	0.017	0.007
L \times C	0.679	0.460	0.309	0.072	0.024
Layers:seedlings at low light				0.617	0.708
Layers:seedlings at high light				0.008	0.002

^a Contrasts are shown for significant light (L) by cutting type (C) interactions ($\alpha = 0.10$).

ilar to those observed in situ for cedar trees growing in cliff and swamp habitats in southern Ontario (Matthes-Sears and Larson 1991).

The photosynthetic light responses of rooted cuttings from layers and seedlings differed slightly when grown under high-light conditions, but not low light conditions, providing partial support for our hypothesis that northern white-cedar trees grown from layers and seeds have comparable light-use efficiency. As pointed out by Boardman (1977), the adaptability of plant species to light is largely controlled by their genotype. We contend that the northern white-cedar seedlings and layers used in this study, which were collected within 100 m of one another, are probably from the same population and are genetically similar. The higher A_{max} and Q_{sat} for cuttings from

layers cultivated under high-light conditions suggest a reduced capacity of seedlings to adapt to high-light conditions. The slight but significant differences between seedlings and layers in these two parameters could be due to ontogenetic effects on light-use efficiency (layers are physiologically older and more developmentally mature; Valladares and Niinemets 2008). For example, Farnsworth and Ellison (1996) reported different photosynthetic capacities at high-light irradiance between seedlings and saplings in red mangrove (*Rhizophora mangle* L.).

Our observations on light-use efficiency of rooted cuttings of layers and seedlings under controlled, near-optimal environmental conditions are not directly applicable to natural field conditions, where regeneration is exposed to varying air temperature, vapor pressure deficit, and soil moisture conditions, and layers remain connected to parent trees (Hofmeyer et al. 2009). The comparative physiology of northern white-cedar layers and seedlings has not been investigated in situ, but research on black spruce suggests a strong positive influence of the larger root systems of layers on gas exchange and water relations. The higher net photosynthetic rate, maximum capacity of ribulose-1,5-bisphosphate carboxylase oxygenase for CO₂ fixation, and shoot water status in black spruce layers than in recently planted seedlings was attributed to greater root system development and enhanced access to soil moisture of layers (Paquin et al. 2000). Conversely, little difference in photosynthetic capacity was found between layers and older, naturally established seedlings, presumably due to relatively similar root system size (Paquin et al. 1999).

The assertion of Curtis (1946) that cedar layers are comparatively shade tolerant based on observations that they endure prolonged periods of low light in the forest understory, is probably attributable to the benefits of their large root systems for survival. That northern white-cedar regeneration of seed origin is intermediate in shade tolerance because of its poor survival and low canopy recruitment in open, exposed habitats is probably primarily the result of small root systems and predisposition to water stress-induced mortality of cedar seedlings during early establishment. Northern white-cedar seedlings in more open microsites of managed forests, such as skid trails (Johnston 1977), also experience more extreme microclimatic conditions than layers. Higher irradiance, daytime temperature, and vapor pressure deficit and more frequent and severe night frosts in spring and fall (Childs and Flint 1987, Man and Lieffers 1999) in exposed habitats can negatively affect photosynthetic performance of seedlings and trees (Man and Lieffers 1997a, 1997b, Man and Greenway 2011). Our field observation that the foliage of seedlings was slightly chlorotic in late June when the cuttings were collected could be associated with higher microclimatic damage to photosynthetic systems and/or slower recovery from this injury in more exposed, higher light environments (Dang et al. 1992).

Regardless of ontogenetic or environmental differences, we suggest that the slight differences in photosynthetic capacity exhibited between rooted cuttings grown from seedlings and layers when exposed to full sun are temporary and will disappear over time. Once fully established, seedlings in open habitats are likely to grow faster than layers shaded by a forest canopy even though seedlings may be subject to more frequent environmental stresses that reduce their photosynthetic capacity. Northern white-cedar seedlings attain maximum height growth at 45–70% of full sunlight, and the greatest shoot and root biomass occurs under full sunlight (Logan 1969, Larouche et al. 2011). Similarly, photosynthetic suppression of layers may occur for the first few years after canopy disturbance because

of the sudden change in understory environment (Gnojek 1992, Dumais and Prévost 2007), but advance regeneration from seed and vegetative origin shows a strong positive growth response to increased light after natural canopy disturbance, harvest, or release treatments (Johnston 1990, Hofmeyer et al. 2009).

Conclusions

Collectively, our results suggest that any assumed difference in shade tolerance between layer and seedling-origin northern white-cedar regeneration is probably not related to leaf-level physiological traits associated with photosynthetic light-use efficiency. We conclude that differences in the persistence of these two forms of regeneration in habitats that vary in light availability are largely associated with the comparative size of their root systems and access to soil moisture during the establishment period, rather than inherent differences in photosynthetic capacity. To ensure the presence of cedar on the landscape and maintain a sustainable wood supply, cedar management on upland sites is best accomplished using partial harvest systems in combination with mechanical site preparation to promote regeneration through natural seeding or can be augmented by planting (Buda et al. 2011, Boulfroy et al. 2012). Forest floor disturbance by mechanical site preparation can create preferred seedbeds for germination, whereas partial canopy retention moderates understory environmental conditions, improves early seedling establishment, and provides adequate light to support competitive height growth and canopy recruitment of cedar regeneration (Buda et al. 2011, Boulfroy et al. 2012).

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