Scandinavian Journal of Forest Research

ISSN: 0282-7581 (Print) 1651-1891 (Online) Journal homepage: http://www.tandfonline.com/loi/sfor20

Modified exponential nitrogen loading to promote morphological quality and nutrient storage of bareroot-cultured Quercus rubra and Quercus alba seedlings

Zonda K. D. Birge , K. Francis Salifu & Douglass F. Jacobs

To cite this article: Zonda K. D. Birge , K. Francis Salifu & Douglass F. Jacobs (2006) Modified exponential nitrogen loading to promote morphological quality and nutrient storage of bareroot-cultured Quercus rubra and Quercus alba seedlings, Scandinavian Journal of Forest Research, 21:4, 306-316, DOI: 10.1080/02827580600761611

To link to this article: http://dx.doi.org/10.1080/02827580600761611

Published online: 18 Feb 2007.

Submit your article to this journal

Article views: 62

View related articles

Citing articles: 16 View citing articles

Full Terms & Conditions of access and use can be found at
http://www.tandfonline.com/action/journalInformation?journalCode=sfor20

Download by: [Purdue University Libraries] **Date:** 09 March 2017, At: 11:46

Scandinavian Journal of Forest Research, 2006; 21: 306–316

Taylor & Francis
Taylor & Francis Group

ORIGINAL ARTICLE

Modified exponential nitrogen loading to promote morphological quality and nutrient storage of bareroot-cultured *Quercus rubra* and *Quercus alba* seedlings

ZONDA K. D. BIRGE, K. FRANCIS SALIFU & DOUGLASS F. JACOBS

Hardwood Tree Improvement and Regeneration Center, Department of Forestry and Natural Resources, Purdue University, West Lafayette, Indiana, USA

Abstract

Exponential nutrient loading has been used to improve nursery fertilizer uptake efficiency of conifer seedlings, but the technique has received little attention in the culture of temperate deciduous hardwoods. This study examined responses of northern red oak (*Quercus rubra* L.) and white oak (*Q. alba* L.) seedlings to modified exponential nitrogen loading during bareroot nursery culture using a broad range of nutrient supply from 0 to 3.35 g nitrogen (N) per plant per season for 18 weeks in Indiana, USA. Seedling growth and nutritional parameters followed a curvilinear pattern that ranged from deficiency to toxicity with increased fertilization consistent with trends depicted in the proposed model for nutrient loading. Fertilization increased plant dry mass by 113–260% for red oak and 49–144% for white oak. Severe nutrient deficiency occurred under indigenous soil fertility, and limited phosphorus and potassium uptake were found to inhibit seedling growth at higher N supply. The sufficiency and optimum rates were determined to be 0.84 and 1.68 g N per seedling per season, respectively, under the current cultural conditions. Fertilization at 1.68 g N per plant increased N content by 40% in red oak and 35% in white oak. This approach may be used to help refine nursery fertilization practices in hardwood culture to produce high-quality seedlings for field planting.

Keywords: *Luxury consumption, nitrogen, northern red oak, nutrient loading, reforestation, white oak.*

Introduction

Recent trends in the declining proportions of natural oak regeneration in many stands is of concern and is partly the result of fire suppression (Olson, 1996). In addition, present-day silvicultural practices such as single and group tree selection harvests limit oak regeneration because canopy openings are insufficient to allow shade-intolerant oak seedlings to compete with co-occurring shade-tolerant species (Dey & Parker, 1997; Larsen & Johnson, 1998; Rogers & Johnson, 1998; Jenkins & Parker, 2001). Conservation tree plantations may be a viable option to maintain or increase relative proportions of oak species in future forests (Jacobs et al., 2004). Many of these plantations are established on former agricultural fields or mine reclamation sites where seedlings must overcome intensive weed competition (Crow, 1988), animal browsing (Stange & Shea, 1998; Tripler et al., 2002) and harsh soil conditions (Bussler et al., 1984; Andersen et al., 1989). Seedling performance on these sites is often poor (Belli et al., 1999; Clark et al., 2000; Ward et al., 2000). A recent survey in Indiana, USA, reported mean survival rates of 66%, with only 33% of northern red oak (*Quercus rubra* L.) and 53% of white oak (*Quercus alba* L.) surviving seedlings deemed free to grow at 5 years of age (Jacobs et al., 2004).

Nitrogen (N) availability is one key factor limiting seedling development (Nambiar & Sands, 1984; Burdett, 1990; Margolis & Brand, 1990). Hence, judicious nursery N fertilization can lead to the production of high-quality seedlings with adequate stored nutrient and carbohydrate reserves to ensure satisfactory survival and growth under field conditions (Ingestad, 1979; Imo & Timmer, 1992). Thus, high-quality seedlings can be raised through nursery

---

Correspondence: D. F. Jacobs, Hardwood Tree Improvement and Regeneration Center, Department of Forestry and Natural Resources, Purdue University, 715 West State Street, West Lafayette, IN 47907, USA. E-mail: djacobs@purdue.edu

(Received 17 August 2005; accepted 12 April 2006)

ISSN 0282-7581 print/ISSN 1651-1891 online © 2006 Taylor & Francis
DOI: 10.1080/02827580600761611

fertilization to promote early establishment success of hardwood plantations. Conventional nursery fertilization practices in bareroot nursery culture often involve the supply of N fertilizers in equal doses at regularly spaced intervals over the growing season. This practice creates a surplus of nutrients at the beginning of culture and a deficiency by the end of the growing season owing to growth dilution (Imo & Timmer, 1992). Exponential fertilization better synchronizes nutrient supply with crop demand, which induces stable internal N concentration in plant tissues over time, referred to as steady-state nutrition (Ingestad, 1979; Imo & Timmer, 1992).

Nutrient loading (Timmer, 1997) is another approach that induces luxury nutrient uptake in excess of growth demand. Acquired excess nutrients are stored in seedling tissues as reserves for subsequent utilization following outplanting (Malik & Timmer, 1995; Salifu & Timmer, 2001). Nutrient loading is more compatible with exponential than with conventional fertilization, as shown in Figure 1 (Timmer et al., 1991; Timmer, 1997). The model shows that growth is limited at low fertility, increases rapidly to sufficiency with increased fertilization, remains constant at luxury nutrient application, but eventually declines at toxic addition. Trends in nutrient content are similar to biomass, except that luxury uptake occurs beyond sufficiency until toxicity, when levels decline owing to toxic accumulation (Imo & Timmer, 1992). By contrast, nutrient concentration continues to rise through the range of nutrient supply, slowly in the deficiency range owing to growth dilution and more rapidly in the toxic range owing to excess accumulation (Ingestad & Lund, 1986; Timmer et al., 1991). Improved outplanting performance of exponentially cultured seedlings has frequently been reported and attributed to the depletion of stored excess N, which is retranslocated to support growth until roots establish and can exploit native soil resources (Malik & Timmer, 1995; Salifu & Timmer, 2001, 2003*a*). Exponentially cultured seedlings may also be more competitive with surrounding vegetation than conventionally reared cohorts (Malik & Timmer, 1995; McAlister & Timmer, 1998).

Exponential fertilization has been successfully tested in culture of conifer species including white spruce [*Picea glauca* (Moench) Voss] (McAlister & Timmer, 1998), black spruce [*Picea mariana* (Mill.) BSP] (Salifu & Timmer, 2003*b*), Norway spruce [*Picea abies* (L.) Karst.] (Rytter et al., 2003) and a tropical angiosperm (Close et al., 2005). By contrast, little is know about nutrient storage and remobilization processes in temperate deciduous species, especially in relation to how exponential nutrient loading may influence these processes. Oak species, in particular, have received little attention in nutritional research (Tinus, 1978; Struve, 1995). Exponential nutrient loading may benefit deciduous species because about 50–90% of nutrients are resorbed from foliage (Aerts, 1996; Tagliavini et al., 1998) into root and shoot tissues (Dickson, 1989; Lacointe et al., 1994; Aerts, 1996; Duchesne et al., 2001) before senescence. Conserved nutrients are drawn upon immediately in spring to meet increased sink demand, especially for red oak during episodic growth events (Reich et al., 1980; Crow, 1988; Dickson et al., 2000).

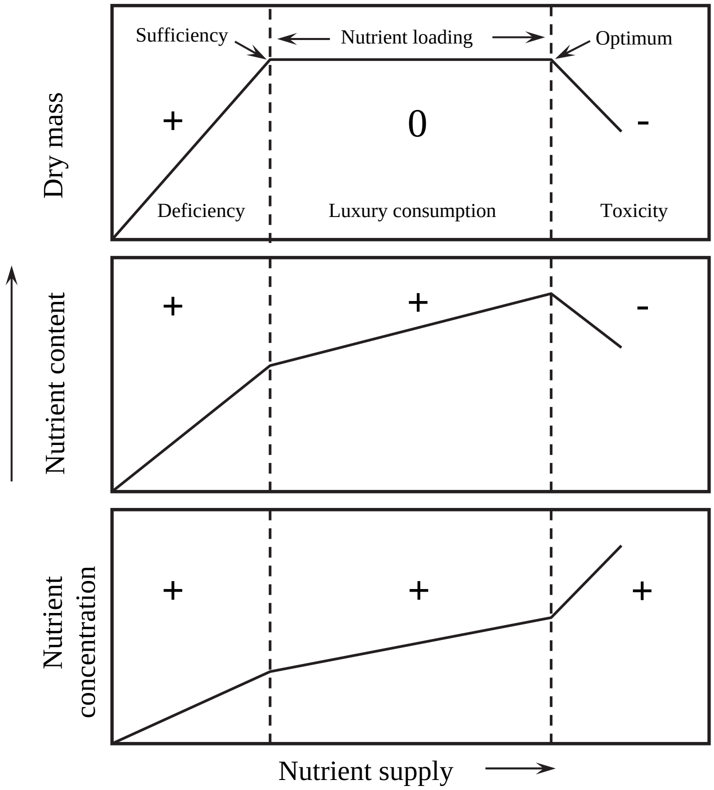
Furthermore, except for the study by McAlister and Timmer (1998), the authors are not aware of other studies that examined exponential nutrient loading in bareroot nursery production systems, the standard practice for growing hardwood seedlings in most regions of the USA. Therefore, the objectives of this study were: (1) to evaluate the suitability of the exponential nutrient loading model for application in hardwood tree seedling culture using a broad range of N supply from deficiency to toxicity; (2) to determine optimum fertilizer prescriptions for growing bareroot northern red oak and white oak during nursery culture; and (3) to quantify the contribution of native soil fertility to seedling growth and nutrition. The focus is on northern red oak and white oak because of their economic importance and frequent use in conservation tree plantings (Jacobs et al., 2004).

Materials and methods

Plant material and growing conditions

Bareroot northern red oak and white oak seedlings were grown for 18 weeks at the Indiana Department of Natural Resources Vallonia State Nursery (38°85′ N, 86°10′ W) in southern Indiana, USA. Initial soil samples were collected and analyzed to characterize native fertility. The soil textural class was a sandy loam with 65% sand, 23% silt and 12% clay. Average soil pH was 6.2 and available phosphorus (P) was 61.9 mg kg^{-1} soil. Mean soil organic matter was 1.2%. Mean potassium (K), calcium (Ca) and magnesium (Mg) were 12.4, 41.5 and 20.9 cmol(+) kg^{-1}, respectively. Seeds were obtained from local sources, uniformly mixed within species and mechanically sown in the fall (autumn) of 2003 at 81–90 seed m^{-2}. Beds were covered with straw to improve moisture retention and prevent seed predation. Germinants were thinned within 1.2×1.5 m^2 study plots to 120 seedlings per plot to ensure uniform densities.

The experimental design was a randomized complete block design with four replications (blocks).



Diagnostic interpretation	Change in plant		
	Growth	Nutrient content	Nutrient conc.
Deficiency	+	+	+
Luxury consumption	0	+	+
Toxicity	-	-	+

Figure 1. Relationships between nutrient supply and plant growth, tissue nutrient content and concentration. Nutrient supply maximizes growth at the sufficiency rate. Fertilization beyond sufficiency may induce luxury consumption where growth remains unchanged but tissue nitrogen (N) status increases. Increased tissue N concentration during luxury uptake allows the excess N to be stored as reserves. Toxicity is induced once plant growth begins to decline at increasing tissue N concentration. The optimum fertilization rate maximizes seedling growth and tissue N content. Adapted from Salifu (2003).

The 10 treatments examined were represented in each of the four beds, resulting in a total of 480 seedlings per treatment per species. Treatment plots were separated by 0.6 m buffers. In addition, one bed to either side of the study, one 7.5 m in front of the plots and one 4.5 m behind the plots were retained as unfertilized buffers to prevent fertilizer drift. Each species was grown separately and represents a separate experiment.

Fertility treatments and fertilizer models

Seedlings were grown under operational conditions (Jacobs, 2003), except for the fertilizer treatments. The standard practice at this nursery is to supply a total of 0.84 g N per seedling per season in seven equal amounts (fortnightly, i.e. every 2 weeks), which represents the conventional (C) treatment in this study. A treatment of 0 g N per seedling served as a control to examine the effect of indigenous soil fertility on seedling growth. The other eight treatments (0.42, 0.84, 1.26, 1.68, 2.10, 2.52, 2.94 and 3.35 g N per seedling) followed exponential (E) functions to match nutrient supply with seedling growth (Timmer & Aidelbaum, 1996; Timmer, 1997; Salifu & Timmer, 2003*b*) using eq. (1):

$$N_T = N_S(e^{rt} - 1) \tag{1}$$

where r is the relative addition rate required to increase N_S (N content in seed) to a final N content ($N_T + N_S$), and N_T was the desired amount to be added over the number of fertilizer applications ($t =$ 7). Average N_S determined from samples of five seeds per species ranged from 20 to 24 mg N per seed. The quantity of fertilizer to apply on a specific day (N_t) was computed using eq. (2):

$$N_t = N_s(e^{rt} - 1) - N_{t-1} \tag{2}$$

where N_{t-1} is the cumulative amount of N added up to and including the previous application. A modified exponential function was used to increase initial nutrient additions to facilitate nutrient exploitation by small root systems early in the season and to reduce application near the end of the season and avoid overfertilization, which could induce potential nutritional imbalances close to the end of nursery culture (Imo & Timmer, 1992; Jacobs & Timmer, 2005). The amount of N compensation (N_c) was initially subtracted from the last two applications calculated from eq. (2) and was delivered exponentially to correspond with exponential expansion of the root system based on eq. (3):

$$N_c = N_0(e^{-rt} - 1) \tag{3}$$

where N_0 is the final amount of N added during the compensation period. Fortnightly N applications to seedlings in each treatment are summarized in Table I. Ammonium nitrate (34–0–0) in crystal form was broadcast manually on treatment plots followed by irrigation for about 1.5–2 h to incorporate the fertilizer after each broadcast application. The water was applied by an above-ground irrigation system with a double nozzle impact head. About 5 cm of irrigation water was supplied per 0.41 ha per week, which required irrigating twice a week for 4 h at each event. Rainfall was taken into account. For example, if it rained 2 cm, subsequent irrigation was adjusted by that amount.

Seedling sampling, chemical and statistical analysis

Following seedling emergence and first leaf flush (representing the baseline or time 0), five seedlings per plot (20 per treatment) were harvested and placed in coolers (2°C) for further processing at Purdue University (West Lafayette, IN, USA). Samples were washed and measured for stem height and root-collar diameter (RCD). Samples were pooled into shoot or leaf parts, dried for 72 h at 70°C and weighed for dry mass determination. Plant samples were subsequently ground and sent for chemical analysis (A&L Great Lakes Laboratories, Fort Wayne, IN, USA), which followed standard analytical protocols. Total N was determined by combustion ("Dumas" procedure; AOAC 968.06) using a LECO nitrogen analyzer (LECO Corporation, St. Joseph, MI, USA). Plant samples were digested in nitric acid plus perchloric acid (AOAC 935.13) and other elements determined using inductively coupled argon plasma (ICAP) analysis (AOAC 985.01). P, K, Ca and Mg were determined by ICAP using extracted aliquots from soils as detailed in Brown (1997). Morphological and nutritional data were evaluated by separate analysis of variance (ANOVA) for each species based on Anderson and McLean's (1974) linear model (eq. 4) using SAS (SAS Institute, 2001):

$$Y_{ij} = \mu + t_i + \varepsilon_{(i)j} \tag{4}$$

where Y_{ij} is the measured seedling response associated with the jth block or replicate ($j = 1, 2, 3, 4$) from the ith fertility treatment ($i = 1, 2, \ldots, 10$), μ is the overall mean, t_i is the fixed effect of the ith fertility treatment and ε is the error (random effect) associated with measured response from replicates. Significant treatment means were ranked according to Waller–Duncan's multiple range tests at $\alpha = 0.05$.

Results

Total above-ground plant dry mass, leaf and stem components increased with fertilization compared with controls, which clearly demonstrates the benefits of supplemental nutrient enrichment in

Table I. Fortnightly fertilizer nitrogen (N) applied to seedlings under conventional (C) or exponential (E) fertilization regimens for 14 weeks during an 18 week nursery culture.

	Fortnightly N applied (g per seedling)									
Week	0.00	0.42E	0.84C	0.84E	1.26E	1.68E	2.10E	2.51E	2.93E	3.35E
0	0.000	0.031	0.120	0.078	0.138	0.209	0.287	0.369	0.459	0.554
2	0.000	0.033	0.120	0.065	0.098	0.132	0.165	0.198	0.231	0.264
4	0.000	0.039	0.120	0.068	0.093	0.115	0.136	0.154	0.172	0.188
6	0.000	0.051	0.120	0.089	0.121	0.149	0.174	0.197	0.220	0.240
8	0.000	0.066	0.120	0.124	0.179	0.230	0.279	0.325	0.371	0.416
10	0.000	0.100	0.120	0.207	0.315	0.423	0.529	0.633	0.738	0.843
12	0.000	0.100	0.120	0.207	0.315	0.423	0.529	0.633	0.738	0.843
Total	0.000	0.420	0.840	0.840	1.260	1.680	2.100	2.510	2.930	3.350

Note: the 0.84C treatment is the standard operational rate used for raising bareroot oak planting stock at this nursery. Higher rates represent loading treatments.

promoting seedling growth (Figure 2). Similarly, dry mass production increased over time and differed ($p = 0.0001$) between treatments by the end of the growing season (4 months after fertilization). Red oak (Figure 2, left) showed increased sink strength compared with white oak (Figure 2, right), as indicated by differences in scale. The 0.84E and 1.68E treatments had the highest above-ground biomass regardless of tissue part examined for red oak (Figure 2, left). By contrast, the white oak data show that seedlings fertilized exponentially, except for 3.35E, had greater growth than did the conventional treatment (Figure 2, right). The remainder of the paper presents detailed results and discussion of the data sampled at 4 months after fertilization.

Figure 3 for red oak and Figure 4 for white oak demonstrate that seedling growth and nutritional responses to increased fertilization conformed closely to the trends shown in the conceptual model (Figure 1). For example, seedling growth significantly increased ($p = 0.001$) with N supply in the deficiency range (<0.84 g N per plant), remained fairly stable in the luxury consumption range (0.84–1.68 g N per plant) and began to decline at higher N addition (>1.68 g N per plant) (Figure 3). Compared with unfertilized seedlings (controls), fertilization increased ($p = 0.001$) plant biomass by 113–260% for red oak and 49–144% for white oak (Figures 3 and 4, top). Similarly, shoot height and RCD increased with N supply relative to controls (Table II). Shoot height increased by 99–162% for

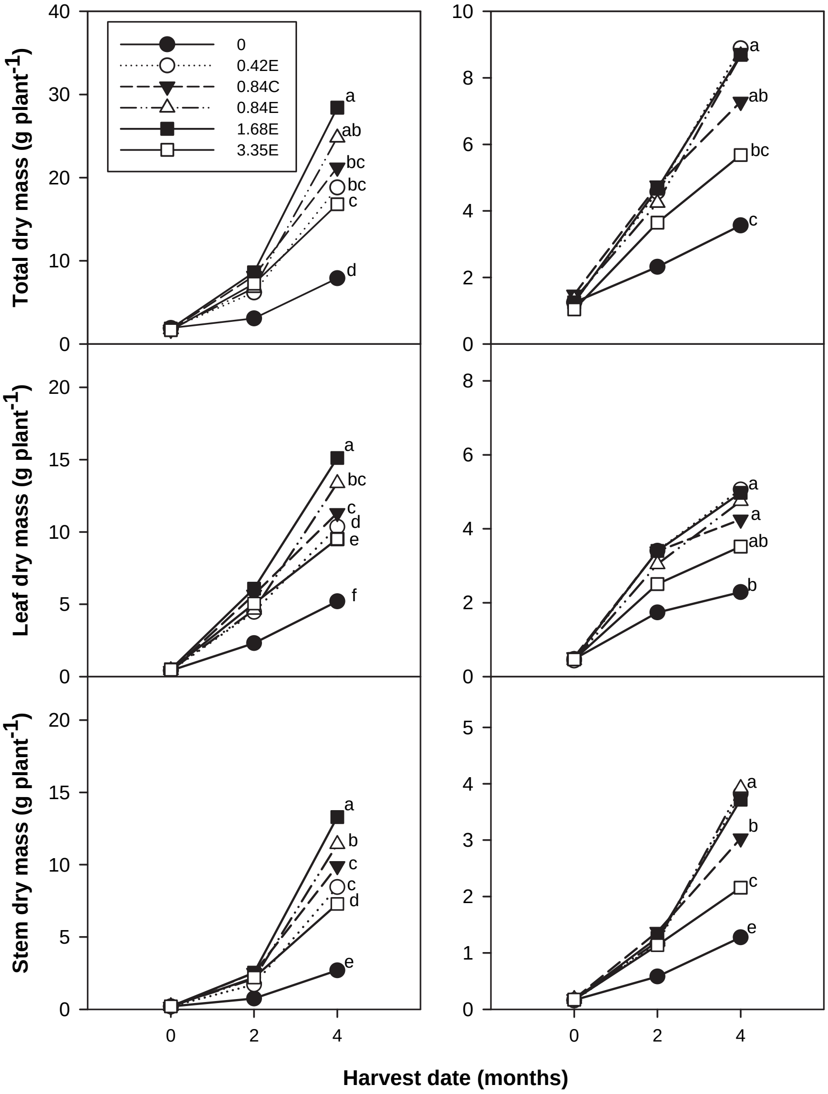


Figure 2. Above-ground seedling growth in response to increasing nutrient supply over one growing season (18 weeks) and sampled at 0, 2 and 4 months for red oak (left) and white oak (right). Treatments marked with different letters at the 4 month sampling event are statistically different according to Waller–Duncan's multiple range tests at $\alpha = 0.05$.

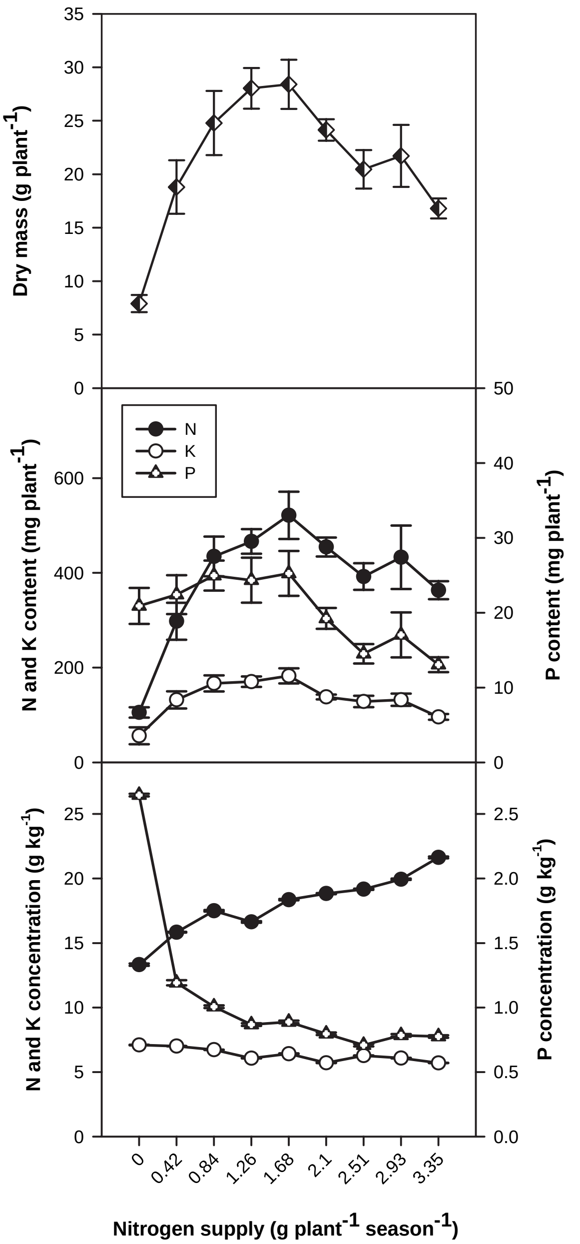


Figure 3. Red oak seedling shoot dry mass (top), nutrient content (middle) and concentration (bottom) in relation to increasing nitrogen (N) supply for one growing season (18 weeks) in the nursery. Trends suggest 1.68 g N per seedling as the optimum loading target.

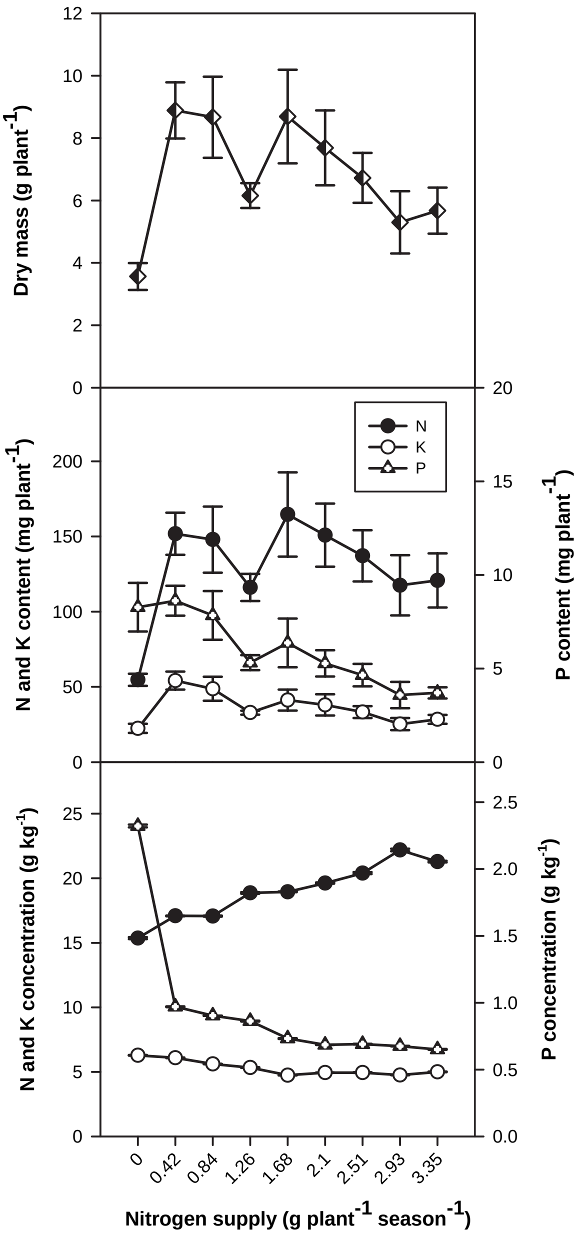


Figure 4. White oak seedling shoot dry mass (top), nutrient content (middle) and concentration (bottom) in relation to increasing nitrogen (N) supply for one growing season (18 weeks) in the nursery. Trends suggest 1.68 g N per seedling as the optimum loading target.

red oak and by 5–66% for white oak relative to unfertilized seedlings (Table II).

Tissue N concentration increased with increasing fertilization (Figures 3 and 4, bottom), consistent with the trends shown in Figure 1. For example, N concentration increased ($p = 0.001$) from 13 to 22 g kg^{-1} for red oak and from 15 to 23 g kg^{-1} for white oak (Figures 3 and 4, bottom) across the treatments relative to controls. Similarly, leaf N concentration ranged from 18 to 30 g kg^{-1} in red oak and from 20 to 29 g kg^{-1} in white oak and differed within species (Table II). The results for seedling nutrient content also followed the conceptual model and maximum nutrient uptake occurred at the 1.68 g N per seedling rate for both species (Figures 3 and 4, middle). Seedlings reared at 1.68E were able to store more N, P and K, by 40, 32 and 30% for red oak and 35, 2 and 5% for white oak, respectively, than those grown at 0.84C (Figures 3 and 4, middle). Nutrient content declined beyond the 1.68 g rate, suggesting induced toxicity at higher fertility and/or P and K limitation.

Table II. Morphological and leaf nitrogen (N) data for red oak and white oak seedlings in response to conventional (C) or exponential (E) fertilization for 14 weeks during an 18 week nursery culture.

	Red oak			White oak		
Fertilizer rate	Shoot height (cm)	RCD (mm)	Leaf N (g kg^{-1})	Shoot height (cm)	RCD (mm)	Leaf N (g kg^{-1})
0.00	34.4±3.2d	5.2±0.2d	18±1.1d	22.0±1.6d	3.8±0.2c	20±0.8c
0.42E	80.3±3.4ac	6.4±0.4cd	24±0.5c	34.2±2.4ab	5.6±0.3a	24±0.5b
0.84C	79.0±1.4ac	6.8±0.2ab	27±0.5b	28.4±3.4ac	5.3±0.3ab	24±1.1b
0.84E	82.1±4.4ab	7.2±0.3ab	27±0.5b	36.6±4.3a	5.7±0.2ab	25±0.9b
1.26E	90.2±4.2a	7.5±0.2a	27±0.9b	28.9±1.0ac	5.2±0.2ab	27±1.0ab
1.68E	85.3±3.9ab	7.6±0.3a	27±0.8b	32.8±4.1ab	5.6±0.4a	27±1.0ab
2.10E	77.7±1.5ac	6.8±0.1ab	28±1.1ab	32.8±1.6ab	5.2±0.4ab	27±0.8ab
2.51E	73.6±3.3bc	6.7±0.2ab	28±0.5ab	27.1±1.6ac	5.4±0.3ab	28±0.5a
2.93E	78.4±6.5ac	6.8±0.2ab	29±1.1a	23.1±1.7d	4.5±0.5ab	29±1.3a
3.35E	68.4±5.3c	6.2±0.2cd	30±1.4a	24.4±3.2cd	4.8±0.2ab	29±0.9a
ANOVA $p > F$						
Fertilizer rate	0.0001	0.0001	0.0001	0.0067	0.0033	0.0001

Note: the 0.84C treatment is the standard operational rate used for culturing bareroot oak planting stock at this nursery. Higher rates represent loading treatments. Data are means±SE. RCD = root-collar diameter.
Means in the same column with different letters differ significantly according to Waller–Duncan's multiple range tests, $\alpha = 0.05$.

For the same fertilizer rate (0.84 mg N per plant), the exponential delivery schedule (0.84E) increased total above-ground N uptake by 16 and 21% for red and white oak, respectively, than when applied conventionally (0.84C) (Figure 5, bottom). The observed differences can be explained by the different fertilization strategies adapted. The C treatment received more N early in the season than could be used; thus, substantial N quantities were leached out of the system and not available to plants. Later in the season, N became increasingly limited in the C treatment, resulting in growth decline. By contrast, the E treatment matched N supply with plant demand, which led to efficient uptake and utilization, resulting in larger plants with higher nutrient contents (Figure 5, bottom).

In addition, component dry mass increased with nutrient enrichment (Figure 5), consistent with the trends shown in Figure 1. Greater proportional N allocation to leaves relative to stems (Figure 5, bottom) suggests that the former act as primary sinks for nutrients. Average initial seed N content ranged from 20 to 24 mg for red and white oak. The amount of N contributed by native fertility to above-ground seedling growth can be calculated from the total N content in control seedlings minus N content in seed (N_s, see eq. 1), which equals 83 mg N per seedling per season for red oak and 34 mg N per seedling per season for white oak.

Discussion

The proposed conceptual model of nutrient loading suggests that plant growth and nutrient status will conform to a curvilinear pattern ranging from nutrient deficiency to toxicity with increased fertilization (Figure 1). Close correspondence of experimental data (Figures 3, 4 and 5) with the trends in Figure 1 demonstrates the model's suitability for application in hardwood bareroot seedling culture. Similar results have been noted for black spruce (Salifu & Timmer, 2003*b*) and red oak (Salifu & Jacobs, 2006) seedlings grown in containers. Thus, exponential nutrient loading can be effectively translated from a controlled greenhouse setting to practical bareroot nursery production systems, as demonstrated here and elsewhere (McAlister & Timmer, 1998). Exponential N loading induced luxury nutrient uptake and storage in plant tissues, which is in agreement with the results of other studies (Imo & Timmer, 1992; McAlister & Timmer, 1998; Qu et al., 2003; Salifu & Timmer, 2003*b*). In addition, the present study results support the contention that increased fertility can induce luxury nutrient uptake in red oak (Kim et al., 1996; Salifu & Jacobs, 2006), differing from the results of studies suggesting that red oak may not exhibit luxury nutrient consumption (Tripler et al., 2002). Exponential fertilization should result in the production of well-balanced seedlings with root:shoot kinetics well adapted to field conditions (Timmer, 1997; Salifu & Timmer, 2003). Although this study lacks root data, strong correlations were noted for RCD versus root volume for northern red oak ($R^2 = 0.75$) and for white oak ($R^2 = 0.68$) seedlings grown at this same nursery facility (Jacobs & Seifert, 2004). Thus, the root volume and biomass data of the studied plants are likely to follow similar patterns across treatments as observed for RCD (Table II).

Leaves of controls exhibited chlorosis reflective of severe N deficiency (Table II). The observed darker

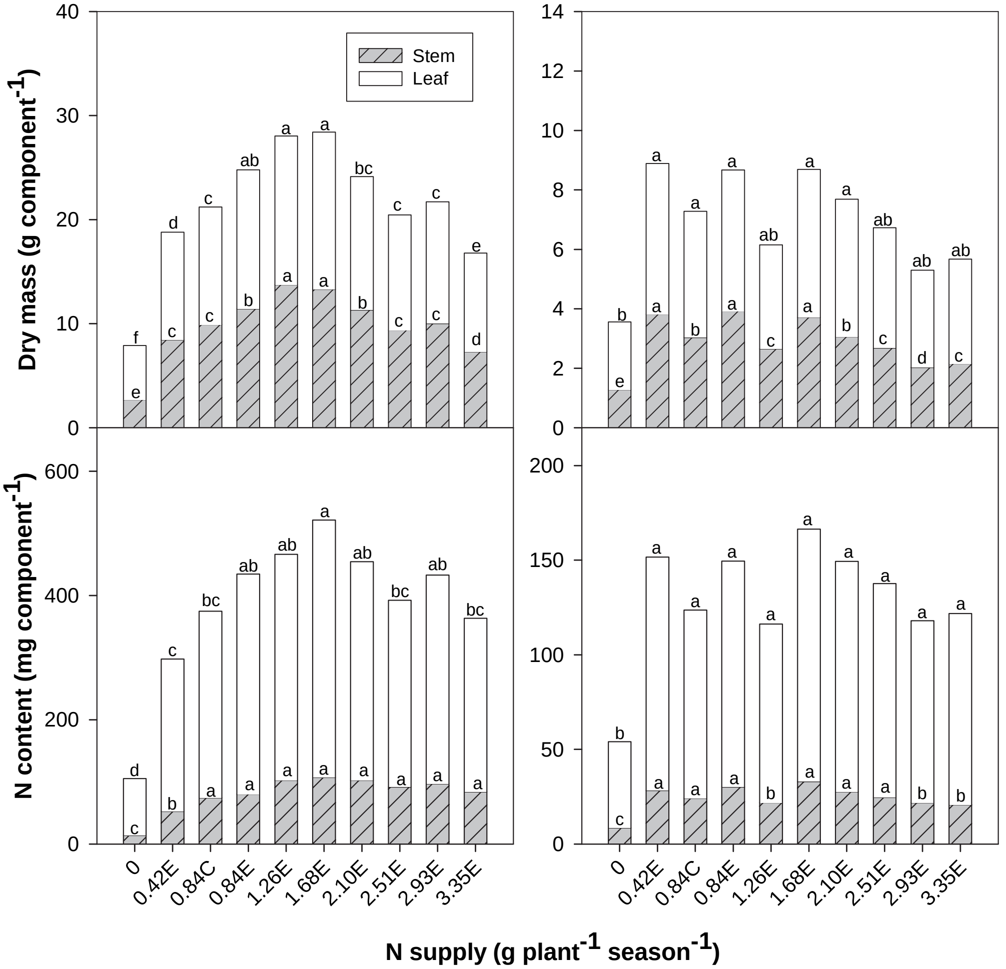


Figure 5. Above-ground seedling dry mass (top) and nitrogen (N) content (bottom) partitioned into stem and leaf components in relation to increasing N supply for one growing season (18 weeks) in the nursery for bareroot red oak (left) and white oak (right). For either stem or leaf components, bars marked with different letters are statistically different according to Waller–Duncan's multiple range tests at $\alpha = 0.05$.

leaf color of exponentially treated plants was likely to be indicative of the presence of more N, chlorophyll and greater photosynthetic ability (Hikosaka & Terashima, 1996). It is anticipated that a greater quantity of N allocated to leaves (Figure 5) will be resorbed (Aerts, 1996; Tagliavini et al., 1998) into root and shoot tissues (Dickson, 1989; Lacointe et al., 1994; Duchesne et al., 2001) before senescence. This could enable plants to provide increased N and carbohydrate reserves to meet increased sink demand (Mattsson, 1997; Tagliavini et al., 1998), especially for red oak during episodic growth events (Reich et al., 1980; Crow, 1988). Episodic or recurrent shoot and root growth results in large changes in sink strength (Crow, 1988; Dickson et al., 2000), which places severe demands on stored carbohydrate and nutrient reserves. Seedlings with higher internal nutrient reserves as conditioned by loading can draw on these critical resources at outplanting to meet increased sink demand, which should facilitate early plantation growth and establishment success.

The modified exponential fertilizer delivery schedule was more effective in promoting nutrient acquisition and storage in seedling tissues than the current constant feed approach used in practice, which corroborates the results of other studies (Timmer & Aidelbaum, 1996; Timmer, 1997; McAlister & Timmer, 1998). For example N, P and K increased by 16, 32 and 19%, respectively, in 0.84E compared with 0.84C for red oak. The reduced growth and N content but elevated tissue N concentration (Figure 6) suggests N toxicity (Salifu & Timmer, 2003*b*). This condition was induced by overfertilization. The ranges of foliar N concentration associated with toxicity (Table II) are similar to values reported previously for black spruce (Salifu & Timmer, 2003*b*).

P and K limitation are other factors limiting seedling growth at higher fertility. This is demonstrated by the reduced growth, and P and K content

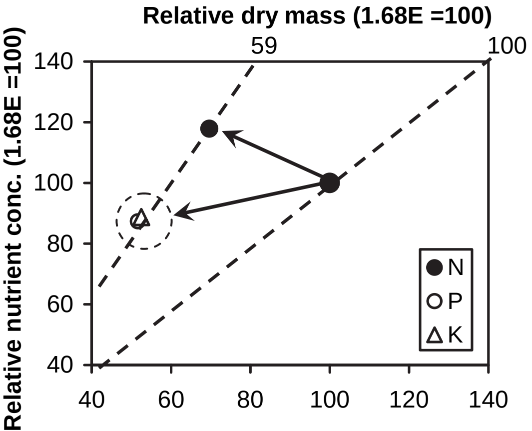


Figure 6. Vector nomogram of relative change in above-ground plant dry mass, nutrient content and concentration in bareroot northern red oak seedlings grown for 18 weeks under operational field conditions. Treatments followed exponential (E) functions. The optimum rate (1.68 g N per plant) was normalized to 100 to allow relative comparison with the toxic rate (3.35 g N per plant). The type of nutritional response induced by treatment is characterized by vector direction and magnitude, described in Salifu and Timmer (2003*b*).

and concentration (antagonistic interaction) in the vector nomogram (Figure 6). Severe competition for a limiting nutrient may cause this condition (Mead & Mansur, 1993). N, P and K dynamics are closely related (Nambiar & Fife, 1991; Munson et al., 1995; Malik & Timmer, 1996). Thus, increased P and K availability could have stimulated more N uptake at the higher fertility treatment levels. The diminished P and K with increased N concentration in plant tissues (Figures 3 and 4, bottom) further suggests the need to use balanced fertilizers containing N, P and K. Therefore, another factor to explain growth reduction is the lack of P and K in the fertilizer source. The observed P and K limitations in this study can be corrected by increased P and K supplementation (van den Dreissche & Ponsford, 1995; Boivin et al., 2002, 2004).

In conclusion, this study is the first of its kind to demonstrate the suitability of the exponential nutrient loading model for application in bareroot culture of red and white oak planting stock. The model can probably be extended to other hardwood species. Specific levels for sufficiency and optimum fertilizer prescriptions were determined to be 0.84E and 1.68E, respectively, for the studied species under the current cultural conditions. Quantified indices may differ for each species and cultural system because of variations in native fertility, cultural practices and species demand for nutrients. The exponential delivery schedule was more effective in promoting nutrient acquisition and storage in seedling tissues than the current constant fertilizer addition approach used in practice. This is exemplified by a 16, 32 and 19% increase in N, P and K, respectively, in 0.84E compared with 0.84C for red oak. Further benefit could be realized by using balanced fertilizers that contain N, P and K in exponential fertilization programs rather than only N-based fertilizers as currently practiced. Native soil fertility proved deficient, contributing about 83 and 34 mg N per seedling per season to support above-ground growth of red oak and white oak seedlings, respectively. Such nutrient limitation was associated with reduced seedling growth at higher N supply. There is a need to extend exponential nutrient loading to other hardwood species to quantify further the optimum fertilizer prescriptions for raising high-quality seedlings for field planting. The importance of resorption for conserving nutrients in stems and root tissues of deciduous species for future utilization in the field also needs investigation. The validated model provides a general framework for rationalizing and quantifying target fertilizer prescriptions, which can guide the production of high-quality hardwood bareroot nursery stock for field plantings.

Acknowledgements

This study was funded by the Hardwood Tree Improvement and Regeneration Center and Purdue University, Department of Forestry and Natural Resources. Indiana Department of Natural Resources Vallonia State Tree Nursery contributed nursery space and seedlings. We appreciate advice, field and (or) laboratory assistance from A. Bear, B. Beheler, L. Birge, M. Birge, B. Hawkins, B. Jewell, S. Jewell, J. McKenna, M. Nicodemus, P. O'Conner, J. Redicker, R. Redicker, M. Spalding, M. Selig, W. Skrobutt, J. Wichman and R. Winks. We thank Mats Hannerz and two anonymous reviewers for appraising the manuscript.

References

Aerts, R. (1996). Nutrient resorption from senescing leaves of perennials: Are there general patterns? *Journal of Ecology*, *84*, 597–608.

Andersen, C. P., Bussler, B. H., Chaney, W. R., Pope, P. E. & Byrnes, W. R. (1989). Concurrent establishment of ground cover and hardwood trees on reclaimed mined land and unmined reference sites. *Forest Ecology and Management*, *28*, 81–99.

Anderson, V. L. & McLean, R. A. (Eds.) (1974). *Design of experiments: A realistic approach*. New York: Marcel Dekker.

Belli, K. L., Hart, C. P., Hodges, J. D. & Stanturf, J. A. (1999). Assessment of the regeneration potential of red oaks and ash on minor bottoms of Mississippi. *Southern Journal of Applied Forestry*, *23*, 133–138.

Boivin, J. R., Miller, B. D. & Timmer, V. R. (2002). Late-season fertilization of *Picea mariana* seedlings under greenhouse culture: Biomass and nutrient dynamics. *Annals of Forest Science*, *59*, 255–264.

Boivin, J. R., Salifu, K. F. & Timmer, V. R. (2004). Late-season fertilization of *Picea mariana* seedlings: Intensive loading and outplanting response on greenhouse bioassays. *Annals of Forest Science*, *61*, 737–745.

Brown, J. R. (Ed.) (1997). *Recommended chemical soil test procedures for the North Central Region* (NCR Publ. No. 221, rev. ed.). Missouri Agricultural Experiment Station SB 1001.

Burdett, A. N. (1990). Physiological processes in plantation establishment and development of specification for forest planting stock. *Canadian Journal of Forest Research*, *20*, 415–427.

Bussler, B. H., Byrnes, W. R., Pope, P. E. & Chaney, W. R. (1984). Properties of mine soil reclaimed for forest land use. *Soil Science Society of America Journal*, *48*, 178–184.

Clark, S. L., Schlarbaum, S. E. & Kormanik, P. P. (2000). Visual grading and quality of 1-0 northern red oak seedlings. *Southern Journal of Applied Forestry*, *24*, 93–97.

Close, D. C., Bail, I., Hunter, S. & Beadle, C. L. (2005). Effects of exponential nutrient loading on morphological and nitrogen characteristics and on after planting performances of *Eucalyptus globulus* seedlings. *Forest Ecology and Management*, *205*, 397–403.

Crow, T. R. (1988). Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*): A review. *Forest Science*, *34*, 19–40.

Dey, D. C. & Parker, W. C. (1997). Overstory density affects field performance of underplanted red oak (*Quercus rubra* L.) in Ontario. *Northern Journal of Applied Forestry*, *14*, 120–125.

Dickson, R. E. (1989). Carbon and nitrogen allocation in trees. *Annals of Forest Science*, *46*, 631–647.

Dickson, R. E., Tomlinson, P. T. & Isebrands, J. G. (2000). Partitioning of current photosynthate to different chemical fractions in leaves, stems, and roots of northern red oak seedlings during episodic growth. *Canadian Journal of Forest Research*, *30*, 1308–1317.

van den Dreissche, R. & Ponsford, D. (1995). Nitrogen induced potassium deficiency in white spruce (*Picea glauca*) and Englemann spruce (*Picea engelmannii*) seedlings. *Canadian Journal of Forest Research*, *25*, 1445–1454.

Duchesne, L., Ouimrt, R., Camire, C. & Houle, D. (2001). Seasonal nutrient transfers by foliar resorption, leaching, and litter fall in a northern hardwood forest at Lake Clair Watershed, Quebec, Canada. *Canadian Journal of Forest Research*, *31*, 333–344.

Hikosaka, K. & Terashima, I. (1996). Nitrogen partitioning among photosynthetic components and its consequence in sun and shade plants. *Functional Ecology*, *10*, 335–343.

Imo, M. & Timmer, V. R. (1992). Nitrogen uptake of Mesquite seedlings at conventional and exponential fertilization schedules. *Soil Science Society of America Journal*, *56*, 927–934.

Ingestad, T. (1979). Nitrogen and plant growth: Maximum efficiency of nitrogen fertilizers. *Ambio*, *6*, 146–151.

Ingestad, T. & Lund, A. B. (1986). Theory and technique for steady state mineral nutrition and growth of plants. *Scandinavian Journal of Forest Research*, *1*, 439–453.

Jacobs, D. F. (2003). *Nursery production of hardwood seedlings* (FNR-212). Department of Forestry and Natural Resources, Purdue University Cooperative Extension Service.

Jacobs, D. F. & Seifert, J. R. (2004). Re-evaluating the significance of the first-order lateral root grading criterion for hardwood seedlings. In *Proceedings of the Fourteenth Central Hardwood Forest Conference*. USDA Forest Service North Central Experiment Station (Gen. Tech. Rep. NE-316, pp. 382–388).

Jacobs, D. F. & Timmer, V. R. (2005). Fertilizer-induced changes in rhizosphere electrical conductivity: Relation to forest tree seedling root system growth and function. *New Forests*, *30*, 147–166.

Jacobs, D. F., Ross-Davis, A. L. & Davis, A. S. (2004). Establishment success of conservation tree plantations in relation to silvicultural practices in Indiana, USA. *New Forests*, *28*, 23–36.

Jenkins, M. A. & Parker, G. R. (2001). Woody species composition of disturbed forests in intermittent stream bottomlands of southern Indiana. *Journal of the Torrey Botanical Society*, *128*, 165–175.

Kim, C., Sharik, T. L., Jurgensen, M. F., Dickson, R. E. & Buckley, D. S. (1996). Effects of nitrogen availability on northern red oak seedling growth in oak and pine stands in northern Lower Michigan. *Canadian Journal of Forest Research*, *26*, 1103–1111.

Lacointe, A., Sauter, J. J., Ameglio, T., Harms, U., Pellicer, V. & Frossard, I. S. (1994). Carbohydrate and protein reserves in trees. In *EUROSILVA—Contribution to forest tree physiology*, INRA, Durban.

Larsen, D. R. & Johnson, P. S. (1998). Linking the ecology of natural oak regeneration to silviculture. *Forest Ecology and Management*, *106*, 1–7.

McAlister, J. A. & Timmer, V. R. (1998). Nutrient enrichment of white spruce seedlings during nursery culture and initial plantation establishment. *Tree Physiology*, *18*, 195–202.

Malik, V. & Timmer, V. R. (1995). Interaction of nutrient-loaded black spruce seedlings with neighboring vegetation in greenhouse environments. *Canadian Journal of Forest Research*, *25*, 1017–1023.

Malik, V. & Timmer, V. R. (1996). Growth, nutrient dynamics, and interspecific competition of nutrient-loaded black spruce seedlings on a boreal mixedwood site. *Canadian Journal of Forest Research*, *26*, 1651–1659.

Margolis, H. A. & Brand, D. G. (1990). An ecophysiological basis for understanding plantation establishment. *Canadian Journal of Forest Research*, *20*, 375–390.

Mattsson, A. (1997). Predicting field performance using seedling quality assessment. *New Forests*, *13*, 227–252.

Mead, D. J. & Mansur, I. (1993). Vector analysis of foliage data to study competition for nutrients and moisture: An agroforestry example. *New Zealand Journal of Forest Science*, *23*, 27–39.

Munson, A. D., Margolis, H. A. & Brand, D. G. (1995). Seasonal nutrient dynamics in white pine and white spruce in response to environmental manipulation. *Tree Physiology*, *15*, 141–149.

Nambiar, E. K. S. & Fife, D. N. (1991). Nutrient retranslocation in temperate conifers. *Tree Physiology*, *9*, 185–207.

Nambiar, E. K. S. & Sands, R. (1984). Competition for water and nutrients in forests. *Canadian Journal of Forest Research*, *23*, 1955–1968.

Olson, S. D. (1996). The historical occurrence of fire in the Central Hardwoods, with emphasis on Southcentral Indiana. *Natural Areas Journal*, *16*, 248–256.

Qu, L., Quoreshi, A. M. & Koike, T. (2003). Root growth characteristics, biomass and nutrient dynamics of seedlings of two larch species raised under different fertilization regimes. *Plant and Soil*, *255*, 293–302.

Reich, P. B., Teskey, R. O., Johnson, P. S. & Hinckley, T. M. (1980). Periodic root and shoot growth in oak. *Forest Science*, *26*, 590–598.

Rogers, R. & Johnson, P. S. (1998). Approaches to modeling natural regeneration in oak-dominated forests. *Forest Ecology and Management*, *106*, 45–54.

Rytter, L., Ericsson, T. & Rytter, R.-M. (2003). Effects of demand-driven fertilization on nutrient use, root:plant ratio and field performance of *Betula pendula* and *Picea abies*. *Scandinavian Journal of Forest Research*, *18*, 401–415.

Salifu, K. F. (2003). *Nitrogen retranslocation of young Picea mariana to varied nitrogen supply and plant nutrient reserves*. PhD Thesis, University of Toronto, Canada.

Salifu, K. F. & Jacobs, D. F. (2006). Characterizing fertility targets and multi-element interactions in nursery culture of *Quercus rubra* seedlings. *Annals of Forest Science*, *63*, 231–237.

Salifu, K. F. & Timmer, V. R. (2001). Nutrient retranslocation response of *Picea mariana* seedlings to nitrogen supply. *Soil Science Society of America Journal*, *65*, 905–913.

Salifu, K. F. & Timmer, V. R. (2003a). Nitrogen retranslocation response of young *Picea mariana* to nitrogen-15 supply. *Soil Science Society of America Journal*, *67*, 309–317.

Salifu, K. F. & Timmer, V. R. (2003b). Optimizing nitrogen loading of *Picea mariana* seedlings during nursery culture. *Canadian Journal of Forest Research*, *33*, 1287–1294.

SAS Institute (2001). *SAS/START user's guide*. Cary, NC: SAS Institute.

Stange, E. E. & Shea, K. L. (1998). Effects of dear browsing, fabric mats, and tree shelters on *Quercus rubra* seedlings. *Restoration Ecology*, *6*, 29–34.

Struve, D. K. (1995). Nitrogen, phosphorus and potassium recovery of container-grown red oak and blackgum seedlings under different fertilizer application methods. *Journal of Environmental Horticulture*, *13*, 169–175.

Tagliavini, M., Millard, P. & Quartieri, M. (1998). Storage of foliar-absorbed nitrogen and remobilization for spring growth in young nectarine (*Prunus persica* var. *nectarina*) trees. *Tree Physiology*, *18*, 203–207.

Timmer, V. R. (1997). Exponential nutrient loading: A new fertilization technique to improve seedling performance on competitive sites. *New Forests*, *13*, 279–299.

Timmer, V. R. & Aidelbaum, A. S. (1996). Manual for exponential nutrient loading of seedlings to improve outplanting performance on competitive forest sites (NODA/NFP Tech. Rep. TR25). Sault Ste Marie, ON: Natural Resources Canada, Canadian Forest Service.

Timmer, V. R., Armstrong, G. & Miller, B. D. (1991). Steady-state nutrient preconditioning and early outplanting performance of containerized black spruce seedlings. *Canadian Journal of Forest Research*, *21*, 585–594.

Tinus, R. W. (1978). Production of container-grown hardwoods. *Tree Planters' Notes*, *29*, 3–9.

Tripler, C. E., Canham, C. D. & Inouye, R. S. (2002). Soil nitrogen availability, plant luxury consumption, and herbivory by white-tailed deer. *Oecologia*, *133*, 517–524.

Ward, J. S., Gent, M. P. N. & Stephens, G. R. (2000). Effects of planting stock quality and browse protection-type on height growth of northern red oak and eastern white pine. *Forest Ecology and Management*, *127*, 205–216.