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Effects of Fertilization on Media Chemistry and *Quercus rubra* Seedling Development under Subirrigation

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***Abstract*. Excessive fertilization may induce physiological drought and/or ion toxicity, which can reduce growth or cause mortality in cultured plants. Although nursery subirrigation produces stock of forest trees of equal or better quality to conventional overhead irrigation, detailed analyses of fertilization responses specific to these systems are lacking. We evaluated the effects of fertility applied as a 15N–9P–12K controlled-release fertilizer at rates equivalent to 0, 1.2, 1.8, 2.4, 3.0, or 3.6 g nitrogen (N) per plant on media properties and northern red oak (*Quercus rubra* L.) seedling development grown with subirrigation. Aboveground plant growth and nutrient content of seedlings increased up to 1.8 g N/plant but declined at higher rates and total mortality occurred for treatments of 2.4 to 3.6 g N/plant by the end of cultivation. Root biomass generally declined with increasing fertilization. Media electrical conductivity (EC) increased with increasing fertility, particularly in the upper media layers, where values exceeded 3.0 $dS \cdot m^{-1}$ at the highest rates. Fertilization had little effect on media pH. Predawn leaf water potential and osmotic potential (ψ_S) were reduced at high nutrient applications. Thus, increasing fertility beyond $\approx$1.8 g N/plant in this subirrigation system apparently resulted in accumulation of excessive fertilizer salts in media and/or ion toxicity, which caused plant mortality. Because subirrigation systems are prone to persistence of residual fertilizer salts in the medium and holding tanks, fertilization prescriptions must be carefully tailored to species and cultural systems to prevent potential for plant damage associated with overfertilization.**

Increased demand for container nursery stock for commercial forestry, restoration/ wildlife plantings, and landscaping has generated a need to optimize watering methods, media types, and nutrient management (Oliet and Jacobs, 2012). Subirrigation has recently been demonstrated as an effective alternative to overhead irrigation, especially for container seedling propagation of broadleaves (Davis et al., 2011a; Schmal et al., 2011). In subirrigation systems, irrigation water is delivered from beneath container trays and (optionally) recycled, which reduces wastewater, nutrient-leaching losses, and uneven water distribution associated with overhead systems (Morvant et al., 1997; Schmal et al., 2011). Subirrigation has been shown to substantially conserve irrigation water (Dumroese et al., 2006; Landis and Wilkinson, 2004) and promote plant growth at reduced nutrient applications compared with overhead systems (Beeson and Knox, 1991; Pinto et al., 2008). Subirrigated forest tree seedlings are usually of equal or better quality to those produced under comparable culture using overhead irrigation systems (Davis et al., 2008, 2011a) with these differences being maintained after field establishment (Bumgarner et al., 2008; Davis et al., 2011b).

Supplemental nutrition through fertilization is essential in these soilless media nursery systems (Landis et al., 1989). When not optimized for a given species and cultural conditions, however, fertilization can result in nutritional disorders such as induced deficiency of other nutrients and/or ion toxicity (Salifu and Jacobs, 2006; Salifu and Timmer, 2003). Despite the demonstrated potential of subirrigation, detailed analyses of fertilization responses specific to these systems is lacking (Schmal et al., 2011). This may be particularly important given observations of persistent residual fertilizer salts in the medium and holding tanks under subirrigation systems that recycle runoff water for multiple irrigation cycles (Dumroese et al., 2006, 2011).

Fertilization in any form can alter rhizosphere chemical and physical properties including pH, EC, ion availability, and ψ_S. For example, when nitrate (NO_3^-) is taken up preferentially over ammonium (NH_4^+), OH^- will be released from the root to maintain charge balance and the media pH will increase. The opposite is true if NH_4^+ is taken up (Jacobs and Timmer, 2005). Changes in pH result in altered ion availability, which can create deficiency of important nutrients and toxicity of other ions, such as aluminum, reducing root growth and development (Jacobs and Timmer, 2005).

EC of media solution is an indication of fertilizer salts in the medium (Landis et al., 1989) and higher EC levels reflect greater salt buildup. Greater fertilizer inputs and decreased media moisture exponentially increase EC of the media solution, which can be detrimental to plant growth (Jacobs and Timmer, 2005; Landis et al., 1989). Furthermore, the addition of fertilizer can lower media solution ψ_S, resulting in a disrupted water potential gradient. A disturbed gradient can cause physiological drought in plants, and plants may close stomata in response. Although stomatal closure conserves tissue water and could prevent lethal desiccation, it is done at the cost of CO_2 assimilation (Burdett, 1990). Consequently, optimal plant growth is not achieved because of limitations in net photosynthesis.

Problems associated with reduced ψ_S may become exaggerated for plants grown in subirrigation systems as a result of the upward flow of ions with water by capillarity, resulting in high soluble salt levels in the upper layers of growing media (Davis et al., 2008; Dumroese et al., 2006, 2011; Pinto et al., 2008). Tolerance to high EC is species-specific, although tolerance levels among broadleaves are not well understood (Jacobs and Timmer, 2005). Thornton et al. (1988) reported that EC levels greater than 1.0 $dS \cdot m^{-1}$ caused damage to northern red oak (*Quercus rubra* L.) seedlings including foliar discolorations and reduced leaf dry mass production, suggesting the potential sensitivity of this species.

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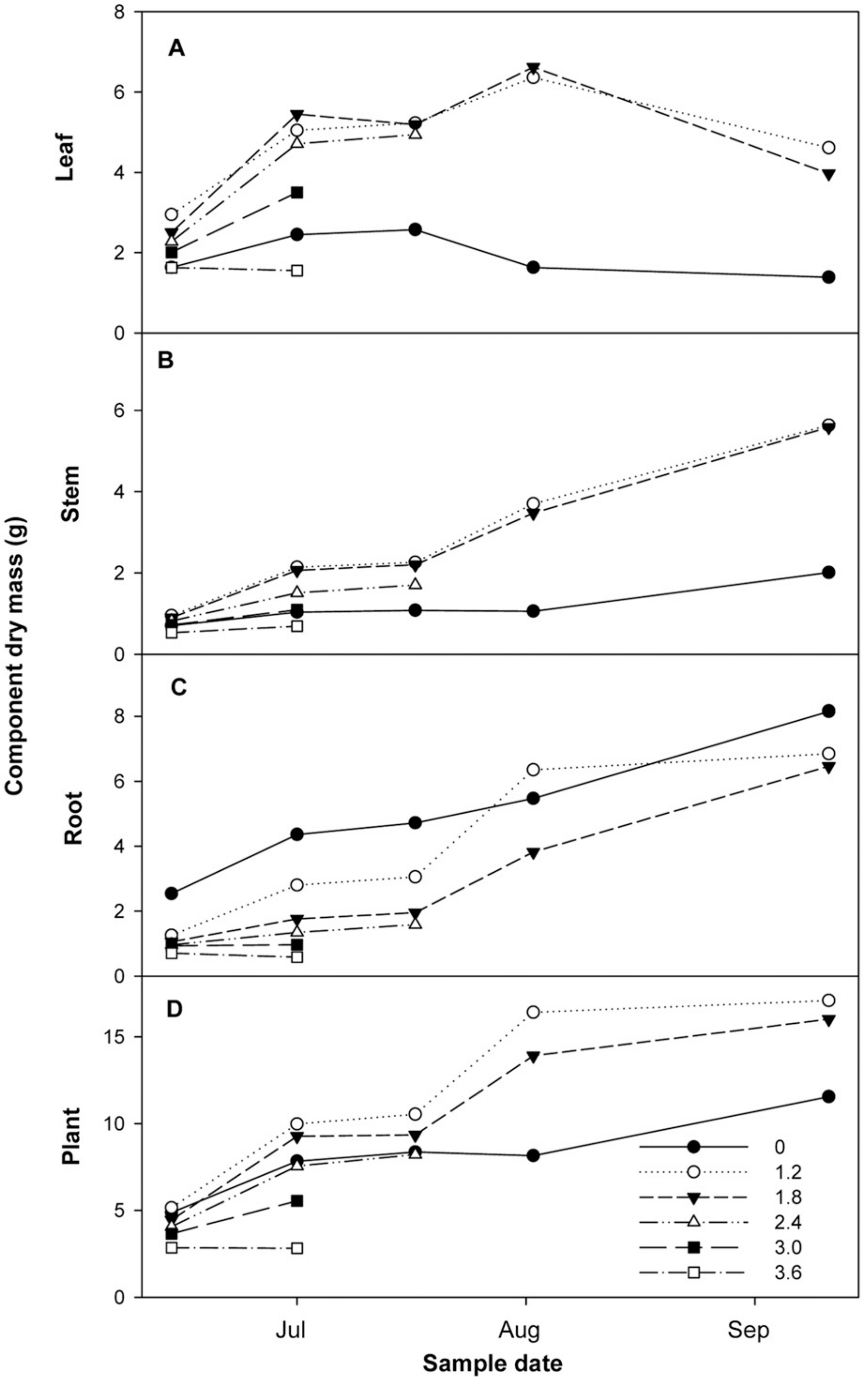

Fig. 1. Effects of fertilizer on northern red oak seedling leaf (**A**), stem (**B**), root (**C**), and whole plant (**D**) dry mass sampled over time (n = 6). Rates given are grams nitrogen (N)/plant.

In a previous study (Bumgarner et al., 2008), we examined the effects of media composition and fertility on growth of northern red oak seedlings under subirrigation vs. overhead irrigation systems. Subirrigated seedlings had greater field diameter growth, although nursery fertilization (1.2 g N/plant) resulted in reduced seedling field survival and height growth compared with the control (unfertilized treatment). Thus, the current study was designed to more closely examine the effects of a wide range of fertility rates applied during subirrigation on media pH, EC, and on the physiology and morphology of container-grown northern red oak seedlings.

Methods

Growth conditions and experimental design. Northern red oak acorns were collected in Fall 2006 from a single mother tree on the Purdue University campus, West Lafayette, IN (lat. 40°25′ N, long. 86°55′ W). Seeds were germinated on mist benches in trays covered with burlap and grown on a greenhouse bench in the Purdue Department of Horticulture and Landscape Architecture Plant Growth Facility. Germinated acorns were sown into containers of 656-cm^3 volume and dimensions of 6.4 cm × 25 cm (diameter × length) (D40 Deepot; Stuewe and Sons, Tangent, OR) in a 60% peatmoss:40% perlite soilless mix on 7 May 2007. Osmocote Plus (15N–9P–12K) 5-6 month controlled-release fertilizer (The Scotts Company, Marysville, OH) was incorporated into the medium at one of six rates: 0 (control), 8, 12, 16, 20, or 24 g per container, which is equivalent to 0, 1.2, 1.8, 2.4, 3.0, or 3.6 g N/plant, respectively. All containers were watered overhead by hand to saturation until shoots emerged, which occurred within 2 weeks of sowing, and subirrigation was used thereafter. Six subirrigation trays were used. Each subirrigation tray represented a replicate block and all six fertility treatments were randomly arranged within each tray.

The experimental design was a randomized complete block design with six fertility treatments replicated in six blocks. Thirty seedlings of each treatment were grown per block. Each block consisted of one 1.22 m × 1.22-m subirrigation tray (Spencer-Lemaire, Edmonton, Alberta, Canada) with a 208-L water reservoir (Mid-West Grow Master, St. Charles, IL) connected to a submersible pump and timer. The reservoirs were replenished with water weekly. Seedlings were grown for 16 weeks under mean day/night temperature of 24/20 °C and ambient light conditions. Container weights were used in three randomly selected trays per block to determine irrigation needs using the gravimetric method as described in Landis et al. (1989). Containers were weighed at saturation every 4 weeks to account for weight of new growth and seedlings were irrigated when containers weighed 75% ± 5% of saturated weight. Irrigation was required every 4 to 5 d during initial seedling establishment and every 2 to 3 d during the remainder of the growing period. Because fertility treatments were distributed randomly across containers within each block, our sampling regime should have helped to account for differing drying rates of fertility treatments. Plants were rotated biweekly within benches to minimize edge effects.

Plant and media sampling, chemical, and statistical analysis. Seedling height, root-collar diameter (RCD), leaf area using a portable leaf area meter (LI-COR 3100C; LI-COR Inc., Lincoln, NE), and dry mass of leaves, stems, and roots (divided into three sections: 0 to 5 cm depth, 5 to 15 cm depth, and 15 to 25 cm depth) were measured on five dates (14 June, 1 July, 17 July, 2 Aug., and 11 Sept. 2007) with a sample size of six seedlings per treatment replication on each sampling date. Plant material was oven-dried for 72 h at 68 °C for dry mass determination and subsequently ground for nutrient concentration analyses. Nutrient analysis of plant samples was conducted by A & L Great Lakes Laboratories, Inc. (Fort Wayne, IN)

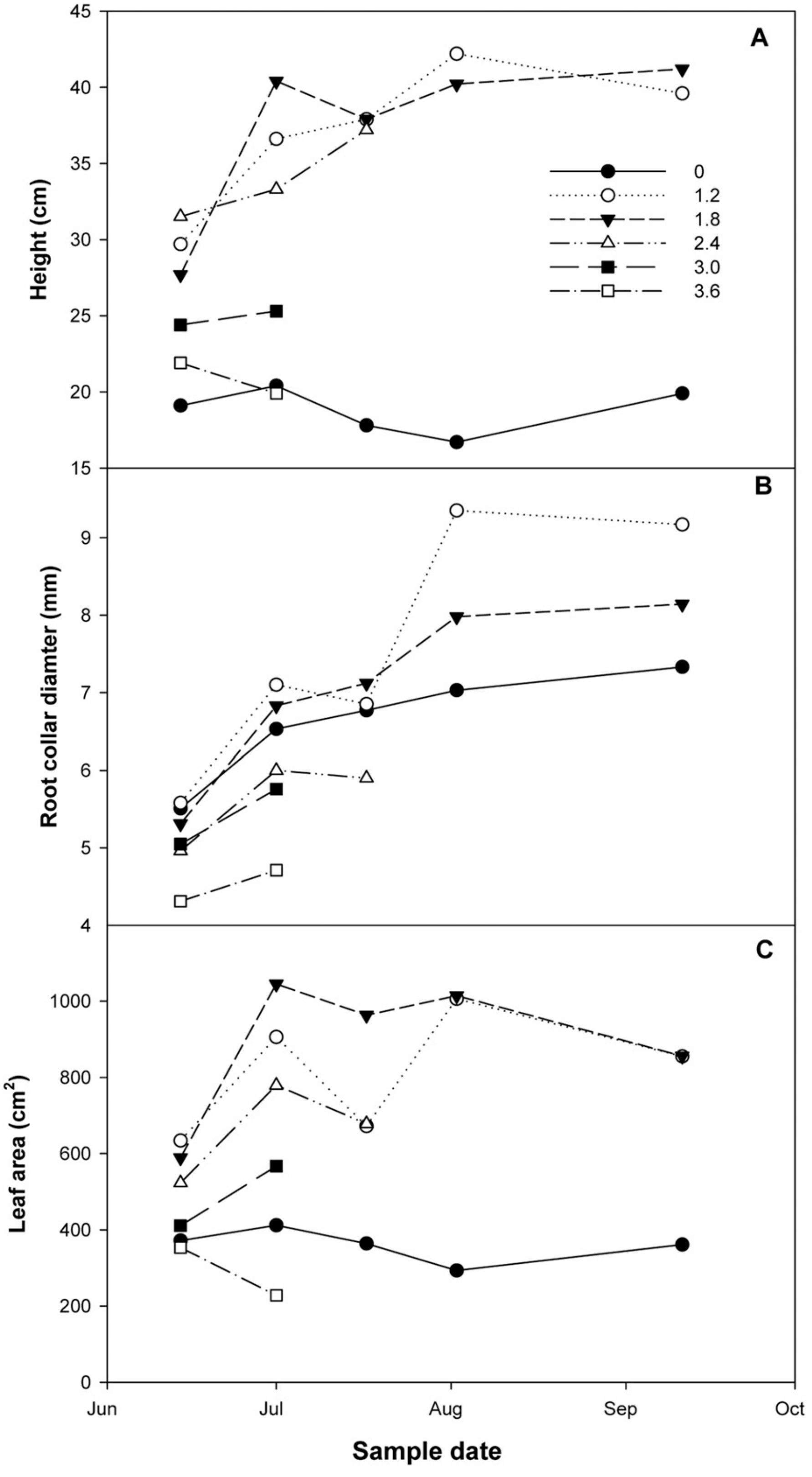

Fig. 2. Effects of fertilizer rate on northern red oak seedling shoot height (**A**), root collar diameter (**B**), and leaf area (**C**) sampled over time (n = 6). Rates given are grams nitrogen (N)/plant.

using the Association of Official Analytical Chemist (AOAC) methods. Total N was determined by the combustion ("Dumas") procedure (AOAC 968.06) using a LECO nitrogen analyzer (LECO Corporation, St. Joseph, MI). Plant samples were digested in nitric and perchloric acids (AOAC 935.13) and phosphorus (P) and potassium (K) were determined using inductively coupled argon plasma analysis (AOAC 985.01).

Saturated media extracts were collected on the same five dates (14 June, 1 July, 17 July, 2 Aug., and 11 Sept. 2007) to monitor changes in root zone EC and pH (Yelanich and Biernbaum, 1994). Procedures for saturated media extracts were as per Warncke (1986). EC and pH were measured on extracted media solutions using a Field Scout EC meter (Spectrum Technologies, Inc., Plainfield, IL) and the Accumet 950 pH/ion Meter (Fisher Scientific, Pittsburgh, PA), respectively.

Seedlings were sampled on a different five dates (21 June, 7 July, 29 July, 14 Aug., and 10 Sept. 2007) for predawn leaf water potential using a Scholander-type pressure chamber (Model 600; PMS Instruments, Inc., Corvallis, OR) as per methodology in Cleary and Zaerr (1980). Osmotic potential was measured on expressed leaf sap on the same leaf used for leaf water potential (Callister et al., 2006). A sample size of six seedlings per treatment replication was used on each sampling date. Sections of leaves were removed, placed into microfuge tubes containing a plastic mesh insert, and immediately placed in liquid N. The tubes were then closed and kept on ice until returning to the laboratory, where they were stored at –4°C and then centrifuged at $\approx$15,000 rpm for 5 min to extract cell sap. The sap was immediately placed in an osmometer (Wescor 5200; Wescor Inc., Logan, UT). Solute concentration was converted to ψ_S using the van't Hoff equation $\psi_s = -RTC$, where R is the gas constant, T is absolute temperature, and C is the molar solute concentration.

Analysis of variance using PROC GLM was conducted on all data using SAS software (SAS Institute Inc., Cary, NC). All models were tested for assumptions of normality, constant variance, and linearity with no transformations needed. Significant treatment means ($P < 0.05$) were ranked according to Tukey's honestly significant difference test at $\alpha = 0.05$.

Results

Visual symptoms of chlorosis and necrosis were apparent by 17 July for seedlings in the higher fertility treatments (i.e., 2.4 to 3.6 g N/plant), resulting in total mortality by 14 Aug. for treatments 3.0 to 3.6 g N/plant and by 10 Sept. for treatments 2.4 to 3.6 g N/plant.

Relative to the control treatment, plant dry mass was 59% lower in the highest fertility treatment (3.6 g N/plant) on the first sample date (Fig. 1D). Similar trends were maintained at the second and third sampling events. By the fourth sample date (that excluded treatments 3.0 to 3.6 g N/plant), plant dry mass of the control plants was 50% to 61% lower than dry mass of plants in the 1.2, 1.8, and 2.4 g N/plant treatments and was still lower than the 1.2 and 1.8 g N/plant treatments at the final sampling (Fig. 1D). Similar trends occurred for stem and leaf attributes (Fig. 1A and B).

Mean root dry mass was highest for plants in the control treatment and generally decreased with increasing fertility with no

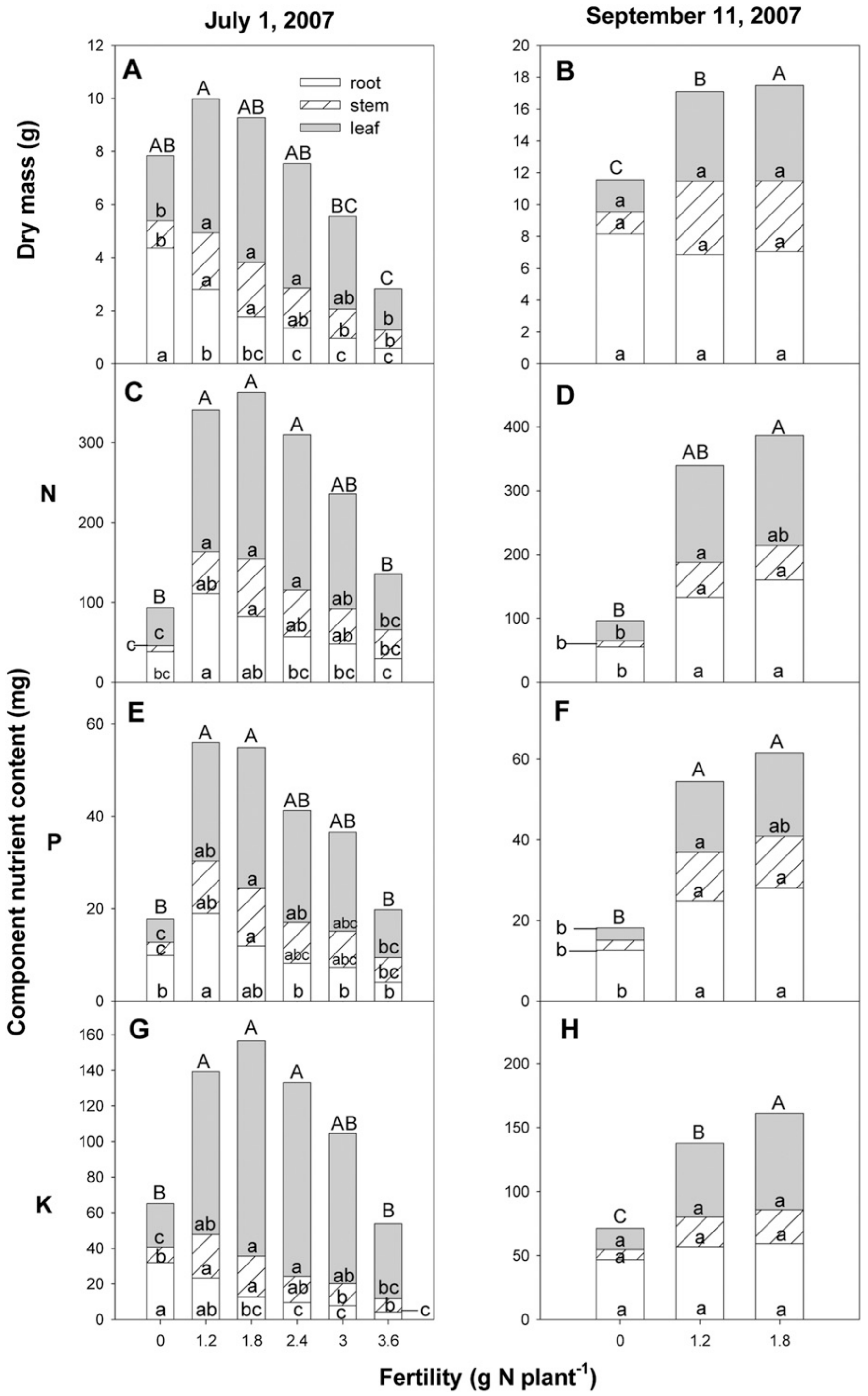

Fig. 3. Effects of fertilizer rate on northern red oak seedling component dry mass (**A–B**), nitrogen (**C–D**), phosphorus (**E–F**), and potassium (**G–H**) content sampled midway (1 July) and at final harvest (11 Sept.) (n = 6). For a given sampling period, different lower- and upper-case letters represent significant differences between treatments within plant organ and for whole plant based on Tukey's honestly significant difference test at $\alpha = 0.05$.

pronounced distinctions according to root zone (Figs. 1C, 3A–B, and 4A–B).

Fertilization up to 1.8 g N/plant resulted in greater seedling shoot height, RCD, and leaf area over time (Fig. 2). In July, nutrient concentration in plant components was affected by fertility treatment except for root K (Table 1). Plant N concentration was highest in leaves and shoots of the higher fertility treatments, whereas N concentration in roots was only lower in control plants (Table 1). Similar trends were observed for P and K in all plant components. N, P, and K were 47%, 102%, and 72% greater, respectively, at 3.6 g N/plant compared with the control treatment (Fig. 5). Nutrient content data, however, showed that although seedlings treated with 1.2 to 2.4 g N/plant had generally higher N, P, and K content compared with the control treatment, fertilization above this rate resulted in N, P, and K content similar to the control treatment (Fig. 3C, E, and G). On the final sample date (11 Sept.), which included only treatments 0 to 1.8 g N/plant, nutrient concentrations followed similar trends according to increased fertility except for stem N, P, and K concentrations, which were unaffected by fertilization (Table 1). Fertilized seedlings had higher plant dry mass and component N, P, and K content compared with seedlings in the control treatment (Fig. 3D, F, and G).

Media solution pH was higher in the control treatment than the fertilized treatments in only the bottom root zone (Fig. 4C). On the final harvest date, however, media pH was unaffected by fertility in any root zone (Fig. 4D). On 7 July, media EC was greatest in the two highest fertility treatments across all root zones; the control had consistently the lowest EC across all root zones (Fig. 4E). At the final sampling, the 1.2 and 1.8 g N/plant treatments had higher EC than the control treatment in the top and middle root zones but no differences were found in the bottom root zone (Fig. 4F).

Plant ψ_S and predawn leaf water potentials decreased with increasing fertility at all sampling dates (Table 2).

Discussion

Fertilization up to 1.8 g N/plant resulted in increased shoot height, RCD, leaf area, dry mass production, and nutrient uptake in northern red oak seedlings, whereas fertilization above this level resulted in reduced growth (Figs. 1–3 and 5). This observation confirms previously reported beneficial effects of fertilization in this species (Jacobs et al., 2005; Salifu and Jacobs, 2006). For example, the trends in Figure 3 conform to a classic dose–response model of fertilization exemplifying nutrient deficiency, sufficiency, luxury consumption, and ion toxicity noted in other studies (e.g., Bigg and Schalau, 1990; Salifu and Jacobs, 2006). Decreased root dry mass production in response to increasing fertility (Figs. 3A and 4A) is consistent with results found in other greenhouse studies with both conifer (Xu and Timmer, 1999) and hardwood (Canham et al., 1996) species, reflecting a common plant response to allocate more dry mass to stimulate root growth on poor soils to increase capacity for site resource exploitation.

Thornton et al. (1988) noted damage to northern red oak seedlings at EC less than 1.0 dS·m^{-1} and a reduction in leaf dry mass at EC less than 0.75 dS·m^{-1}. It is likely that the high EC values (greater than three times these values) in our highest fertility treatments contributed to plant mortality. The vector shift (Fig. 5) demonstrates ion toxicity or toxic nutrient accumulation (Salifu and Timmer, 2003) in leaves at the highest fertility treatment (3.6 g N/plant) compared with 0 g N/plant. The higher EC of the upper media zones in fertilized seedlings is consistent

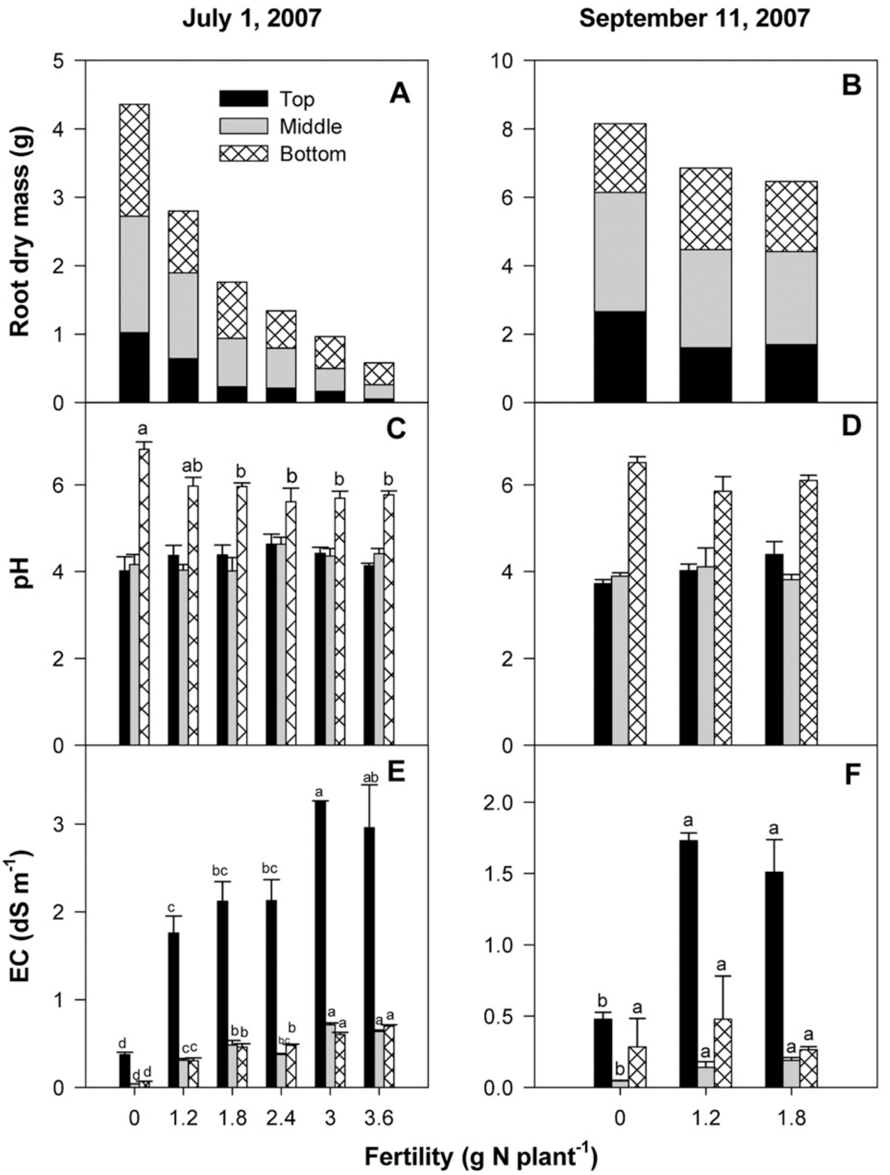

Fig. 4. Effects of fertilizer rate on northern red oak seedling sectioned root dry mass (top 0 to 5 cm, middle 5 to 15 cm, and bottom 15- to 25-cm depths) (**A–B**) and associated pH (**C–D**) and electrical conductivity (EC) (**E–F**) at these depths sampled midway (1 July) and at final harvest (11 Sept.) (n = 6). For a given sampling period, treatments marked with different letters are statistically different according to Tukey's honestly significant difference test at α = 0.05.

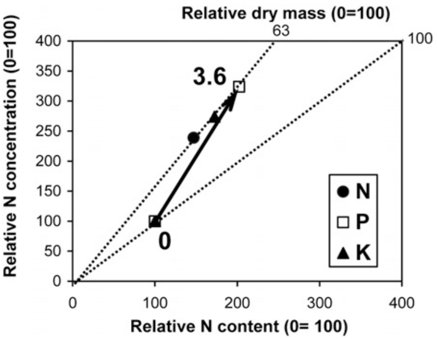

Fig. 5. Vector nomogram of relative change in leaf dry mass, nutrient content, and concentration in northern red oak seedlings fertilized at 3.6 g nitrogen (N)/plant or unfertilized (control). Corresponding value at each point indicates seasonal dose rate applied (milligrams N/plant). The type of nutritional response (toxic accumulation) induced by treatment is demonstrated by the vector direction and magnitude as detailed in Salifu and Jacobs (2006) and in Salifu and Timmer (2003).

with results noted in other subirrigation trials (Davis et al., 2008; Dumroese et al., 2006, 2011; Pinto et al., 2008) and may be explained by the upward movement of salts through capillary flow to upper media layers. In addition to media EC being an important proxy of potential for plant damage, media EC is an effective indicator of overall plant development, accounting for 39% and 68% of the variation in northern red oak shoot height and dry mass, respectively, in response to fertility (Salifu et al., 2006).

Lopushinsky (1990) noted that plant water potential may be close to 0.0 MPa at high moisture availability, which decreases with moisture stress (more negative). Our seedlings were not exposed to a drought treatment nor did we ever observe pre-dawn water potentials below –0.8 MPa. However, our higher fertility treatments had significantly lower water potential values (Table 2), suggesting potential for moisture stress resulting from excessive fertility. Shumway et al. (1993) found reduced leaf area in drought-stressed northern red oak plants. Although none of the plants in this study were drought-stressed, a trend of lower leaf area was noted in the highest fertility treatments, which was associated with the lowest water potential (Fig. 2; Table 2). Compared with well-watered plants, Humara et al. (2002) observed reductions up to 50% in height, dry mass, and leaf area in *Eucalyptus globulus* Labill. under drought treatments. Results noted in this study (Figs. 1 and 2) are consistent with these findings. Additionally, pre-dawn water potentials for well-watered *Quercus petraea* [Matt.] Liebl. and *Quercus robur* L. (Thomas and Gausling, 2000) were similar to our results (Table 2). However, these authors also observed osmotic pressures that were five to 10 times greater than the values we observed at maximum turgor. Accumulation of fertilizer salts in media reduces ψ_S and can result in reduction of root length and dieback of laterals (Baligar et al., 1998), not observed in this study.

Conclusions

Under this subirrigation system, fertilization with controlled-release fertilizer increased biomass of northern red oak seedlings up to 1.8 g N per plant; but most physiological and morphological parameters were reduced at nutrient input above this rate. Thus, increasing fertility beyond ≈1.8 g N per plant apparently resulted in toxicity, which caused plant mortality. Observed responses to fertility conformed to a classic dose–response model, which suggested a broad range of fertility from deficiency to toxicity. Increased fertility was associated with high EC levels, especially in the upper media layers consistent with published information on subirrigation. These levels were inversely related to root dry mass production, inferring detrimental effects of EC on root development. Altered fertility did not significantly affect pH in this study.

Subirrigation has shown excellent potential to produce forest tree seedlings of equal or better quality to overhead irrigation while simultaneously reducing water and nutrient waste. Our study results indicate, however, that growers must carefully calibrate fertilizer inputs based on species and cultural systems to avoid potential for plant toxicity, which may be partly associated with the accumulation of residual fertilizer salts in the upper media layers that is characteristic of this irrigation system. Additional studies are needed to rigorously evaluate effects of media ψ_S on water availability and on plant growth and development, especially under

Table 1. Effects of increased fertility on northern red oak seedling component nutrient concentration and associated $P > F$.[z]

	Nutrient concn (g·kg^{-1})								
	Nitrogen			Phosphorus			Potassium		
Sample date/source	Leaf	Shoot	Root	Leaf	Shoot	Root	Leaf	Shoot	Root
1 July									
Fertility rate									
0	19.35 d	6.75 d	8.65 b	2.14 c	2.66 c	2.23 b	10.08 d	8.33 b	7.26 a
1.2	35.08 c	24.50 cd	37.76 a	4.96 b	5.23 bc	6.74 a	18.08 c	11.50 ab	8.03 a
1.8	37.97 bc	34.48 bc	47.52 a	5.48 ab	5.82 ab	6.95 a	21.69 bc	10.96 ab	7.31 a
2.4	41.30 abc	38.78 abc	42.35 a	5.18 b	5.88 ab	6.15 a	23.26 ab	10.12 ab	7.20 a
3.0	41.75 ab	43.23 ab	49.77 a	6.19 ab	7.43 ab	7.48 a	24.67 ab	11.92 a	8.09 a
3.6	46.23 a	56.60 a	48.03 a	6.93 a	8.40 a	6.72 a	27.62 a	11.98 a	6.85 a
ANOVA $P > F$	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0178	0.5851
11 Sept.									
Fertility rate									
0	15.87 b	7.15 a	6.75 b	1.54 b	1.78 a	1.55 b	8.33 b	5.54 a	5.70 b
1.2	27.05 a	12.05 a	19.58 ab	3.11 ab	2.66 a	3.68 ab	10.21 ab	5.07 a	8.28 a
1.8	29.42 a	13.94 a	26.40 a	3.66 a	3.30 a	4.59 a	13.28 a	6.42 a	8.47 a
ANOVA $P > F$	<0.0001	0.0677	0.0008	0.0016	0.0284	0.0017	0.0026	0.3830	0.0002

[z]Fertility rate is grams nitrogen per plant. For a given sampling period, column means followed by different letters within a given treatment differ significantly according to Tukey's honestly significant difference test at $\alpha = 0.05$ (n = 6).
ANOVA = analysis of variance.

Table 2. Effects of increased fertility on red oak seedling pre-dawn leaf water potential and osmotic potential and associated $P > F$.[z]

	Water potential (MPa)					Osmotic potential (MPa)				
Source	21 June	7 July	29 July	14 Aug.	10 Sept.	21 June	7 July	29 July	14 Aug.	10 Sept.
Fertility rate										
0	–0.21 b	–0.18 d	–0.23 d	–0.26 b	–0.28 b	–0.23 b	–0.36 c	–0.87 b	–0.36	–0.35
1.2	–0.21 b	–0.32 d	–0.40 cd	–0.42 a	–0.46 a	–0.33 ab	–0.51 bc	–1.27 ab	–0.47	–0.44
1.8	–0.35 b	–0.35 bc	–0.43 bc	–0.46 a	–0.50 a	–0.45 ab	–0.63 abc	–1.51 a	–0.54	–0.63
2.4	–0.44 ab	–0.43 bc	–0.45 bc	–0.51 a		–0.69 a	–0.90 ab	–1.36 a	–0.58	
3.0	–0.52 ab	–0.52 ab	–0.57 ab			–0.53 ab	–0.64 abc	–1.40 a		
3.6	–0.78 a	–0.65 a	–0.70 a			–0.56 a	–1.03 a	–1.33 a		
ANOVA $P > F$	0.0002	<0.0001	<0.0001	0.0003	0.0001	0.0169	0.0011	0.0036	0.1843	0.1046

[z]Fertility rate is grams nitrogen per plant. For a given sampling period, column means followed by different letters within a given treatment differ significantly according to Tukey's honestly significant difference test at $\alpha = 0.05$ (n = 6).
ANOVA = analysis of variance.

subirrigation systems. Although this study used controlled-release fertilizer, there is also a need to examine seedling responses under subrrigation using soluble fertilizers and to more precisely quantify fertilizer use efficiency among treatments.

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