Original article

Characterizing fertility targets and multi-element interactions in nursery culture of *Quercus rubra* seedlings

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Abstract – We quantified and characterized fertility targets for nursery culture of container northern red oak (*Quercus rubra* L.) seedlings. Plants were supplied with a 15N-5P$_2$O$_5$-15K$_2$O fertilizer at eight rates ranging from 0–150 mg N plant^{-1} and reared for 18 wk in a greenhouse. Plant growth and nutritional response to increased fertilization followed a curvilinear pattern depicting phases that ranged from deficiency to toxicity. Seedling dry mass production was maximized at sufficiency (25 mg N plant^{-1} season^{-1}) while optimum N and P uptake occurred at 100 mg N plant^{-1} season^{-1}. The 150 mg N plant^{-1} seasonal dose rate induced N and P toxicity, but resulted in antagonistic K interaction. Nutrient loading raised plant N and P contents by 27 and 55%. This new approach demonstrates promise to help refine fertility targets for nursery production of *Q. rubra* planting stock and may have application to other hardwood species or cultural systems.

antagonistic interaction / exponential fertilization / growth / luxury uptake / northern red oak / vector diagnosis

Résumé – Caractérisation des objectifs de fertilité et des interactions multiéléments chez des semis de *Quercus rubra* cultivés en pépinière. Des objectifs de fertilité ont été quantifiés et caractérisés pour des semis de chêne rouge d'Amérique (*Quercus rubra* L.) cultivés en pépinière. Les semis ont été alimentés avec un engrais 15N-5P2O5-15K2O selon huit taux de 0–150 mg N plant^{-1} et ont poussés pendant 18 semaines dans une serre. La croissance des semis, leur réponse nutritionnelle à un accroissement de la fertilisation a suivi un modèle curvilinéaire décrivant des phases rangées depuis la carence jusqu'à la toxicité. La production en matière sèche des semis a été maximale à la dose suffisante correspondant à 25 mg N plant^{-1} saison^{-1}, tandis que l'optimum de consommation s'est situé à 100 mg N plant^{-1} saison^{-1}. La dose saisonnière de 150 mg N plant^{-1}a induit une toxicité N et P, mais il en est résulté une interaction antagoniste avec K. Le prélèvement de nutriments par les plants a augmenté le contenu en N et P de 27 % et 55 %. Cette nouvelle approche démontre la possibilité d'espérer perfectionner les objectifs de fertilité pour une production en pépinière de plants de *Quercus rubra* et peuvent avoir une application pour d'autres espèces feuillues et d'autres systèmes culturaux.

interaction antagoniste / fertilisation exponentielle / croissance / consommation de luxe / chêne rouge / vecteur diagnose

1. INTRODUCTION

Poor seedling quality has been identified as one major cause of the failure of hardwood afforestation and reforestation plantings [24, 27]. Although mineral nutrition is a critical aspect of seedling quality, this topic has received little attention in hardwood culture [52]. Current trends reflect increased interest to use fertilizers in the nursery to improve the nutritional quality of hardwood seedlings, but recommended guidelines are relatively unavailable for quantifying and characterizing fertility targets in hardwood seedling culture.

Timmer [44] proposed a conceptual model (Fig. 1) that can be used to quantify and characterize fertility targets in cropping systems. The model suggests plant growth and nutrient status will increase with increased fertilization, but separated here to distinguish nutrient deficiency, sufficiency, luxury consumption and toxicity in plants. Traditionally based on biomass or yield parameters alone [17, 29], this model has now been configured to include nutrient uptake and nutrient concentration to improve diagnostic capacity. Salifu and Timmer [38] validated the application of this model across a broad spectrum of soil N fertility ranging from nutrient deficiency to toxicity in conifer production systems. The model has yet to be tested under multi-element interaction scenarios and in the culture of temperate deciduous forest tree species. Additionally, this model can help quantify and define target rates (*n, f, l* and *e*: Fig. 1) for production of forest tree seedlings for field planting [7, 15, 44]. As shown in the model, fertilizer (*f*) is usually added to supplement native fertility (*n*), which averts nutrient deficiency to maximize growth at sufficiency. Extra high fertilization, or

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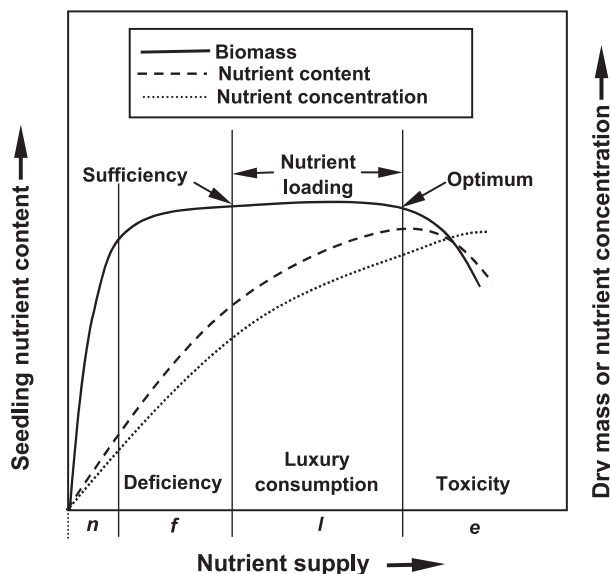
Figure 1. Plant growth and nutrient status conform to a curvilinear pattern with increased fertilization, but partitioned here into phases to distinguish nutrient deficiency, sufficiency, luxury uptake and toxicity. Fertilizer (*f*) supplements native fertility (*n*) to avert nutrient deficiency to maximize growth at sufficiency. Extra high fertilization or nutrient loading (*l*) induces luxury uptake in excess of growth demand, which are stored as reserves for later utilization. Excess fertilization (*e*) may induce toxicity signified by diminished plant growth and N content at increasing tissue N concentration (adapted from [38]).

nutrient loading (*l*), induces luxury uptake in excess of growth demand and nutrients are stored as reserves for later utilization. Excess fertilization (*e*) may induce toxicity, often indicated by decreased plant growth and N content but elevated tissue N concentration. Higher internal nutrient reserves acquired during nutrient loading have correlated well with improved field performance of seedlings [28, 37].

Exponential rather than conventional fertilization is most compatible with nutrient loading because the former approach exposes seedlings gradually and progressively to high nutrient inputs. This helps avert plant damage associated with ion toxicity or inhibitory rhizosphere electrical conductivity levels [25, 26], as well as enhances the acclimation of seedling tolerance to intensive fertilization [32, 44, 45]. Exponential fertilization has been extended to several evergreen forest tree species [8, 30, 50], yielding specific fertilizer recommendations for given cultural regimes. For example, about 64 mg N plant^{-1} season^{-1} maximized growth and N uptake in container black spruce (*Picea mariana* [Mill.] BSP) seedlings [38] and is recommended for commercial production of this species in Ontario, Canada. Although exponential nutrient loading has been examined in deciduous conifers [31] and a tropical angiosperm [8], no published information is available on temperate deciduous species. Exponential nutrient loading may benefit deciduous species because significant quantities of nutrients are resorbed (50–90%) from foliage into root and shoot tissues [1, 13, 41] prior to leaf senescence. Thus, roots and shoots serve as important sinks for N storage during senes-

cence and sources of N for new growth the following spring [12, 41].

One objective of this study was to test application of the dose response model over a broad range of N supply from deficiency to toxicity to quantify and characterize fertility targets for growing northern red oak (*Quercus rubra* L.), a deciduous forest tree species increasingly used for environmental plantings in the Central Hardwood Region, USA [24]. An absolute need exists to determine these indices for each species and cultural system because of the variation in species demand for nutrients, cultural practices and native fertility (*n*) of growing substrates [16, 48]. Another objective was to quantify the contribution of substrate fertility to seedling growth. Additionally, we used vector diagnosis to explain multi-element interactions on seedling growth in response to increasing nutrient enrichment [18, 38].

2. MATERIALS AND METHODS

2.1. Plant material and growth conditions

Two stratified northern red oak seeds from one seed source were sown in 2.8 l Treepots™ (Stuewe and Sons, Corvallis, OR, USA) filled with Scotts Metro-Mix® 560 growing medium (The Scotts Company, Marysville, OH, USA). This medium is comprised of 35–54% composted pine bark, 20–30% processed coconut coir pith, 10–20% sphagnum peat moss, 5–15% processed bark ash and 5–15% horticultural perlite. Nine 2.8 l pots were fitted into one crate and two of such crates represented an experimental unit. Crates were arranged onto a greenhouse bench (mean day/night temperature of 24/20 °C) under ambient light conditions in the Department of Horticulture and Landscape Architecture Plant Growth Facility at Purdue University, West Lafayette IN, USA (40° 25'N, 86° 55'W). Each pot was irrigated to container capacity determined gravimetrically at planting [47, 51]. Two weeks after planting, seedlings were thinned to leave one plant per pot.

Fertilization commenced at week two and continued for 16 wk. Seasonal dose rates ranged from 0–150 mg N plant^{-1}, applied conventionally (25 mg N plant^{-1}) or at exponentially increasing rates (25–150 mg N plant^{-1}). The conventional treatment was chosen to represent the average rate generally used for production of container *Q. rubra* seedlings [2, 40] and was calculated and supplied at a constant weekly rate (1.56 mg N plant^{-1}). Weekly applications were based on exponential functions previously described by [44, 45] designed to synchronize fertilizer supply with exponential growth and nutrient uptake of seedlings [22, 23].

Exponential fertilization delivered nutrients at exponentially increasing addition rates [23, 45] according to equation (1):

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

where *r* is the relative addition rate required to increase N_S (initial N content in seed) to a final N content ($N_T + N_S$), and N_T (ranges from 25–150) was the desired amount to be added over the number of fertilizer applications (*t* = 16 wk). N_S was determined to be 23 mg N seed^{-1} from three replicates each comprising 5 seeds at planting. The quantity of fertilizer to apply on a specific day (N_t) was computed using equation (2):

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

where N_{t-1} is the cumulative amount of N added up to and including the previous application.

A commercial water-soluble fertilizer (Miracle Gro® Excel® 15N-5P_2O_5-15K_2O plus other macro- and micro-elements [The Scotts Company, Marysville, OH, USA]) was applied in solution. Total N consisted of NH_4-N (1.20%), NO_3-N (11.75%) and urea-N (2.05%). Supplemental irrigation was supplied twice weekly at similar rates by periodic weighing of pots to determine amount of water to be added to return pots to container capacity [47, 51] to avoid potential confounding effects of irrigation on treatment responses. The eight fertilizer treatments (0, 25C, 25E, 50E, 75E, 100E, 125E and 150E mg N plant^{-1} season^{-1}) were randomly assigned to a group of two crates and arranged in a randomized complete block design with three replicates. The blocks were placed on raised benches as described before and were rotated bi-weekly to minimize edge effects.

2.2. Plant sampling, chemical and statistical analysis

Growth and nutritional response data were sampled at the pre-hardening phase of nursery culture (18 wk). Two seedlings per treatment replication were destructively sampled at harvest and separated into shoots and roots, measured individually for height and root collar diameter (RCD) but averaged for growth assessment. Plant material was oven-dried for 72 h at 68 °C and ground. Chemical analyses on plant samples was conducted by A&L Great Lakes Laboratories (Fort Wayne IN, USA) based on the Association of Official Analytical Chemist (AOAC) methods. Total N was determined by combustion ("Dumas") procedure (AOAC 968.06) using a LECO nitrogen analyzer (LECO Corporation, St. Joseph, MI, USA). Additionally, plant samples were digested in nitric + perchloric acids (AOAC 935.13), and P and K determined using inductively coupled argon plasma (ICAP) analysis (AOAC 985.01). A one-way analysis of variance was conducted on growth and nutritional response data using SAS [39]. Significant treatment means were separated by Tukey's honestly significant difference test at $\alpha = 0.05$.

2.3. Vector diagnosis

Vector diagnosis allows for simultaneous comparison of plant dry mass and nutrient status of plants or plant components contrasting in growth in an integrated graphic format known as a vector nomogram [18, 38, 43]. The approach offers comprehensive and accurate diagnostic information and facilitates detection of nutritional effects of growth dilution, deficiency, luxury uptake, toxicity and nutrient interactions that tend to complicate conventional diagnostic techniques [21, 46]. Plant growth and nutritional response data for vector analysis can be manipulated in two modes: (i) an instantaneous mode that compares plant samples taken at one point in time to identify different nutritional states [38], and (ii) a dynamic mode that compares treatments over time to identify steady-state nutrition [20, 21], and retranslocation processes [36]. Instantaneous vector diagnosis was employed here to facilitate interpretation of multi-element interactions on seedling growth in response to increased fertilization.

3. RESULTS AND DISCUSSION

3.1. Seedling growth and nutrition

Fertilization increased seedling shoot dry mass by 44–65% ($P < 0.0021$) relative to the control (Fig. 2), which signifies nutrient deficiency in controls and the need for nutrient supplementation [20]. Generally, seedling growth increased with increased fertilization at the deficiency range, remained relatively stable during luxury uptake, but declined at very high N rates associated with induced toxicity (Figs. 1 and 2). Similarly,
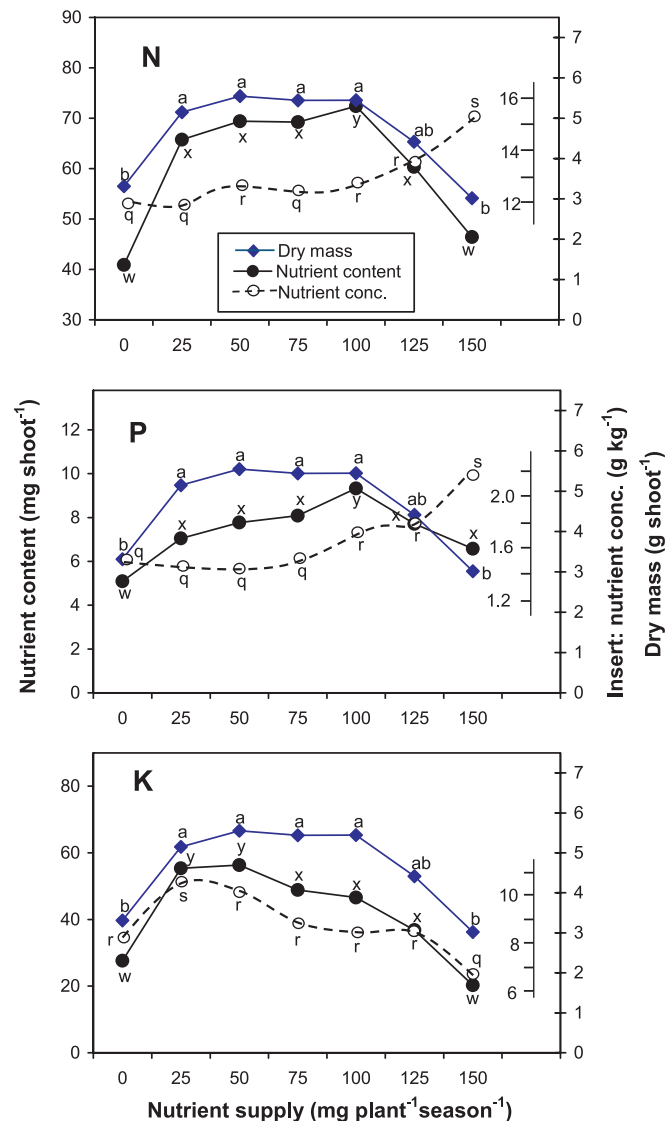
Figure 2. Responses of seedling shoot dry mass, nutrient content and concentration in relation to increasing N supply for one growing season (18 wk) in the greenhouse. The vertical scale insert represents nutrient concentration (g kg^{-1}). For each parameter, means followed by same letter (biomass *a* to *b*; content *w* to *y*, and concentration *q* to *s*) are not statistically different according to Tukey's honestly significant difference test at $\alpha = 0.05$. Fertilization followed exponential (E) addition schedules.

shoot height and RCD (Tab. I) were also consistent with model trends (Fig. 1). Additionally, Table I suggests that luxury uptake does not significantly stimulate growth [44]. Mean root:shoot biomass declined with increased N fertilization, though not significant ($P = 0.4740$), except for the shoot stunting noted at higher fertilizer inputs (Fig. 3A and Tab. I). Diminished root:shoot with increasing substrate fertility has been noted previously [6, 9, 38].

Plant nutrient uptake (Fig. 2) increased with substrate fertility by 39–78% for N ($P = 0.0333$), 20–80% for P ($P = 0.1000$) and by 61–68% for K ($P = 0.0008$) up to the 100 mg N plant^{-1}

Table I. Mean (± SE) of northern red oak seedling shoot height, root collar diameter (RCD), root:shoot and component nutrient content in response to increasing nutrient supply for 18 wk in the greenhouse. Fertilization followed conventional (C) or exponential (E) addition schedules.

Treatment	Shoot height	RCD	Root:shoot	Nutrient content (mg component^{-1})			
				Shoot		Root	
				P	K	P	K
0	18.00 (1.20)	5.42 (0.30)b	2.96 (0.20)	5.08 (0.34)b	27.60 (3.17)bc	13.66 (0.29)	53.63 (2.11)
25C	21.00 (0.80)	5.48 (0.01)ab	2.45 (0.01)	6.02 (0.56)ab	45.14 (1.50)ab	14.37 (1.10)	53.91 (6.69)
25E	22.00 (0.80	6.32 (0.02)ab	2.65 (0.20)	7.05 (0.70)ab	55.39 (3.82)a	17.97 (2.88)	75.74 (8.66)
50E	23.00 (0.90)	6.20 (0.20)ab	2.33 (0.10)	7.77 (0.24)ab	56.32 (2.90)a	16.83 (1.72)	63.05 (14.99)
75E	22.00 (0.10)	6.73 (0.40)ab	2.56 (0.20)	8.08 (0.57)ab	48.88 (6.96)ab	18.93 (1.70)	68.58 (10.01)
100E	22.50 (2.40)	7.03 (0.40)a	2.26 (0.12)	9.33 (1.39)a	46.58 (8.02)ab	19.68 (2.51)	67.01 (11.16)
125E	20.00 (2.90)	6.05 (0.50)ab	2.49 (0.40)	7.71 (1.30)ab	36.81 (5.85)abc	19.12 (1.71)	69.72 (8.60)
150E	16.00 (2.80)	5.73 (0.46)ab	2.76 (0.42)	6.58 (0.97)ab	20.30 (3.96)c	17.15 (1.04)	58.29 (6.49)

Column means marked by same or no letter are not statistically different according to Tukey's honestly significant difference test at $\alpha = 0.05$.
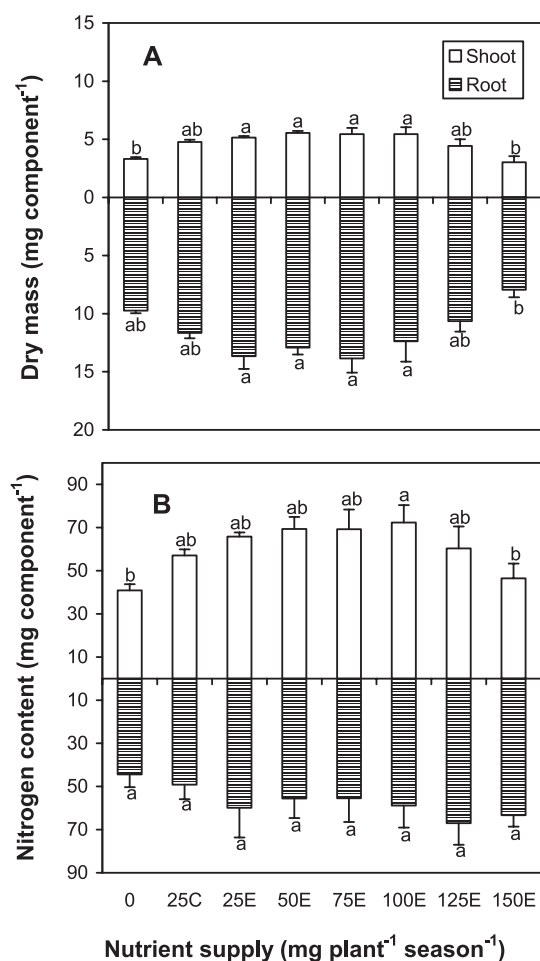
Figure 3. Seedling dry mass (A) and nitrogen content (B) in response to increasing N supply for one growing season (18 wk) in the greenhouse. For each parameter, bars marked by the same letter are not statistically different according to Tukey's honestly significant difference test at $\alpha = 0.05$. Fertilization followed conventional (C) or exponential (E) addition schedules.

rate, and then declined thereafter presumably due to toxicity [42, 43]. Trends in plant nutrient concentration (Fig. 2) were similar to those shown in Figure 1, increasing gradually with N supply at the deficiency range due to growth dilution and rapidly at toxic additions due to accumulation effects [19, 44]. Apparently, acute toxicity induced stunting in seedlings raised at the 150 mg N regime (Fig. 3A and Tab. I). The consistent pattern in Figure 2 with trends in the conceptual model (Fig. 1) confirm suitability of the dose response model as a useful framework for quantifying and characterizing fertility targets for *Q. rubra* seedling culture as previously validated for black spruce [38].

3.2. Quantifying and characterizing fertility targets

Seed N content (N_s) was 23 mg in *Q. rubra* contrasting markedly with about 0.2 mg estimated for black spruce [45]. Assuming that the N accumulated in non-fertilized trees reflected availability from the growing substrate, the native (n) supply (Fig. 1) was calculated as total N in the control minus N_s which equals 18 mg N seedling^{-1} season^{-1} (Fig. 2). This index is higher than 1–8 mg seedling^{-1} season^{-1} estimated for black spruce [38, 45]. Although n is high in this study, it was inadequate to meet the rapid growth demand of *Q. rubra* seedlings. Supplemental fertilizer (f) countered deficiency and increased seedling growth to the sufficiency level at the 25 mg N seedling^{-1} season^{-1} rate (Fig. 2). The deficiency response is characterized by 56, 61, 40 and 96% increases in dry mass, and N, P and K contents, respectively (Fig. 2). The sufficiency level found here for *Q. rubra* is within the 10–32 mg N plant^{-1} season^{-1} target rates commonly use for conventional production of container planting stock [3, 33].

The loading rate (l) induced luxury nutrient uptake along a broad fertility range (25–100 mg plant^{-1} season^{-1}), which increased seedling N content ($P = 0.0333$) and concentration ($P = 0.0367$) without significantly changing dry mass (Fig. 3) when compared with the sufficiency index. Compared with the standard 25C treatment (Tab. I), the maximum target rate (100 mg N plant^{-1} season^{-1}) (Fig. 2) induced 27 and 55% increases in N and P uptake, respectively. This target threshold

is higher than the 64 mg N plant^{-1} seasonal dosage estimated for nutrient-loaded black spruce seedlings [38]. Induced luxury uptake in red oak seedlings should not be lost through leaf fall because of resorption. This important nutrient conservation mechanism can recover 50–90% of nutrients from senescing leaves and store them as reserves in stem and root tissues, which are remobilized for new growth in spring [1, 10, 41]. Thus, it is likely that increased internal nutrient reserves resulting from nutrient loading in red oak seedlings may be readily exploited later to facilitate new growth at outplanting [1, 41]. Nitrogen supply in excess (*e*) of target levels (Figs. 1 and 2) induced toxicity associated with diminished plant growth [19, 43]. For example, red oak seedling dry mass and nutrient content declined, while N and P concentration were elevated at toxic application (Fig. 2), exemplifying the need to determine target fertilizer rates for effective nutrient loading. Quantified target rates will help avoid over fertilization and potential nutritional imbalances in plants. Additionally, defined target rates may result in production of high quality seedlings with stable internal tissue nutrient concentration free from nutrient stress, which should help to optimize seedling field performance.

3.3. Multi-element interactions

Vector diagnosis is used to interpret and improve understanding of multi-element interactions at the deficiency (Fig. 4A) and toxicity (Fig. 4B) ranges (Figs. 1 and 2). Nitrogen and K deficiency (shift C, Fig. 4A) is associated with increased growth, nutrient uptake and concentration (See Fig. 2 in [38]), suggesting that nutrient uptake rate is higher than growth rate. Such response reflects improved plant growth and nutrient status. Potassium is the most responsive nutrient at deficiency as shown by its vector magnitude (Fig. 4A). Growth dilution associated with increased growth and nutrient uptake but diminished tissue nutrient concentration occurred with P (Fig. 4A). The highest dose rate induced N and P toxicity (shift E, Fig. 4B) associated with reduced growth (45%) and nutrient uptake but elevated tissue nutrient concentration. For example, nutrient toxicity increased shoot N and P concentration by 17 and 30% but decreased N and P content by 36 and 30%, respectively (Figs. 2 and 4B). Antagonistic interaction of K (shift F, Fig. 4B) occurred when a decline in K concentration (21%) reduced growth and K uptake (56%). The greater N accumulation in shoots may partly explain K reduction at higher dose rates because increased NH_4^+ uptake has been found to reduce K uptake [4, 49]. Higher K supplementation can be used to correct K dilution [5, 49].

3.4. Improving diagnostic precision

Interpretations of plant response to fertilization are often based on plant tissue nutrient concentration alone [14, 43] or on dry mass alone using the traditional dose response model [17, 29]. The more integrated approach utilizing plant dry mass and nutrient status (Figs. 1 and 2) can improve diagnostic reliability [38, 47]. For example, elevated tissue nutrient concentration associated with increased fertilization is often wrongly diagnosed as a positive fertilizer response, but may in fact reflect an induced toxicity. This fact is illustrated in Figure 4B, where the highest dose rate (150 mg N plant^{-1} season^{-1}) raised N and P concentration but decreased growth (45%), and N and P uptake by 36 and 30%, respectively. Additionally, studies
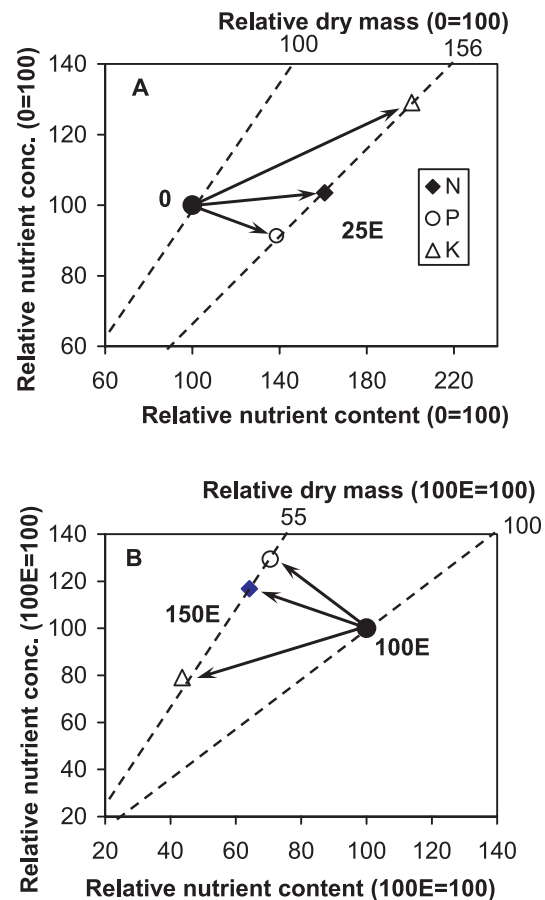
Figure 4. Vector nomogram of relative change in shoot dry mass, nutrient content and concentration in northern red oak seedlings at the deficiency phase (A) or at the toxic range (B). Corresponding value at each point indicates seasonal dose rate applied (mg N seedling^{-1}; 0 represents unfertilized or the control treatment). The 25, 100 and 150 treatments followed exponential (E) addition schedules. The type of nutritional response induced by treatment is characterized by vector direction and magnitude, described by [38, 43].

have shown that field performance of seedlings may be more closely related to pre-plant nutrient status than morphological indicators [34, 44]. The above information and further examples in [38] have important implications for current stock quality assessment programs, which are primarily based on seedling morphological attributes such as dry mass, shoot height or RCD [11, 35, 52]. Incorporating nutritional as well as morphological standards (Figs. 1 and 2) in planting stock quality assessment programs could improve diagnostic reliability. Although the quantified indices in this study are influenced by substrate native fertility, they provide needed quantitative information and a rationale to help characterize fertility targets in nursery culture of forest tree seedlings. The conceptual model (Fig. 1) demonstrates potential as a useful diagnostic tool, which provides a framework for quantifying and characterizing fertility regimes for forest tree seedlings. The model should be calibrated for other production systems and additional tree species to account for the variability in substrate native fertility, growing methods and species demand for nutrients.

4. CONCLUSIONS

Study results demonstrate suitability of the dose response model for quantifying and characterizing fertility targets for the culture of northern red oak seedlings. The sufficiency rate (25 mg N plant^{-1} season^{-1}) maximized seedling dry mass production in the studied species. Maximum N and P accumulation occurred at 100 mg N plant^{-1} season^{-1}. The 150 mg N plant^{-1} seasonal dose rate induced N and P toxicity in cultured plants, demonstrating the susceptibility of crops to over fertilization and the need to determine fertility targets in cropping systems. Toxicity increased plant N and P concentration by 17 and 30%, respectively, but reduced growth (45%), N content (36%) and P content (30%). Native fertility contributed about 18 mg N to support seedling growth. Vector analysis effectively diagnosed growth dilution, antagonistic interactions and toxicity of nutrients in cultured plants, which improves understanding of red oak seedling response to increased fertilization. The dose response model demonstrates promise as a useful tool for quantifying and characterizing fertility targets in seedling culture, and can help improve diagnostic precision in nutritional studies of forest tree seedlings.

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