Fertilizer-induced changes in rhizosphere electrical conductivity: relation to forest tree seedling root system growth and function

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Abstract. Fertilization is standard practice in forest tree seedling nursery culture. Additionally, fertilization at outplanting has potential to facilitate nutrient uptake and reduce transplant shock. Fertilization, however, may dramatically alter rhizosphere chemical properties such as pH, ion availability, and electrical conductivity (EC). These changes may inhibit root system growth and function by reducing soil osmotic potential and creating specific ion toxicities. The risk of root damage associated with high EC levels appears to be dependent on species, age of root system, and soil moisture availability. Root inhibition in container nursery culture of conifers is likely to occur above 2.5 dS m^{-1}, though threshold EC levels for bareroot culture and field plantings are largely unavailable. Fertilization at outplanting has the added risk that drought conditions may prevent leaching of excess fertilizer salts, which can increase rhizosphere EC beyond safe levels and ultimately impair root uptake of water or nutrients. For fertilization programs to be successful, a critical threshold balance must be maintained between optimizing seedling nutrient availability in the rhizosphere, while minimizing potential for root damage. Future research is needed to identify optimal EC levels for a range of species across all stages of the reforestation process, from nursery culture through plantation establishment.

Introduction

Fertilization is an essential component of producing high quality stock for reforestation. Fertilization during nursery culture can enhance plant growth, nutrient storage reserves, root growth potential, and resistance to drought stress, freezing temperatures, and diseases (Landis 1985; Rook 1991; van den Driessche 1991). Additionally, there has been renewed interest in fertilization at time of outplanting (Brockley 1988; Haase and Rose 1997) as a means to minimize seedling transplant shock and accelerate initial plantation development (Carlson 1981; Carlson and Preisig 1981). Encouraging optimal root system development is also a critical factor in nursery culture, and vigorous root system growth following field planting contributes to the ability of seedlings to overcome transplanting stress (Grossnickle 2005).

Fertilization can have a profound effect on seedling root system development, promoting root growth and function under well-balanced cultural scenarios but potentially creating inhibitions when conditions are unfavorable. To facilitate optimal seedling root growth and maximize subsequent reforestation success, a critical threshold balance must be maintained between optimizing nutrient availability and minimizing root system damage due to toxicities associated with over-fertilization (Salifu and Timmer 2003b). Root damage may be a function of toxic concentrations of specific ions and/or detrimental changes in soil osmotic potential (Baligar et al. 1998; Bernstein and Kafkafi 2002). Maintaining this critical balance may largely dictate the capacity for a positive seedling growth response from fertilization prescriptions applied in both the nursery and field. Given the apparent significance of this relationship to reforestation success, relatively little research has been accomplished in this area for forest tree seedlings and no thorough synthesis of the topic has been constructed.

The objectives of this review are to (i) illustrate the effects of fertilization on rhizosphere chemical activity (emphasizing changes in electrical conductivity) and resulting impact on forest tree seedling root system growth and function, (ii) describe methods by which fertilization regimes may be monitored to concurrently maximize nutrient availability and optimize seedling root development, (iii) synthesize the literature regarding seedling root development and fertilization during both nursery culture and at the time of outplanting, and (iv) suggest opportunities for future research to improve our understanding of these interactions. Because nitrogen tends to be the nutrient upon which most fertilization regimes are based, specific examples within this manuscript focus primarily on this element.

Fertilization and rhizosphere properties

Most fertilizers used in nursery culture and at outplanting are synthetically produced and occur as inorganic salts. The effects of common fertilizers on soil salinity are listed in Table 1. Fertilizer nutrients are released as ions after application and targeted for delivery to the rhizosphere (defined here as the area of media within the immediate vicinity of, and with direct influence on, the root system). They may then either undergo uptake by the root, adherence to media particles for possible exchange with roots (i.e., through cation exchange), or are leached away from the root system. Fertilization may have profound effects on chemical properties within the seedling rhizosphere, such as soil electrical conductivity (EC), pH, and occurrence or availability of different soil nutrients. These changes may affect root system growth and function, and thereby impact the ability of seedlings to exploit the soil to extract water and nutrients. A specific understanding of the mechanisms by which fertilization affects rhizosphere properties and how these changes may be monitored and corrected may help to optimize seedling response to fertilization.

Table 1. Effect of some common inorganic fertilizers on salt index and relative salinity, each expressed as relative to the effect of sodium nitrate (adapted from Bunt 1988).

Fertilizer	Analysis	Salt index[a]	Relative salinity[b]
Sodium nitrate	16.5 N	100.0	100.0
Ammonium nitrate	35 N	104.7	49.4
Ammonium sulphate	21 N	69.0	53.7
Calcium nitrate	11.9 N, 17 Ca	52.5	30.1
Urea	46 N	75.4	26.7
Diammonium phosphate	21 N, 23 P	34.2	12.7
Monoammonium phosphate	12 N, 27 P	29.9	12.7
Superphosphate (single)	7.8 P	7.8	16.5
Superphosphate (triple)	19.6 P	10.1	8.5
Potassium chloride	49.8 K	116.3	38.5
Potassium nitrate	13 N, 38 K	73.6	23.6
Potassium sulphate	45 K	46.1	17.0
Calcium carbonate	40 Ca	4.7	1.9
Calcium sulphate	23 Ca	8.1	5.8
Magnesium sulphate	16 Mg	44.0	44.5

[a]Calculated from the increase in osmotic pressure of equal weights of fertilizer.
[b]Calculated from the increase in osmotic pressure per unit of plant nutrient.
Note that actual increases in osmotic potential from a given amount of fertilizer will vary depending on medium characteristics.

Fertilization may alter rhizosphere pH by changing the relative concentration of different ions in the soil solution. This effect is further confounded by the influence of fertilizer nutrients on ion exchange between root and soil along with root metabolic processes, which may lead to as much as a $2-3$ unit change in rhizosphere pH compared to bulk soil (Neumann and Romheld 2001). For instance, N is available to plants in both cationic (NH_4^+) and anionic (NO_3^-) forms. Uptake of primarily NO_3^- promotes excess uptake of anions over cations (and release of OH^- from the root) and a subsequent rise in rhizosphere pH, while uptake of NH_4^+ leads to extrusion of H^+ and soil acidification (Neumann and Romheld 2001).

As pH fluctuates, the availability of different ions changes as certain ions are chemically bound (e.g., P) while others become more available (e.g., Fe and Al). This may affect root system development, as high concentrations of Al, for example, tend to be toxic to roots. Symptoms of root Al rhizotoxicity include stunting, poor hair development, swollen apices, and less lateral branching (Baligar et al. 1998). Ammonium nitrate topdressed to white spruce (*Picea glauca* (Moench) Voss) seedlings acted to acidify the soil and increased extractable levels of soil Al, which reduced root length, specific root length (root length per unit of dry matter), and number of root tips (Teng and Timmer 1995). Similarly, fertilization with high levels of ammonium-based fertilizer decreased root biomass, root length, and specific root length of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings (Olsthoorn et al. 1991; De Visser and Keltjens 1993).

Because fertilizer nutrients are salts that conduct an electrical charge, they act to alter the EC of the soil solution. EC is the reciprocal of electrical resistance, which is measured using the equation $E = I \times R$, where E is the electrical potential, I is the current, and R is the resistance (Tinus and McDonald 1979). For the purposes of monitoring solution EC during plant propagation, measurements are generally reported in terms of specific conductance (e.g., dS m^{-1}, as presented herein). Understanding the relationship between rhizosphere EC and root system development is crucial to formulating successful nursery and field fertilization protocols, and we focus the remainder of the paper on this concept.

Monitoring rhizosphere electrical conductivity

Monitoring EC levels of a soil solution provides an indication of fertilizer salts present (Landis et al. 1989) and therefore serves as a reliable means to help evaluate fertilization protocols. A primary advantage of EC sampling is that measurements may be conducted on a consistent basis and results are rapid, allowing for prompt management decisions. Assessment of EC during nursery culture and following outplanting can be easily conducted with a hand-held meter using displacement of the growing solution or following growing medium extraction (Bunt 1988; Landis et al. 1989). Analysis may be improved further when combined with diagnosis of limiting or excess nutrients in media extracts and comparing these levels with established optimum or critical concentrations (Timmer and Parton 1984).

The "pour-through" technique for EC_{pt} sampling is relatively easy to perform in container nurseries and may be conducted regularly without the need for media extraction (Wright 1986). Using this method, a specified amount of distilled water is added to the surface of growing media and the leachate is collected from beneath the container and analyzed (Landis et al. 1989). The saturated media extract procedure was developed for field soils (Bunt 1988), and therefore has direct application to bareroot nurseries and field sites, but is also effectively used in container systems. A known volume of growing media is extracted and saturated with distilled water. After equilibration for two hours, the water and dissolved salts are separated from the medium with a vacuum or water pump and the solution is analyzed for EC_e (at 25 °C). Alternatively, a larger proportion of water can be added to the medium sample to make a suspension for extraction (EC_w). No universal standard for ratio of medium to water has been established, but 1:2 or 1:5 dilutions by volume are most common (Bunt 1988; Landis et al. 1989). To avoid the need to vacuum extract or water pump the medium solution, EC_p can be measured directly in a soil-water paste (Brady and Weil 2002), or a press extract (EC_{pe}) can be obtained by "squeezing" root plugs or peat-based substrates after irrigation to container capacity (Caberra 1998; Scoggins et al. 2001, 2002). Sonneveld et al. (1974), early proponents of the press procedure, claimed that EC_{pe} measures are "closest to the actual root zone solution."

The saturated media extract (EC_e) method is usually preferred because it provides an assessment of both the applied salinity load as well as the concentration of accumulated unused fertilizer salts (Landis et al. 1989). Additionally, the amount of water used is directly proportionate to the amount held by the media at saturation; thus, the measured salinity largely reflects that experienced by the plant under nursery culture (Bunt 1988). The dilution factor is key for comparative purposes; hence it is important to document how much water is added to the medium, such that test results may be accurately compared to reference values. For instance, salinity values attained using the 1:5 volume procedure will be approximately 40% of those obtained using the 1:2 method (Bunt 1988). For horticultural applications, the various methods are closely interrelated (Caberra 1998; Scoggins et al. 2001, 2002).

Variation in EC levels throughout the soil profile is another critical factor affecting the accuracy of EC sampling techniques, particularly when applied to bareroot nursery culture. Surface soil layers tend to accumulate higher concentrations of salts following evaporation or seedling transpiration of water containing soluble salts (Landis 1988). Thus, while EC determination from composite samples taken from the entire plow layer may show moderate EC values, the EC of the surface soil can reach much higher levels that may be toxic during germination and emergence (Landis 1988). Examination of EC_e changes in various soil zones in a bareroot nursery in Colorado, USA found that EC_e at soil depth $0-5.1$ cm was approximately 8.0 dS m^{-1}, while that of each sampled zone below that depth was less than 2.0 dS m^{-1} (Landis 1980).

Electrical conductivity and seedling root development

Sensitivity of forest tree species to high EC levels

EC levels tend to rise exponentially with increasing fertilizer inputs and decreasing soil moisture (Bunt 1988; Landis et al. 1989). Although sensitivity of agronomic crop and horticultural species to salinity is well documented, much less is known about salt sensitivity in forest tree species (Thornton et al. 1988; Allen et al. 1994). Most agricultural crops are not affected by soil salinity until EC_e levels reach 4.0 dS m^{-1} (Landis 1988), which is also the minimum EC_e value for classifying soils as saline (U.S. Salinity Laboratory Staff 1969). Woody plants, and forest tree seedlings in particular, are very sensitive to high EC levels and damage can occur quickly (Landis et al. 1989; Maynard et al. 1997), with EC_e values as low as 1.4 dS m^{-1} potentially causing growth reduction (Landis 1988). This sensitivity is a complex phenomenon, the mechanisms of which are poorly understood (Allen et al. 1994), but is likely a function of specific cation or anion toxicities (i.e., the ion under consideration causes an additional depression of growth beyond

what could be expected from the osmotic effect of its solution alone as per Bernstein and Kafkafi 2002) and/or changes in soil osmotic potential, which may act to limit water and nutrient uptake through reduced soil water potential and damage to root function and elongation (Bunt 1988; Thornton et al. 1988; Allen et al. 1994; Maynard et al. 1997; Baligar et al. 1998; Bernstein and Kafkafi 2002). It is often difficult to assess the relative contributions of these factors on growth inhibitions (Marschner 1995), which may be further complicated by variation in plant response associated with type of salt input (Allen et al. 1994).

Physiological drought resulting from high solute concentrations can occur even at field capacity, although this effect is more pronounced under dry conditions (Kozlowski 1987). Following fertilizer application, fertilizer salts diffuse outward acting to decrease soil osmotic potential (Drew 1975). This may kill elongating root apical meristems via desiccation and thereby limit root system expansion (Bernstein and Kafkafi 2002), resulting in decreased root length and dieback of laterals (Baligar et al. 1998). Root apical meristems are anatomically suited to act as critical points of nutrient and water uptake (Peterson et al. 1999). Thus, an inhibitory response at these sites may negatively affect root system function in addition to retarding root growth, and ultimately lead to limitations in whole-plant development.

Tolerance to high EC levels appears to vary among species; an EC_e as low as 2.5 dS m^{-1} may cause a 50% growth reduction in very sensitive species such as Douglas-fir or blue spruce (*Picea pungens* Engelm.), but would not affect more tolerant species such as ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) (Landis et al. 1989). Susceptibility to root damage also varies according to developmental stage, with tolerance to high EC levels increasing as roots age (Zekri 1993). This suggests that seedling roots during nursery culture and immediately following outplanting would be exceptionally vulnerable to elevated EC levels from fertilizer inputs. Tinus (1984) applied solutions of variable EC levels to 10 deciduous tree and shrub species and reported that total germination and germination energy (average percent per day to 50% of maximum germination) were more adversely affected by high EC levels than was subsequent seedling growth over a 45-day period.

Seedling response to changes in EC associated with fertilizer addition

Recommended EC levels associated with fertilization that maximize nutrient uptake and seedling growth have been provided by several authors, yet are based on a limited number of research trials with only a few species. Black spruce (*Picea mariana* (Mill.) B.S.P.) and white spruce seedlings had optimal growth up to 2.5 dS m^{-1}, but stunting was noted above this level, and mortality occurred above 4.0 dS m^{-1} (Phillion and Bunting 1983). These authors recommended maintaining an EC_e range between 1.2 and 2.5 dS m^{-1} under this cultural regime. Similarly, maximum plant growth occurred at EC_e levels
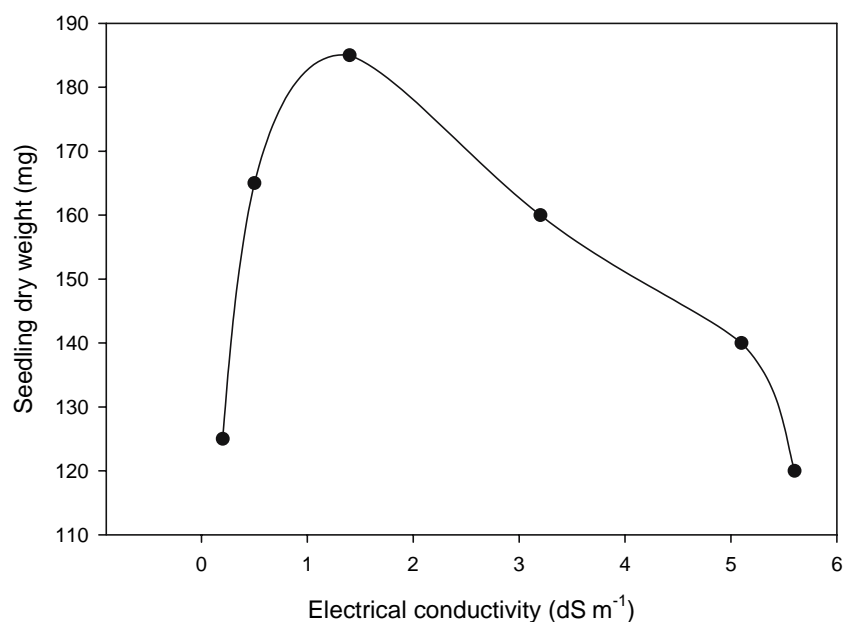
Figure 1. Response of red pine (*Pinus resinosa* Ait.) seedlings grown in containers with a peat-vermiculite media to increasing media electrical conductivity (EC_e) levels resulting from fertilization using a balanced nutrient solution (adapted from Timmer and Parton 1984). Critical EC_e levels were identified as ranging between 1.0 and 2.2 dS m^{-1}.

ranging between 1.8–2.2 dS m^{-1} for container-grown red pine (*Pinus resinosa* Ait.), while toxicity was identified at 2.5 dS m^{-1} (Timmer and Parton 1984) (Figure 1). In each of these studies, a balanced fertilizer solution was applied to attain a range of EC_e levels, and the peat-vermiculite media was analyzed using a saturated media extract.

A limitation in interpreting the relationship between fertilizer-induced changes in EC and root development is that reported toxicities are most commonly associated with reduction in whole-plant mass or visual foliar symptoms, which are presumed to be a result of specific cation or anion toxicities (Timmer and Armstrong 1987a), and/or root system damage associated with osmotic pressure changes (Thornton et al. 1988). Few experiments have directly examined the relationship between media EC and seedling root growth. A study investigating response of Douglas-fir seedlings to transplanting above a localized layer of Osmocote$^{®}$ 15:9:12 (N:P:K) controlled-release fertilizer (CRF) found that root penetration below the CRF layer was reduced with increasing CRF rate (Jacobs et al. 2003a). No restriction in rooting was observed at 2.0 dS m^{-1}, but as EC_w levels rose above 2.6 dS m^{-1}, both root penetration and root tip proliferation were inhibited (Figure 2).
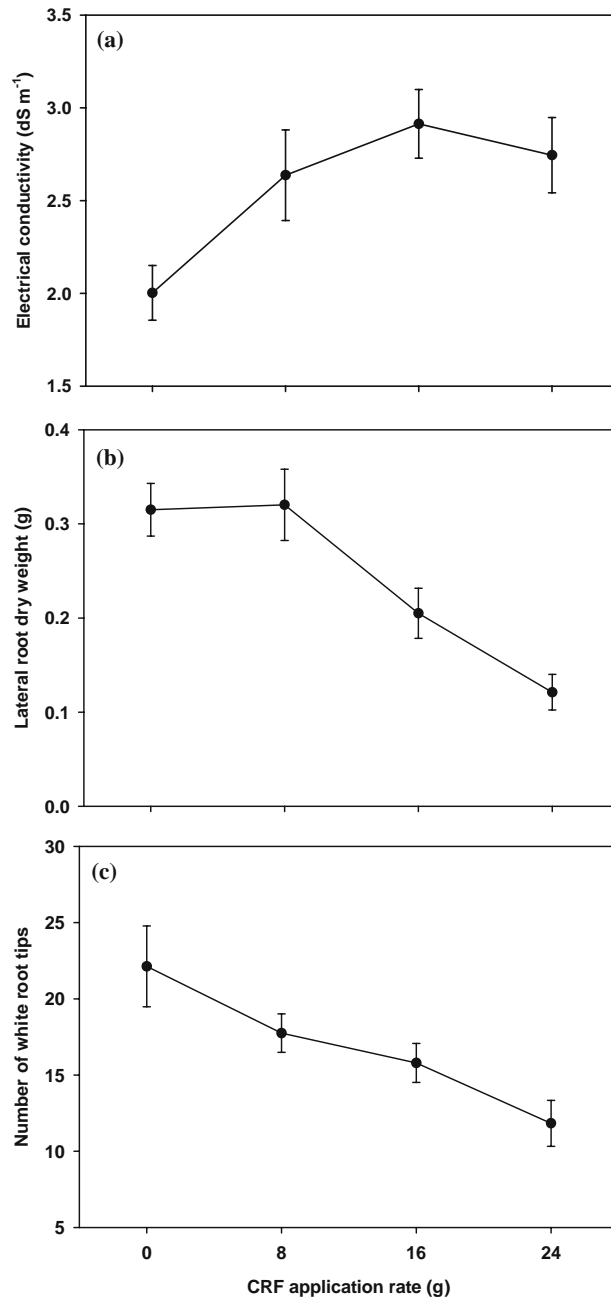
Figure 2. Changes in media electrical conductivity (EC_w) (a), lateral root dry weight (b), and number of white root tips (c) within an 8-cm rooting zone of localized controlled-release fertilizer (CRF) placement, sampled 6 months following Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedling transplant (adapted from data presented in Jacobs et al. 2003a).

Seedling response to changes in EC associated with sodium addition

Other studies have examined changes in rhizosphere EC and corresponding effects on forest tree seedling development by applying Na^+ in solution (typically with Cl^- or SO_4^{2-} as the anion) in addition to a fertilizer solution, often to simulate saline environmental conditions resulting naturally or from anthropogenic causes such as mine reclamation (Croser et al. 2001; Franklin et al. 2002) or roadway deicing (Fostad and Pedersen 2000). In these cases, results may be partly a function of toxicity to excessive Na^+ concentrations (Thornton et al. 1988; Maynard et al. 1997; Franklin et al. 2002), limiting the contribution of these reports in helping to pinpoint threshold fertilized-induced EC levels that optimize root growth and whole plant vigor. However, careful extrapolation to potential response under fertilizer culture may be useful. An early study examined germination and young seedling development of blue spruce, Scots pine (*Pinus sylvestris* L.), and Siberian elm (*Ulmus pumila* L.) to saturation extract EC_e levels of 1, 4, 7, or 10 dS m^{-1} (obtained primarily by addition of NaCl) under two levels of moisture (near field capacity at 22% and 15%) using a clay loam mineral soil (Werkhoven et al. 1966). Emergence, survival, plant height, and dry mass decreased with increasing EC_e levels, particularly in the drier treatment. Croser et al. (2001) examined emergence and early growth of black spruce, white spruce, and jack pine (*Pinus banksiana* Lamb.) seedlings in response to Na^+ addition and found that root development was more adversely affected with increasing salinity than was shoot growth, with mean number of lateral roots and root length tending to decrease at solution EC levels above about 2.0 dS m^{-1} (assuming that a 10 mM NaCl solution approximates 1.0 dS m^{-1} EC as per Thornton et al. 1988). Maynard et al. (1997) grew white spruce seedlings in containers for 12 weeks with Na_2CO_3 in addition to a fertilizer solution, creating a range of five solution EC levels up to 3.4 dS m^{-1}. Growing medium EC_e sampled at the end of the study increased with solution EC treatments and varied from 1.1 to 4.6 dS m^{-1}. Damage increased with increasing EC_e levels, but the lowest treatment (substrate EC_e of 1.3 dS m^{-1}) reduced emergence by 8%, and both shoot and root growth by 50% compared to controls (substrate EC_e of 1.1 dS m^{-1}). Because all growing medium EC_e levels, with the exception of the highest treatment, fell within the range recommended by Phillion and Bunting (1983) for white spruce, the authors speculated that the growth reduction noted in the lower treatment levels was attributable to specific toxicity of Na^+ and CO_3^{2-}, rather than to EC_e levels. This again emphasizes the potential limitation of these studies in helping to formulate fertilizer prescriptions that target tolerable ranges of EC. Table 2 provides a summary of the reported literature regarding forest seedling development in relation to growing media EC levels.

Table 2. Summary of selected literature regarding effects of media electrical conductivity (EC) on development of forest tree seedlings.

Species	Media type	Type and rate of salt addition	Range of EC levels tested[a]	Reported effects on shoot or root development	Reference
Black spruce, White spruce	Peat-vermiculite	50–2000 ppm N using balanced fertilizer	Approximately 0.5 to 8.0 dS m^{-1}	Healthy to 2.5 dS m^{-1}, damage between 2.5–4.0 dS m^{-1}, and mortality above 4.0 dS m^{-1}	Phillion and Bunting 1983
Red pine	Peat-vermiculite	Balanced fertilizer solution at 0–9 times suggested rate	Approximately 0.25 to 5.5 dS m^{-1}	Maximum growth at 1.8–2.2 dS m^{-1}, while toxicity identified at 2.5 dS m^{-1}	Timmer and Parton 1984
Douglas-fir	Peat-vermiculite	Osmocote® 15:9:12 (N:P:K) at 0, 8, 16, or 24 g per seedling	1.9 to 2.9 dS m^{-1} varying by treatment and soil zone	Root penetration inhibited above 2.6 dS m^{-1}	Jacobs et al. 2003a
Ten different deciduous trees and shrubs	Peat-vermiculite	Varying levels of nutrient solution plus Na$_2$SO$_4$, NaCl, and NaHCO$_3$	1.6, 4.5, 7.2, 12.1, and 16.6 dS m^{-1}	Variable, with some species sensitive and others very tolerant	Tinus 1984
White spruce	Peat-perlite	Na$_2$CO$_3$ at 0, 0.2, 0.4, 0.9, or 1.8 g L^{-1} plus balanced fertilizer solution	1.1, 1.3, 1.6, 2.0, and 4.6 dS m^{-1}	Lowest (1.3 dS m^{-1}) treatment reduced emergence by 8%, and both shoot and root growth by 50% vs. controls	Maynard et al. 1997
Blue spruce, Scots pine Siberian elm	Clay loam mineral soil	Primarily NaCl at 0, 0.2, 0.4, or 0.8 g per 454 g dry soil and two moisture levels	1, 4, 7, and 10 dS m^{-1}	Emergence, survival, and plant growth decreased with increasing EC$_e$; Effect magnified in drier treatment	Werkhoven et al. 1966

[a]In each study, EC levels were determined from saturated media extracts (EC$_e$), with the exception of EC sampling of the added solution in Tinus 1984 and of extracted media solution (EC$_w$) in Jacobs et al. 2003a.

Application to nursery culture

Conventional fertilization

Conventional fertilization practices in container seedling nurseries are often based upon either constant or periodic fertilizer addition using soluble fertilizers (Landis et al. 1989). With a constant fertilizer regime, a moderate fertilizer rate is identified that promotes desired morphological characteristics (i.e., nutrient sufficiency) and nutrient supply during the growing cycle remains relatively constant. This rate may be applied as a dilute fertilizer solution each time the crop is irrigated, beginning several weeks following germination, and throughout the primary growing period. In contrast, periodic fertilization involves application of a more concentrated (i.e., several times that of constant addition) fertilizer solution at less frequent intervals. Nutrient levels in growing media tend to vary more substantially in periodic compared to constant fertilizer regimes, creating greater potential for nutrient deficiencies or toxicities associated with fluctuating media EC levels (Landis et al. 1989). Conventional fertilization practices in bareroot nurseries differ from that of container nurseries in that fertilizer prescriptions are adjusted according to native soil fertility (van den Driessche 1984).

Under conventional fertilization regimes, the greatest risk for root damage associated with high growing media EC occurs in the early stages of seedling development when plant demand is low and susceptibility of succulent young roots to damage is high. Fertilizer inputs in container nurseries are often delayed for 4–8 weeks following sowing until the germinant becomes established (Landis et al. 1989). Fertilizer formulations may then be adjusted for relative proportions of nutrients based on seedling developmental growth phases. For instance, N inputs may be relatively low soon after germination and at bud set, and moderate to high during juvenile and rapid growth phases (Landis et al. 1989). In bareroot nurseries, crops are often grown for two or more years and fertilizer regimes may be adjusted for seedling age in addition to growth stages. For instance, application of N fertilizer to May-sown seedlings is often delayed until late-June, while seedlings in their second year of growth may be fertilized beginning in March (van den Driessche 1984). Similarly, addition of N is not recommended beyond July during the first season of growth, while in subsequent years, N may be applied later in the season after bud set (van den Driessche 1984).

Root damage associated with high EC during all phases of nursery culture can best be avoided by consistent monitoring of substrate EC and application as necessary of controlled leaching in container culture (Bunt 1988; Landis et al. 1989) or "deep" irrigation (i.e., application of excess water to carry salts out of the plow layer) in bareroot culture (Landis 1988). Concurrently, when low EC levels are detected, fertilizer inputs should be increased accordingly and EC levels re-assessed thereafter to ensure optimal nutrient availability.

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Nutrient loading

Although operationally convenient, conventional fertilizer regimes may not match seedling requirements adequately because of the exponential growth and nutrient consumption of plants. A tendency for decline in foliar nutrient concentration due to growth dilution as the season progresses has been noted in some conventionally grown seedlings, suggesting potential for nutrient stress due to excess fertilization at the beginning of the growing period and possible under-fertilization at the end of culture (Timmer and Armstrong 1987b; Timmer 1997). Thus, exponential fertilization has been suggested as an option for nursery fertilization whereby nutrient additions are increased exponentially during the growing cycle in an attempt to match plant nutrient demand, representing steady state nutrition (Timmer and Aidelbaum 1996; Timmer 1997). Theoretically, total fertilizer inputs may be increased relative to conventional fertilization to the point where an optimum N dose is identified that results in maximum storage of N without compromising plant mass (i.e., exponential nutrient loading) (Salifu and Timmer 2003b). These internal reserves may then be retranslocated within the plant to support growth following field transplant (Salifu and Timmer 2001, 2003a). Nutrient-loaded seedlings of several conifer species have consistently outperformed conventional counterparts across a variety of ecological conditions in Ontario, Canada (Timmer and Aidelbaum 1996; Timmer 1997). Exponential nutrient loading (50 mg N per seedling) of *Eucalyptus globulus* Labill. seedlings increased foliar N concentration and outplanting performance compared to conventionally grown plants (25 mg N per seedling) across three sites in northwest Victoria, Australia (Close et al. 2005). Though most often studied in container production, this method has also been applied to bareroot nursery systems (McAlister and Timmer 1998).

Exponential fertilization may help minimize risks of root damage from over-fertilization because fertilizer inputs are matched to plant demand, reducing potential for salt buildup in media during periods of low demand. For example, fertilizer inputs are relatively low soon after germination and through initial stages of seedling development, reducing risks for root impairment associated with high EC levels during this sensitive stage. The gradual exposure to greater fertilizer inputs under exponential nutrient loading, combined with increasing plant age, helps ensure tolerance to relatively higher nutrient additions applied toward the end of culture (Quoreshi and Timmer 2000). However, frequent use of high fertilization levels during final stages of nursery culture increases potential for buildup of fertilizer ions in the growing media (Timmer and Aidelbaum 1996), necessitating consistent monitoring of media EC. Examples of calculating fertilizer additions at a given time for modified exponential loading regimes are presented in Timmer and Aidelbaum (1996).

Late-season fertilization is a form of nutrient loading, whereby conventionally grown seedlings are fertilized at relatively high rates following apical bud initiation in fall while roots may still actively extract nutrients, contrasting with traditional cultural practices that reduce fertilizer inputs during this

period for hardening-off purposes (Landis et al. 1989). Similar to exponential nutrient loading, no significant change in plant mass generally occurs. However, late-season fertilization may induce luxury consumption by increasing foliar N concentration (van den Driessche 1985, 1988; Boivin et al. 2004; VanderSchaaf and McNabb 2004) and can lead to improved seedling out-planting performance (Margolis and Waring 1986; van den Driessche 1988; VanderSchaaf and McNabb 2004). As with exponential fertilization, there are concerns that application of high fertilizer rates at the end of nursery culture may induce toxicity. For instance, while late-season fertilization of black spruce with 24 mg N per seedling stimulated growth following transplant compared to controls, application of 48 mg N per seedling reduced survival by 30% (Boivin et al. 2004).

Guidelines for maintaining acceptable ranges of EC in nursery culture, as defined earlier, are also likely applicable to nutrient loading systems. Nutrient loading (75 mg N per seedling) of red pine raised media EC_e values from 0.6 to 0.8 dS m^{-1} in conventionally grown (25 mg N per seedling) seedlings to 2.0–2.1 dS m^{-1} (Miller and Timmer 1994), resulting in an EC_e level within the recommended range for this species (Timmer and Parton 1984). In this case, nutrient loading was accomplished without affecting root mass. However, nutrient loading has potential to enhance root growth. For instance, exponential nutrient loading (39 mg N per seedling) of red pine increased root dry weight from 29 to 34 mg compared to conventional fertilization at this same rate (Timmer and Armstrong 1987b). Root mass in the 50 and 25% strength exponential loading treatments increased to 37 and 41 mg, respectively.

Another potential advantage of nutrient loading in container production is that the seedling root plug may become a significant source of nutrition following outplanting, as nutrients may be retained within media for future root exchange. It was estimated that root plugs of nutrient-loaded black spruce seedlings contributed as much as 22% of N uptake during the season following transplant (Idris et al. 2004). In this case, nutrient loading raised the EC_e of the media (sampled prior to transplant) from 0.6 dS m^{-1} (conventional) to 1.0 dS m^{-1}. Even under the loading treatment, these media EC levels are below maximum recommended levels for container-grown black spruce seedlings (2.5 dS m^{-1}) (Phillion and Bunting 1983), and those that are likely to begin to inhibit root growth (2.6 dS m^{-1}) (Jacobs et al. 2003a), as detailed above.

Root plug EC appears to decrease during the hardening and storage periods when fertilizer is discontinued yet plant uptake and leaching losses still occur (see citations in Timmer and Teng 2004). Thus, there may be potential to further enhance root plug fertility by raising plug EC levels prior to transplanting (i.e., nutrient spiking) to levels approaching maximum recommended values. The feasibility of this practice was recently studied with black spruce in Ontario in which extensive calibrations involving root plug soaking in various concentrations of a 20:20:20 (N:P:K) plus micronutrients water-soluble fertilizer solution were conducted over a range of time intervals (Timmer and Teng 2004). A 1.0% dilution rate (2000 mg N L^{-1}) at 30 min was identified as the

optimal combination to achieve the target 2.0 dS m^{-1} root plug EC_e level. Spiking with this dose (60 mg N per seedling) was as effective at stimulating growth and nutrient uptake efficiency following transplanting as topdressing of transplanted seedlings at a much higher rate (300 mg N per seedling), presumably because of close proximity of a non-toxic fertilizer dose to roots.

Controlled-release fertilizer applied to root plug

Another practice that has gained recent interest is incorporation of polymer-coated CRF into container media prior to sowing. Fertilizer nutrients are released during nursery culture and additional nutrient release may occur following field transplanting. Proximity of CRF in the container plug allows nutrients to be released within the immediate vicinity of the root system, but with the risk that toxicities associated with rapid release of fertilizer salts could occur. Success is therefore dependent upon a proper combination of fertilizer formulation, nutrient release rate (typically ranging from 3 to 16 months), and environmental conditions during nursery culture and following outplanting.

Because nutrient release of polymer-coated CRF is primarily dependent on media temperature (Kochba et al. 1990), variation in greenhouse temperatures may result in rapid flushes of nutrient release during warm periods. When 3–4 month Osmocote® and Nutricote® were used under conditions where average maximum media temperatures exceeded 30 °C, the most rapid N and K release occurred within the first 2 weeks after potting when plant demand was low, resulting in significant nutrient leaching (Huett 1997a, b). This suggests that proper monitoring of EC when using this technique, and supplementing with fertigation and/or controlled leaching to help maintain optimal EC levels may be necessary. When several Australian groundcover species were grown in containers with CRF and subjected to various controlled-leaching treatments, cessation of leaching elevated media EC_e to 2.1 dS m^{-1} and caused significant reduction in both shoot and root dry weight, while a leaching fraction of 25–39% maintained EC_e between 1.1 and 1.5 dS m^{-1} and prevented growth depression (Huett 1997a).

Caution must also be used during storage of seedlings with CRF in the media. Though the temperature-dependent mechanism of nutrient release of polymer-coated CRF should reduce risks of excessive nutrient release during cooler storage, freezing temperatures may create osmotic pressure changes within the soluble fertilizer core that can cause prill damage and allow fertilizer salt leakage, potentially resulting in lethal EC levels within the plug. This has been the presumed cause of several operational outplanting failures using seedlings that had been freezer-stored with CRF in the media (T.D. Landis, personal communication).

Another risk to root development using this method occurs when seedlings are subjected to hot, dry conditions during summer following field transplant. Drought conditions may result in buildup of fertilizer salts within the

rhizosphere, causing potential for root damage and greater transplant stress. Studies reporting substantial growth gains from application of CRF to container media with forest tree seedlings have generally been conducted under non moisture-limiting field conditions (Reddell et al. 1999; Haase et al. 2005).

Fertilization at outplanting: root system considerations

Fertilization at outplanting has gained renewed interest in reforestation programs, particularly with increased availability and refinement of CRF technology (Jacobs et al. 2003b). This process may be particularly attractive for use with bareroot seedlings, which preclude options such as nutrient spiking or incorporating CRF into media. Fertilizer may either be placed in the planting hole, put into an adjacent hole, localized on the surface near the tree, or broadcast (van den Driessche 1991).

Reports of growth response to fertilization at outplanting vary considerably, however, ranging among positive, neutral, and negative results across many tested combinations of fertilizer type, species, stocktype, and outplanting environmental conditions (Brockley 1988). Because initiation of new roots and root extension following outplanting is critical to minimizing transplanting stress (Sands 1984; Brockley 1988; Grossnickle 2005), root system inhibitions associated with excessive rhizosphere fertilizer salts might serve as a limiting factor in dictating response to fertilization at outplanting. This may be of particular concern when fertilizer is placed in the planting hole, which has been suggested by numerous authors as a means to facilitate the release of fertilizer nutrients within the vicinity of the root zone (see citations in Jacobs et al. 2004). This technique may be more efficient than adjacent-hole placement, which supplies nutrients to only a portion of the rooting zone where roots may or may not be present (Carlson 1981; Carlson and Preisig 1981; Rose and Ketchum 2003). However, potential risk for root damage associated with planting-hole fertilization cannot be avoided with the mechanisms of soluble nutrient salt release characteristic of most CRF types (Brockley 1988; van den Driessche 1991). Root damage may be amplified with increasing fertilizer dose, rapidity of nutrient release, proximity to roots, and moisture-limiting conditions.

On a drought-prone site in the Coast Range of Oregon, USA, a relatively high application rate of 60 g (5.22 g N) per seedling of 19:6:12 (N:P:K) Polyon® CRF to the planting hole inhibited root system development of Douglas-fir seedlings, resulting in reduced lateral root length, numbers of root tips, and biomass compared to non-fertilized seedlings (Jacobs et al. 2004). In many cases, comparison of root volume prior to outplanting with that following excavation indicated that there was a mean reduction in root volume for fertilized seedlings during the first growing season. Poor root system development of fertilized seedlings was correlated with reductions in xylem water potential and stomatal conductance compared to non-fertilized seedlings. In contrast,

fertilization with 21 g (1.89 g N) per seedling in the planting hole with a composite Osmocote® CRF improved shoot and root system development compared to controls for both western hemlock (*Tsuga heterophylla* Raf. Sarg.) on the Olympic Peninsula of Washington, USA (Carlson 1981) and Douglas-fir in northwestern Oregon (Carlson and Preisig 1981). For each species, planting-hole fertilization increased the number, and in some cases the diameter of lateral roots. In a series of studies involving several species across five sites in the Pacific Northwest, USA, planting-hole fertilization with two different combined formulations of Woodace® IBDU (isobutylidene diurea) CRF (3.9 g N per seedling) increased seedling stem volume only at the two sites with adequate soil moisture (Rose and Ketchum 2002).

Thus, potential for fertilization at outplanting to accelerate whole-plant growth while promoting root system development exists, but is dependent on maintaining a critical threshold balance that maximizes nutrient availability in the root zone while minimizing potential for root damage. Because control over moisture availability to facilitate nutrient uptake and/or leach excessive fertilizer salts from the root zone is generally not practical in the field, conservative application rates are advisable, particularly on dry sites.

Synthesis and future directions

Fertilization is a critical component of producing high quality nursery seedlings that are likely to establish and grow rapidly following outplanting. Interest in building nutrient reserves of nursery seedlings, as well as increased use of fertilization at outplanting is likely to persist in the future as expectations for reforestation productivity continue to rise.

Fertilization may create profound changes in rhizosphere chemical properties, acting to alter pH, make certain ions more or less available, and increase EC. High rhizosphere EC levels may inhibit root system proliferation and limit the ability of roots to extract water or nutrients. This is likely a combined function of specific ion toxicities and reduction in soil osmotic potential though precise mechanisms, particularly for tree species, need more complete study (Allen et al. 1994). A limited number of trials with container-grown seedlings using a peat-based media have identified EC ranges that maximize plant response during the first year of growth and found that root damage is likely above 2.5 dS m^{-1} for several common conifer species.

Inconsistencies in response to fertilization at outplanting, along with evidence for root system toxicities suggest that the inter-relationship between rhizosphere EC levels, nutrient uptake, root system proliferation, and transplanting shock should be more carefully examined. While threshold EC levels might approximate those reported for container-grown seedlings, there appears to be variation in tolerance of forest seedlings to salinity associated with different substrates (Fostad and Pedersen 2000). Distinctions in soil physical and chemical properties between a peat-based medium compared to mineral soil,

along with corresponding changes in root system tolerance to high EC levels as plants age warrant study under field scenarios. Reliance on precipitation to facilitate nutrient uptake and leach excessive fertilizer salts from the root zone as soils dry in the field is another critical difference between nursery and out-planting conditions, and attaining a positive response from field fertilization is largely dependent on soil moisture availability.

Future studies should be designed to examine changes in forest seedling EC tolerance across all stages of the reforestation process, from shortly after germination through field establishment. Ultimately, this information will provide a means to more competently prescribe fertilizer treatments that promote, rather than deter, root system development and help to maximize reforestation success.

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