

Growth, Gas Exchange, Foliar Nitrogen Content, and Water Use of Subirrigated and Overhead-irrigated *Populus tremuloides* Michx. Seedlings

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Abstract. Because limitations on water used by container nurseries has become commonplace, nursery growers will have to improve irrigation management. Subirrigation systems may provide an alternative to overhead irrigation systems by mitigating groundwater pollution and excessive water consumption. Seedling growth, gas exchange, leaf nitrogen (N) content, and water use were compared between overhead irrigation and subirrigation systems used to produce trembling aspen (*Populus tremuloides* Michx.) seedlings. After 3 months of nursery culture, subirrigation resulted in a 45% reduction in water use compared with overhead irrigation. At the end of the growing season, subirrigated seedlings had lower net photosynthetic assimilation, stomatal conductance (g_s), and leaf area, indicating earlier leaf senescence. However, no significant differences were detected for biomass, leaf N content, height, root-collar diameter, or root volume. Thus, we suggest that subirrigation systems offer promising potential for aspen seedling production when compared with overhead irrigation given the added benefits of water conservation and reduced nutrient runoff. Continuing emphasis on refinement such as determining the plant water requirements based on growth and development as well as container configuration is needed so that the intended benefits of using subirrigation can be realized.

Water scarcity and the increasing competition for water resources are forcing nursery growers to consider more seriously the adoption of water-saving strategies, especially in areas with limited water resources (Beeson and Yeager, 2003; Cabrera, 2005; Costa et al., 2007). In several regions with container seedling production, water is limited, restricted, or both (Beeson, 2006). In addition to the problems associated with the depletion of water resources, the loss of nutrients from excess irrigation during container seedling

production can represent a considerable eutrophication potential (Dumroese et al., 1995; Juntunen et al., 2002; Weatherspoon and Harrell, 1980). Therefore, efficient irrigation is one of the principal concerns in container seedling production. Overhead irrigation is the most widely used form of irrigation in tree seedling nurseries (Landis et al., 1989; Leskovar, 1998) as a result of its simplicity, low-cost installation, and capacity to reduce toxic buildup of fertilizer salts (Argo and Biernbaum, 1995; Biernbaum, 1992; Molitor, 1990).

Despite the wide acceptance of overhead irrigation, some critical features are of concern. Although overhead irrigation is a great tool for leaching the harmful accumulation of soluble salts in growing media, this practice may allow contaminated runoff to enter ground and surface waters (Dole et al., 1994). Similarly, various fertilizer practices can also contribute to harmful runoff or nitrate loading in soils around nurseries (Brand et al., 1993; Rathier and Frink, 1989). In addition, water interception by leaves of broad-leaved plants creates uneven water distribution in overhead systems (Landis and Wilkinson, 2004) such

that only 20% to 40% of the water applied through these systems is retained in the containers (Beeson and Knox, 1991). Thus, 60% to 80% of overhead irrigated water is of almost no value for plant growth.

In light of this, there is an increasing interest in subirrigation as a viable alternative to conventional overhead watering systems for container seedling production (Davis et al., 2008; Dumroese et al., 2006). Being a closed system, water is generally circulated from a reservoir into an application tank where capillary action causes upward water movement into growing medium (Coggeshall and Van Sambeek, 2001). Subirrigation supplies only the water that is used by the plants in transpiration plus a small evaporative loss (Argo and Biernbaum, 1995). When subirrigation is complete, unused water drains back to the reservoir for later recirculation. Subirrigation may be a useful technique for growing broadleaf plants that tend to shed water from a conventional, overhead-applied irrigation system, making it less effective, or where water conservation is of great concern. A variety of agronomic and forest tree species showing similar or better plant growth with subirrigation than overhead irrigation highlights the promise of this technique for tree seedling production (Ahmed et al., 2000; Bumgarner et al., 2008; Davis et al., 2008; 2011; Dumroese et al., 2006, 2011; Pinto et al., 2008). However, little work examining the differences in water use, seedling physiology, and end-of-season morphology of tree seedlings has been completed, limiting the potential for adoption by tree seedling growers.

Aspen (*Populus tremuloides* Michx.) is widely distributed across North America in parts of Canada, Mexico, and the United States. It is an important component of restoration programs and ornamental nursery culture. As a hardwood species with broad foliar canopy, it has a tendency to deflect irrigation water that limits the quantity and uniformity of water reaching the growing medium and was thus selected as the species of interest for this study.

Our objective was to build on the works of Bumgarner et al. (2008), Davis et al. (2008), and Dumroese et al. (2011) regarding the practical significance and suitability of subirrigation for nursery production of broadleaf forest tree species. This promising new technology needs further investigation before being used operationally. If subirrigation was shown to be effective in maintaining seedling quality compared with overhead irrigation, the water conservation benefits should improve tree seedling production efficiency. We hypothesized that seedlings of comparable morphology and physiological status could be produced under subirrigation and overhead irrigation systems.

Materials and Methods

Aspen seeds, wild collected in May 2009 in northern Idaho, were sown in early June 2009 into 164-cm³ Ray Leach “Cone-tainers” (SC-10; Beaver Plastics, Stuewe & Sons, Inc., Target, OR) at the University of Idaho Pitkin

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Forest Nursery in Moscow, ID. The “Cone-tainers” were assembled into 24 trays at 98 cells (each cell being an individual tubular Ray Leach “Cone-tainer”) per tray and filled with growing medium comprised of 45:45:10 peat:vermiculite:bark (v:v:v) “professional growers mix” (Sun Gro Horticulture, Ltd., Bellevue, WA). Based on operational growing practices at the Pitkin Forest Nursery (Kea Woodruff, personal communication), it was determined that seedlings should receive ≈ 250 mg N per individual during the growing season from overhead irrigation. Targeting the same amount of N, 10.8 kg of 5–10–10 controlled-release fertilizer (N–P–K) were hand-mixed into 474 L of growing medium, yielding 4.59 g of the fertilizer per cell (229 mg of N per plant). The fertilizer (Morcrop; Lilly Miller Brands, Walnut Creek, CA) has a 6-week release, which aligns well with the rapid growth phase of aspen seedling production. The same growing medium was used for both subirrigated and overhead-irrigated seedlings.

After sowing, containers were kept in a misted greenhouse for 7 d, which was maintained at a relative humidity of $\approx 80\%$. Subsequently, fogging was suspended and the germinants were watered by hand (gentle misting nozzle on a standard hose) and then by using an overhead system at a reduced flow rate for 3 weeks during the establishment

phase; after this, plants were transferred to the USDA Rocky Mountain Research Station Greenhouse Facility in Moscow, ID. They were then divided by treatment (subirrigation and overhead irrigation), randomized by tray, and placed on their respective tables. Germinants were thinned to leave just a single plant per container.

Irrigation scheduling was determined by gravimetric water content (GWC). Seedlings were irrigated when GWC reached 85% of field capacity for ≈ 6 weeks during the rapid growth phase. During the hardening phase, irrigation was scheduled at a GWC of 75% for 4 weeks followed by 70% for 2 weeks. Containers were randomly rotated within irrigation treatment to minimize edge effects. Irrigation treatments were initiated on 24 June. Subirrigation and overhead irrigation systems were the same as those used by Pinto et al. (2008). For overhead irrigation, the number of passes from the boom was determined based on 1) the need to reach field capacity (FC); and 2) the effects of foliage interception during the rapid growth phase. The number of passes was determined bi-weekly and recorded for later determination of water use. For subirrigation, a submersible pump was used to fill each of the three trays (one tray per block). Once the tray was full, water was allowed to sit until capillary force

allowed for saturation of the growing medium. Exposure time required to reach FC ranged from 1.25 h to 2.5 h throughout the study. After the allotted time for saturation, the valve at the base of the tray was released and the water returned to the storage tank. Because the subirrigation tanks required 196 L of water for proper filling of the tray, water levels were replenished as necessary. Water additions were measured by graduated cylinder and recorded.

The experiment was designed with two irrigation (overhead irrigation and subirrigated) treatments randomized in three blocks. Fifteen seedlings from each irrigation treatment were randomly sampled on six dates (17 July, 1 Aug., 16 Aug., 15 Sept., 30 Sept.). Morphological measurements included height (HT), root-collar diameter (RCD), root volume (RV), leaf area (LA), and tissue dry mass (DM); physiological measurements included tissue moisture contents, gas exchange [net photosynthesis (A); g_s], and foliar N content.

A and g_s were measured using a LI-6400 portable infrared gas analyzer equipped with a red light-emitting diode source (LI6400-02) and a CO₂ mixer control unit (LI-COR, Lincoln, NE). Measurements were taken on uppermost attached, fully expanded leaves on five different seedlings from each treatment for each replicate block (15 seedlings total).

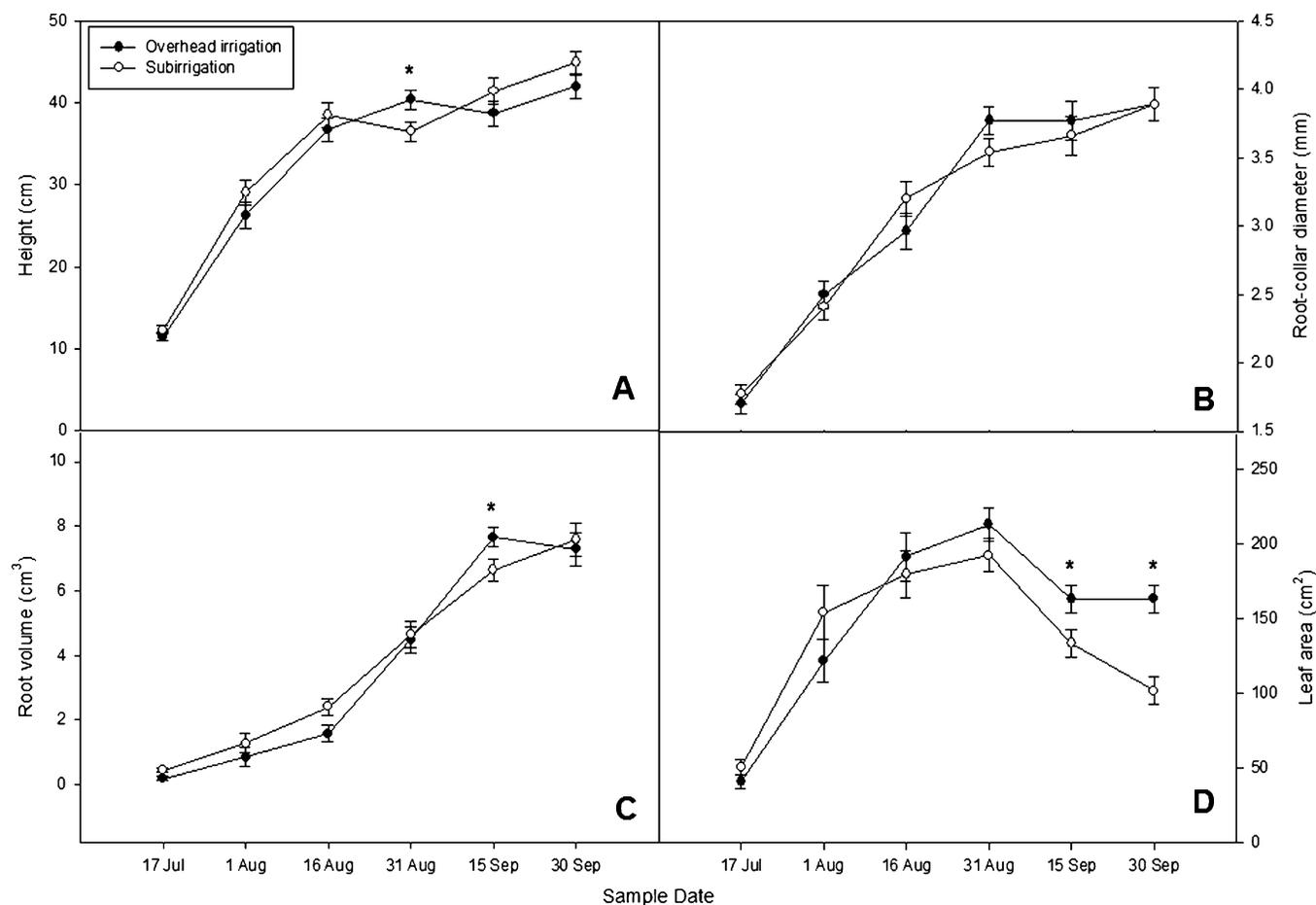


Fig. 1. Height (A), root collar diameter (B), root volume (C), and leaf area (D) of overhead-irrigated and subirrigated aspen seedlings. Each data point represents mean ($n = 15$) \pm SE. Asterisk at each sampling date indicates significant difference at $P < 0.05$. Data were analyzed separately at each sampling date; thus, only pairs of means at each sampling date are being compared with each other.

All gas exchange measurements were made beginning 3 to 5 h after sunrise. Parameters were held stable at photosynthetic photon flux density of $900 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, reference CO_2 concentration of $400 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, leaf temperature of 30°C , relative humidity of 25% to 35%, and flow rate at $500 \mu\text{mol}\cdot\text{s}^{-1}$. After enclosure in the leaf cuvette, data were logged when a leaf reached a steady-state value (cvs of CO_2 and H_2O within the chamber was less than 0.25%).

Morphological data and leaf N content were measured on the same 15 seedlings as those used for leaf gas exchange measurements. Seedlings were washed free of soil and measured for HT, RCD, and RV [through the water displacement method (Burdett, 1979)]. Leaf area was determined with an LI-3100 leaf area meter (LI-COR) and tissue DM was obtained after oven drying at 70°C for 72 h. On 5 Oct., fertilizer salt status in the growing medium was assessed through electrical conductivity (EC) measurements using a Field Scout Soil EC probe and Meter (Spectrum Technologies, Inc., Plainfield, IL). Growing medium EC was determined for five containers within each treatment, per block, at 5, 10, 15, and 20 cm from the top of the growing media. N was determined by the Dumas combustion procedure using a LECO nitrogen analyzer (LECO Corporation, St. Joseph, MI). Leaf N content was calculated by multiplying N concentration with DM.

Tests for normality and constant variance were performed to ensure validity of the assumptions of analysis of variance (ANOVA) and no transformations were necessary. Data were analyzed using a general linear model with SAS 9.2 (SAS Institute Inc., Cary, NC). When ANOVA indicated significant ($P < 0.05$) irrigation treatment effects, Tukey's studentized range test was used to identify significant differences at $\alpha = 0.05$. All measured variables were analyzed for each sampling date. The data presented in figures are means of 15 seedlings from each irrigation treatment ($n = 15$). A t test was used to quantify the difference in water use between overhead and subirrigated seedlings.

Results

Seedling HT was similar between overhead and subirrigation systems throughout the sampling dates with the exception for 31 Aug., when HT in overhead-irrigated plants was significantly ($P = 0.034$) greater than that of subirrigated plants (Fig. 1A). RCD was not significantly different between irrigation treatments throughout the sampling dates (Fig. 1B). RV (Fig. 1C) of subirrigated seedlings was greater on 15 Sept. ($P = 0.030$) but the same at the last measurement point. Mean LA for both overhead and subirrigation were similar from 17 July until 31 Aug. After 31 Aug., mean LA (Fig. 1D) in subirrigated plants was significantly lower than in overhead-irrigated seedlings ($P < 0.0372$). With the exception of the 16 Aug. measurement ($P = 0.001$ and $P = 0.0124$ for shoot and root DM, respectively), shoot DM (Fig. 2A) and root DM (Fig. 2B) were the same across irrigation treatments.

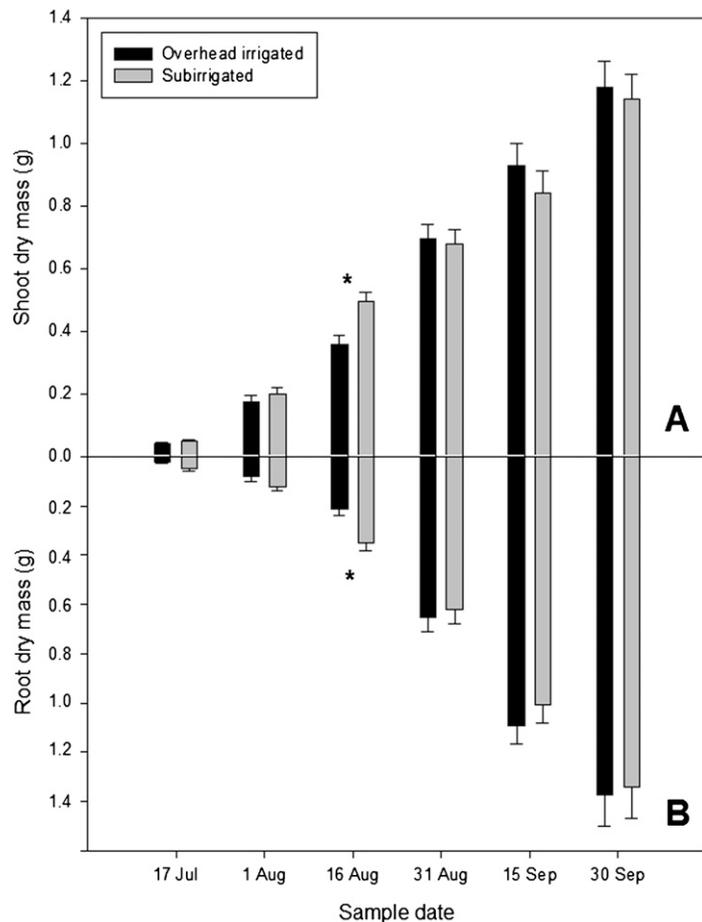


Fig. 2. Shoot dry mass (DM) (A) and root DM (B) of overhead-irrigated and subirrigated aspen seedlings. Each data point represents mean ($n = 15$) \pm SE. Asterisk at each sampling point indicates significant difference at $P < 0.05$. Data were analyzed separately at each sampling date; thus, only pairs of means at each sampling date are being compared with each other.

Mean A values for both irrigation treatments showed decreasing trends from 17 July until 16 Aug. while maintaining similar values (Fig. 3A). By 31 Aug., rates had increased sharply and spiked on 15 Sept. in overhead irrigation ($13.19 \mu\text{mol CO}_2/\text{m}^2/\text{s}$) and significant differences between treatments were detected ($P = 0.001$ on 15 and 30 Sept.) with overhead irrigation having greater mean A values. Mean g_s values showed a comparable but less consistent response patterns than A rates over the sampling dates (Fig. 3B). Similar to A , g_s values were significantly higher in overhead-irrigated seedlings on 15 Sept. ($P = 0.0083$) and 30 Sept. ($P = 0.0058$). In addition, overhead-irrigated plants had significantly ($P = 0.0115$) higher initial g_s , compared with subirrigated plants on 17 July. For leaf N content, the only significant difference between irrigation treatments was on the first sampling date, 17 July (Table 1).

Irrigation method ($P = 0.0230$) and depth from the top of growing medium ($P = 0.0430$) significantly affected growing medium EC. Subirrigated containers had higher EC ($2.34 \pm 0.02 \text{ dS}\cdot\text{m}^{-1}$; mean \pm SE) levels than those irrigated from above ($1.78 \pm 0.01 \text{ dS}\cdot\text{m}^{-1}$). Growing medium EC in both container types was lower at 5 cm ($1.05 \pm 0.02 \text{ dS}\cdot\text{m}^{-1}$) than at 10, 15, and 20 cm ($2.20, 2.62, 2.65 \pm 0.02$

$\text{dS}\cdot\text{m}^{-1}$). Total growing season water use in the subirrigation system was significantly lower ($P = 0.0001$), at $726.67 \pm 6.77 \text{ L}$ of water compared with $1348.3 \pm 0.00 \text{ L}$ in overhead systems.

Discussion

Confirming our hypothesis regarding morphology, we observed that aspen seedlings can be grown in containers using subirrigation yielding plants of similar quality to overhead irrigation-produced seedlings. Although physiological and morphological assessment did not indicate superior performance of subirrigated seedlings, as reported by other studies (Bumgarner et al., 2008; Coggeshall and Van Sambeek, 2001), producing equal quality seedlings under reduced water consumption is of great interest. The similarity in seedling physiological performance throughout the rapid growth phase and end of growing season morphology was not surprising. For example, Davis et al. (2008) observed no significant differences in growth of subirrigated versus overhead-irrigated northern red oak (*Quercus rubra* L.) seedlings. In koa (*Acacia koa* Gray), subirrigated and overhead-irrigated plants had similar gas exchange, height, and RCD (Davis et al., 2011; Dumroese et al., 2011).

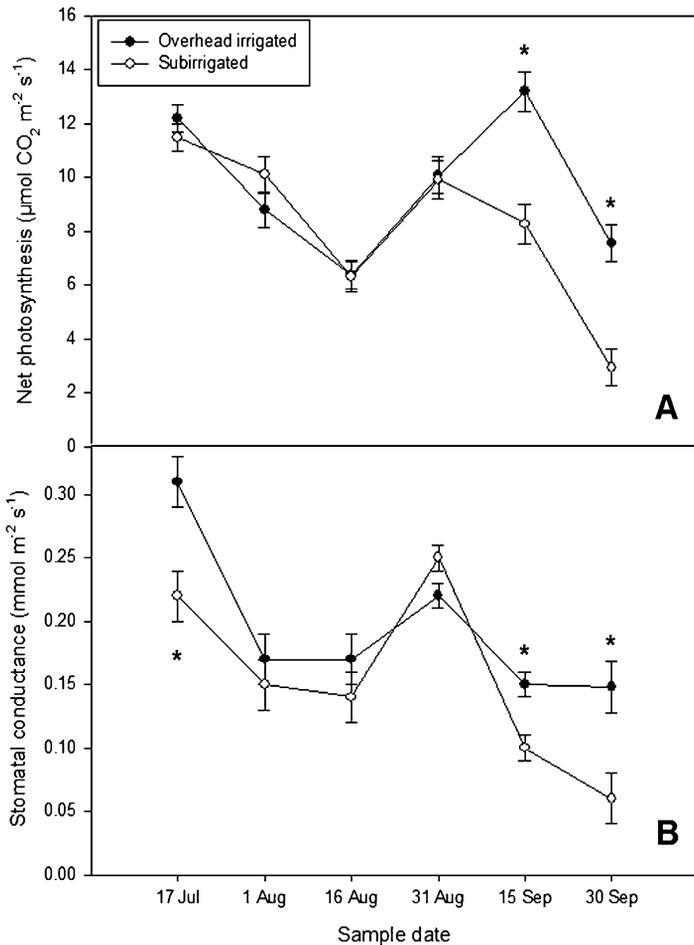


Fig. 3. Net photosynthesis (A) and stomatal conductance (g_s) (B) of overhead-irrigated and subirrigated aspen seedlings. Each data point represents mean ($n = 15$) \pm SE. Asterisk at each sampling point indicates significant difference at $P < 0.05$. Data were analyzed separately at each sampling date; thus, only pairs of means at each sampling date are being compared with each other.

Table 1. Leaf nitrogen (N) content of overhead-irrigated and subirrigated aspen seedlings.^z

Sample date	Leaf N content ($\text{mg}\cdot\text{g}^{-1}$)	
	Overhead irrigation	Subirrigation
17 July	6.67 \pm 0.50	7.71 \pm 0.40*
1 Aug.	4.48 \pm 0.27	4.93 \pm 0.27
16 Aug.	3.28 \pm 0.12	3.13 \pm 0.12
31 Aug.	2.89 \pm 0.11	2.93 \pm 0.11
15 Sept.	2.50 \pm 0.09	2.43 \pm 0.09
30 Sept.	2.34 \pm 0.13	2.45 \pm 0.13

^zEach data point represents mean ($n = 15$) \pm SE. Asterisk at each sampling point indicates significant difference at $P < 0.05$. Data were analyzed separately at each sampling date; thus, only pairs of means at each sampling date are being compared with each other.

Subirrigation has repeatedly been shown to reduce water inputs when compared with overhead irrigation (Ahmed et al., 2000; Dumroese et al., 2006; Weatherspoon and Harrell, 1980) because water is delivered directly to the growing medium within the container (Landis et al., 1989). Ahmed et al. (2000) reported an 86% reduction in water use for subirrigated-grown food crops compared with overhead irrigation, whereas Dumroese et al. (2006) demonstrated a 56% water savings for Ohi'a, Hlan tropical hardwood (*Met-*

rosideros polymorpha Gaudich.). In our study, the subirrigation system yielded a water savings of 45% compared with overhead irrigation. Our results indicated that seedlings grown under subirrigation required 0.64 l H₂O/g of final biomass compared with 1.08 l H₂O/g for overhead-irrigated seedlings. In areas where water is expensive, unavailable readily, or restrictively managed, this notable gain in water use efficiency should be of value in seedling production.

Despite the relatively little difference in seedling size and physiological status throughout the growing season, some of our data allows us to speculate that seedling development was hindered in subirrigated plants in the late growing season. It is possible that disease or insufficient watering in subirrigated seedlings may have contributed to repeated daily stress, as suggested by the results of our work in which subirrigated seedlings had lower A and g_s than overhead-irrigated seedlings. Therefore, plants receiving low irrigation volume in relation to their needs closed their stomata, resulting in reduced photosynthesis and thus decreased plant growth (Apostol et al., 2009; Siemens and Zwiazek, 2003; Wan et al., 1999) and potentially explaining the earlier senescence in subirrigated seedlings. In some ways,

rejecting our hypothesis regarding physiological status (i.e., the differences in late-season gas exchange) highlights the importance of refining irrigation regimes to optimize seedling production. The earlier declines in leaf area and gas exchange indicate more pronounced senescence in subirrigated seedlings. Although this was not enough to create a difference in seedling morphology or N content, it does highlight the ability to manipulate seedling phenology using an irrigation regime. With changes in seedling phenology, investigation of the effects of irrigation method on dormancy status is warranted as Davis (2006) showed dormancy conditioning in northern red oak during nursery culture resulted in more rapid onset of budbreak after overwinter storage.

In our study, we found that growing medium EC was 31% higher in subirrigated containers than in those irrigated from above but that values were below any area of concern for tree seedling production (Jacobs and Timmer, 2005). That irrigation method influenced growing medium EC is indicative of two things. First, less fertilizer was being leached from subirrigated containers than from those receiving overhead irrigation, potentially resulting in subirrigated seedlings requiring less fertilizer applied to produce a seedling of equal quality to overhead-irrigated seedlings (Hickleton and Cairns, 1996). This would yield financial and environmental benefits to seedling producers. Second, seedling growers using subirrigation must consider potential salt distribution throughout. Although several studies have found fertilizer salt buildup occurs near the top of the container (e.g., Argo and Biernbaum, 1995; Davis et al., 2008; Richards and Reed, 2004; Todd and Reed, 1998), the opposite occurred in the present study. The timing of the measurement in our study as well as the novel use of controlled-release fertilizer in subirrigation research could explain this difference with downward movement of fertilizer across the growing season and a relatively low fertilizer rate to begin with. Where high upper-profile EC is an issue, Davis et al. (2008) found it could be quickly remedied through flushing with water. During nursery culture, we observed, but did not quantify, that fewer roots existed in the upper profile of subirrigated containers, concurring with Todd and Reed (1998), who reported less root dry weight in the upper portion of containers for *Impatiens hawker* Bull.

We conclude that subirrigation produces quality aspen seedlings at a significant water savings. Additional research is needed to help refine subirrigation systems for use across a variety of broadleaf forest tree species because tailoring irrigation scheduling and understanding the differences in air flow, pathogen dispersal, and nutrient flux is needed for optimization of this system. Quantifying the savings in reduced nutrient leaching, both economically in terms of saved fertilizer and in terms of reduced pollution, will further help quantify potential benefits of subirrigation systems.

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