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Growth, Biomass, and Nitrogen Use Efficiency of Containerized Fraser Fir (*Abies fraseri*) as Related to Irrigation and Nitrogen Fertilization

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***Abstract.* Growth and nutrient uptake of containerized fraser fir (*Abies fraseri*) seedlings in response to irrigation and fertilization was investigated for 2 years in a greenhouse experiment. Height and stem diameter growth increased 12% to 35% and 4% to 32%, respectively, with increased irrigation. There was an inverse relationship between irrigation and foliar nitrogen content and no irrigation effect on foliar phosphorus, potassium, magnesium, and manganese. Irrigation increased foliar calcium. Approximately 2.0% to 4.5% of applied nitrogen was lost through leaching. Increases in total biomass in high irrigation treatments were caused by higher root and stem biomass. Higher irrigation treatments increased nitrogen use efficiency (NUE) and assimilatory nitrogen use efficiency probably as a result of increase in carbon assimilation efficiency leading to increase in net primary productivity. There was no clear effect on the root weight ratio, but the index nitrogen availability per unit of foliage indicated a higher availability in plants receiving the lowest irrigation. This suggests that under water stress, the decrease in assimilation and NUE may be buffered by an increase in the plant's ability to provide nitrogen and other nutrients to various organs.**

Fraser fir [*Abies fraseri* (Pursh) Poir.] is widely planted for Christmas tree production in the midwest and eastern United States. The species has a unique natural distribution, restricted to high elevations in the southern Appalachian Mountains of southwestern Virginia, western North Carolina, and eastern Tennessee, but intensively planted elsewhere in the United States as a result of its desirable attributes (Beck, 1990; Nzokou and Leefers, 2007). Under current field production practices in the Midwest, the crop is intensively managed with regular applications of inorganic fertilizers and irrigation to satisfy its physiological needs.

Water is an important factor for the numerous physiological and biochemical processes controlling plant growth and productivity (Turner and Begg, 1981). The mechanism of response to water shortage involves stomata closure, which restricts CO_2 uptake and subsequently growth (Jamieson et al., 2009). Water availability, uptake, and utilization also affect nutrient availability, solubility, and use. These processes include element concentrations in the soil solution, because of nutrient diffusion and mass flow to the root surface, absorption of the elements by the roots to shoots, and utilization in the photosynthetic process by the foliage (Alam, 1999).

Nitrogen (N) fertilization and uptake is critical for shoot and root growth. Most N taken up by crops is retained in plant tissues, where it becomes part of the plant structure and is involved in the photosynthesis or in labile storage (Jamieson et al., 2009). During the growing season, N is reallocated according to sink demands and is mobilized from sources to sink tissues (biochemical cycling). In addition, seasonal N resorption is a known mechanism for perennial plants to conserve and reuse stored N that can substantially impact the N use efficiency (Coleman et al., 2004; Hinesley et al., 1991). Nitrogen shortages lead to reduction of the RuBisCo (ribulose-1, 5-bisphosphate carboxylaxe/oxygenase) in leaves, causing remobilization of N to other tissues (Grindley, 1997; Jamieson et al., 2009). This ultimately leads to reduction in light interception and use for photosynthesis (Grindley, 1997).

The capacity of plant roots to absorb water and nutrients is affected by water stress (Alam, 1999). Nutrient uptake tends to decrease under reduced water availability as a result of a decrease in the transpirational rate and subsequent reduction in the nutrient absorption capacity of roots (Alam, 1999; Levitt, 1980). Changes in soil water also affect root permeability and cause disturbance to root metabolism (Gerakis et al., 1975). However, there are conflicting reports in the literature on plant nutrient uptake and utilization under droughty conditions. Tanguilig et al. (1987) reported decreased N concentration, whereas other references showed high N levels in plants under stress attributed either to fast accumulation of proline (Singh et al., 1973) or fast accumulation of free amino acids that are not converted into proteins (Barrett and Naylor, 1966). In addition, the slower growth rate of plants under reduced water conditions can prevent the dilution of nutrients within the plant (Alam, 1999). Studies conducted on various agricultural crops also indicated accumulation of phosphorus, magnesium, potassium, and carbon under drought stress (Jenne et al., 1958).

Another important process that affects the availability and uptake of nutrients under well-watered conditions is the leaching of soluble nutrients below the root zone. When plants are irrigated beyond the soil water-holding capacity, soluble forms of N and other macronutrients will leach from the root zone.

The objective of our study was to determine the growth, nutrient concentration and content, and N use efficiency of containerized *Abies fraseri* in response to watering and N fertilization.

Material and Methods

Site and materials. This 2-year greenhouse study was conducted at the Tree Research Center (TRC) at Michigan State University. The greenhouse growing season and average high temperatures were 27 and 20 °C, respectively, and the daytime average operating temperature was 25 °C.

Three-year-old (plug+2) fraser fir (*Abies fraseri*) transplants were potted in 3-gallon cylindrical black plastic containers. The seedlings averaged 9.3 mm in diameter and 31.4 cm in height. The potting mix used was the Fafard 52 mix (Conrad Fafard, Inc.), which contains ≈60% pine bark along with Canadian sphagnum peat, perlite, vermiculite, dolomitic limestone, and gypsum; the reported pH is 5.5 to 6.5.

Nitrogen was supplied with a granular controlled-release formulation (MESA™; Lebanon Turf) containing 30% N (30N–0P–0K) and 12% sulfur. The fertilizer is a homogenous granule of approximately equal amounts of ammonium sulfate and methylene urea polymers.

Before potting, the seedlings were root-pruned to an approximate root length of 25 cm. Seedlings were potted at root-collar depth on 19 May 2007 and placed in the greenhouse where they received various fertilization and irrigation treatments throughout the growing

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season (described subsequently) until 30 Sept. 2007. At that date, all plants were moved outdoors to a lath house for hardening. The lath house was covered with polyurethane throughout the winter to protect seedlings from extreme temperatures. On 15 Apr. 2008 (before budbreak), plants were moved back into the greenhouse for a second growing season.

Treatments. Three N rates were top-dressed as a single yearly application at the beginning of each of the two growing seasons (6 May 2007 and 14 May 2008). Irrigation was manually applied during the growing season at rates of 386, 257, 122, and 63 mL/pot/d (Monday to Friday) between 140 HR and 1700 HR. Initial analysis showed that irrigation water contained 0.06 ppm manganese, 16.3 ppm magnesium, 68.4 ppm calcium, and 0.02 ppm potassium. Four irrigation treatments (I1 = 386 mL/d, I2 = 257 mL/d, I3 = 122 mL/d, and I4 = 63 mL/d) were combined with three fertilization treatments (F1 = 6 g, F2 = 12 g, and F3 = 18 g) in a factorial arrangement. Each treatment had nine containers replicated three times for a total of 27 plants in each treatment and 324 plants for the entire experiment.

Growth characterization. Baseline tree height from the soil surface and stem diameter (root collar) was measured shortly after potting in May 2007 on all trees. Trees were remeasured at the end of the 2007 and 2008 seasons (11 Sept. 2007 and 26 Sept. 2008). Height and diameter growth were calculated as the difference between the final and initial measurements.

Ten trees were randomly selected and used determination of the initial root, stem, and foliar biomass in May 2007. At the end of the 2008 growing season (30 Sept. 2008), two random specimens were collected from each replicate (six plants total per treatment) to determine final biomass for each treatment. Biomass accumulation for stems, roots, and foliage were calculated as the difference between the final and initial biomass for each treatment.

Plant tissue sampling and analyses. Needles were collected for nutrient analyses at the end of the growing season in each year. Tissues harvested were oven dried at 60 to 65 °C and ground into a fine powder. Approximately 0.3 g of material was placed into the 75-mL digestion tube and acid-digested with a mixture of sulfuric acid (4.5 mL) and hydrogen peroxide (1.5 mL). Samples were pre-digested for 2 h and placed into a block digester (AIM600 Block Digestion System) at 340 ± 10 °C for heat digestion under a programmed temperature schedule.

Total N was determined as described by Christianson and Holt (1986). Aliquots from the digested solution were buffered and after dialysis chlorinated to form a chemical complex measured at 660 nm for total N on a SAN++ segmented flow analyzer (Skalar Inc., Atlanta, GA). The total phosphorous content determination was based on the ammonium heptamolybdate and potassium antimony (III) reaction that form under acidic environment an antimony-phospho-molybdate complex measured at 880 nm on the SAN++ segmented flow analyzer. Other macronutrients, including potassium (K), calcium (Ca), magnesium (Mg), and manganese (Mn), were determined by atomic absorption spectrometry (AAnalyst 400; Perkin Elmer).

Leachate collection and analysis. Leachates were collected from a subset of containers in each treatment (six in 2007 and three in 2008) using plastic trays placed under the containers. Water drained naturally into the collection trays during the week and was collected from the tray twice weekly. The two samples were then combined and their volume measured. An aliquot of 100 mL collected from each container was stored at 4 °C before analysis.

Stored samples were used for determination of the nutrient concentration. Aliquots (15 mL) used for total N and total phosphorous were persulfate (K_2SO_4) digested according to Cabrera and Beare (1993). A second aliquot (30 mL) was filtered (70-μm filter paper) and analyzed for K, Ca, Mg, and Mn using the AAnalyst 400 atomic absorption spectrometer. The total mass (mg) of each nutrient ion leached per week was calculated from the total volume leached and the aliquot ion concentration for each element.

Data analysis. Resource use efficiency parameters were calculated as described by Sheriff et al. (1995), given by:

ANUE: Assimilatory nutrient use efficiency (rate of carbon assimilation, or foliar biomass production per unit of foliar N).
NUE: Whole plant nutrient use efficiency in grams of biomass/g of N per year.
N/RW: Index of N availability (foliar N per unit root weight).
RWR: Root weight ratio (grams of root/g of total biomass).

Growth attributes, biomass, and nutrient content data were first tested for homogeneity of variance and normality. A general factorial model combining main effects and interaction as described in Eq. (1) was used.

$$Y = \beta_0 + \beta_1 A + \beta_2 B + \beta_3 AB \qquad (1)$$

where β_0 is the model intercept, β_1 and β_2 are coefficients associated with factor A and B, and β_3 is the coefficient associated with the combination of factors A and B, representing the interaction in the model. Analysis of variance was performed for a 3 × 4 randomized design with three replications on all response variables using the linear model described previously. A level of significance of α = 0.05 was used for inferring any statistical significance. For growth, when the model was significant, the least significant difference method with a Bonferroni correction at $P \leq 0.05$ was used to make pairwise comparisons between responses. Linear regression analysis was used to evaluate the quantitative impact of the two main effects (irrigation and N applications) on growth, biomass, and organs nutrient content parameters. The GLM procedure for repeated measures ($P \leq 0.05$) was used to analyze the leachate nutrient concentrations. All statistical analyses were performed using Systat 12 statistical software (Systat Software, Inc., Chicago, IL).

Results

Growth response. Two years cumulative growth data indicate a significant effect of irrigation and fertilization on height growth, but root-collar diameter was affected by irrigation and not by fertilization (Table 1). There was no interaction between the irrigation and fertilization on neither height nor root-collar diameter. Irrigation increased height growth by 12% to 35% (from lowest to highest irrigation), whereas diameter growth increased up to 54% (from lowest to highest irrigation).

Total biomass generally increased with irrigation treatments from 40 g to 110 g/tree

Table 1. Growth and biomass accumulation of containerized fraser fir transplants in response to irrigation and fertilization (2 years accumulated).

Treatments	Ht growth (cm)	Diam growth (mm)	Dry wt Stem (g)	Dry wt Roots (g)	Dry wt Needles (g)	Shoot/root
Irrigation[z]						
Level 1	16.3 (0.8)[x]	5.9 (0.5)	49.0 (11.6)	36.0 (4.4)	23.0 (3.1)	1.9 (0.5)
Level 2	14.1 (1.2)	6.0 (0.2)	47.6 (13.9)	35.4 (2.6)	30.8 (1.3)	2.1 (0.2)
Level 3	12.2 (1.2)	4.6 (0.4)	23.5 (2.7)	27.7 (0.9)	16.4 (1.2)	1.4 (0.1)
Level 4	9.4 (0.8)	3.8 (0.1)	13.1 (3.8)	13.1 (1.6)	11.1 (1.5)	1.8 (0.2)
Significance	**r^2 = 0.80	***r^2 = 0.85	**r^2 = 0.71	**r^2 = 0.80	*r^2 = 0.68	NS
Nitrogen[y]						
Level 1	11.0 (1.1)	4.6 (0.5)	20.1 (2.9)	25.5 (3.5)	19.6 (3.7)	1.6 (0.1)
Level 2	12.0 (1.6)	5.1 (0.5)	29.0 (14.2)	27.9 (6.6)	19.3 (5.4)	2.1 (0.4)
Level 3	15.2 (1.8)	5.6 (0.6)	40.9 (10.6)	30.9 (6.3)	22.2 (4.2)	1.9 (0.2)
Significance	NS	NS	NS	NS	NS	NS

[z]Irrigation levels 1, 2, 3, and 4 = 386, 257, 122, and 63 mL per pot per week, respectively.
[y]Nitrogen levels 1, 2, and 3 = 6, 12, and 18 g per pot, respectively.
[x]Numbers in parentheses are SES of the arithmetic mean.
Height and diameter growth and biomass data were analyzed for main effect by simple regression analysis and analysis of variance at $P \leq 0.05$.
NS, *, **, ***Nonsignificant, or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

depending on the treatment. Higher fertilization treatments (12 g and 18 g) generally produced more biomass, especially when combined with high irrigation treatments. The partition of the accumulated biomass indicates that needle biomass accumulation did not increase with higher irrigation and fertilization treatments, but root and stem biomass accumulation were generally positively affected by both factors (Table 1). Irrigation significantly affected only root biomass production, whereas fertilization affected stem, root, and foliage biomass. There was no interaction between the two factors for any of these three organs.

Foliar nutrient concentration. Foliar N concentration generally increased as the applied amount of irrigation decreased with a more pronounced effect in 2007 compared with 2008 (Fig. 1). Increased irrigation reduced the foliar N concentration in 2007 ($P \leq 0.00$) but not in 2008 ($P \leq 0.17$). Increased fertilization increased the foliar N concentration in both 2007 ($P \leq 0.01$) and 2008 ($P \leq 0.00$). The phosphorus (P) concentration was unaffected by either irrigation or fertilization. The N/P ratio varied from 9.8 to 15.5 depending on the treatment. Ratios above 10 are considered adequate for foliar N and P nutrition (Landis, 1989).

Foliar Ca concentration slightly increased with irrigation in both 2007 and 2008 (Fig. 2) with changes statistically significant in both years ($P \leq 0.05$ and $P \leq 0.00$, respectively). Foliar K, Mg, and Mn were unaffected by increased irrigation treatments (Fig. 2).

Nitrogen accumulation. Needle and stem N content were unaffected by irrigation but were significantly affected by fertilization with no interaction (Table 2). Root and total plant N were significantly affected by both irrigation and fertilization. Higher irrigation treatment resulted in enhanced N use efficiency compared with lower water treatments (Table 2).

Nutrient leaching. The computation of the cumulated volume leached indicated a leaching fraction of 3.0% to 23.8% depending on the irrigation treatment (Table 3). Treatments at 386 mL/pot produced average leaching fractions of 21.7% (2007) and 11.0% (2008), whereas 257-mL/pot treatments leached 6.5% (2007) and 9.6% (2008). No leachate was collected in either year on plants treated with 63 mL/pot or 122 mL/pot in either year. The leaching fractions correspond to 4.5% (2007) and 4.0% (2008) total N leached for the 386-mL/pot treatments and 3.1% (2007) and 2.0% (2008) total N leached for the 257-mL/pot treatments (Table 3). The repeated-measures mixed model at 95% confidence interval indicated that the difference in N concentration in weekly leachates collected was not significant in 2007 ($P = 0.49$) but was highly significant in 2008 ($P = 0.00$).

The total cumulative leaching for Ca, K, and Mg (Fig. 3), indicates no statistical difference in total Ca or total K. The total Mg leached was significantly affected by irrigation with the highest irrigation treatment (386 mL/pot) exhibiting much higher cumulated total Mg leached in both 2007 ($P \leq 0.00$) and 2008 ($P \leq 0.01$).

The Mn and orthophosphate concentrations in leachates were negligible and thus are not included in the data reported.

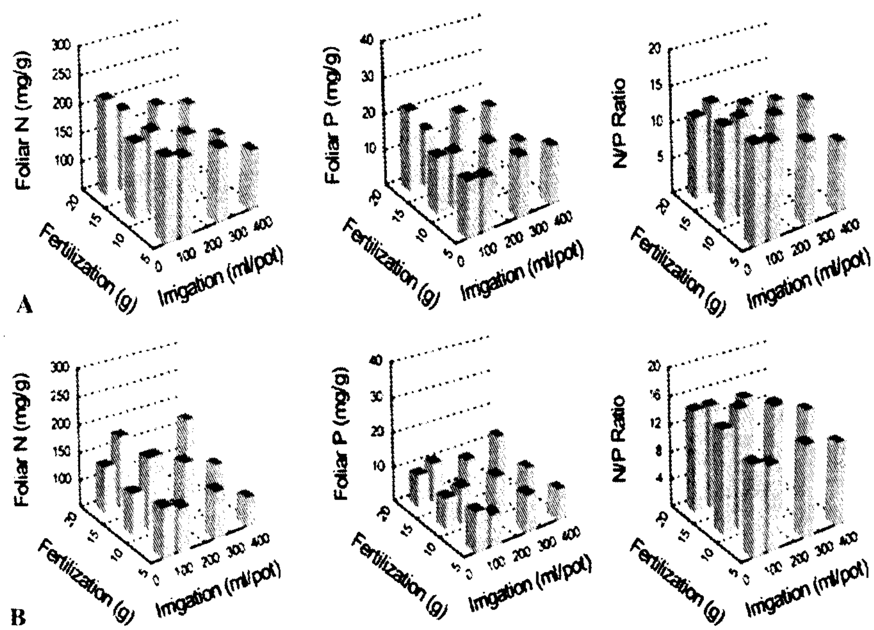

Fig. 1. Change in foliar nitrogen (N) and phosphorous (P) concentrations and N/P ratio as affected by irrigation and fertilization in 2007 on the top three panels (**A**) and 2008 in the bottom three panels (**B**). Foliar N content was affected by irrigation in 2007 ($P = 0.00$) but not in 2008 ($P = 0.18$). The N content was significant affected by fertilization in both 2007 ($P = 0.01$) and 2008 ($P = 0.01$). Irrigation: I1 = 386 mL, I2 = 257 mL, I3 = 122 mL, I4 = 63 mL; fertilization F1 = 6 g, F2 = 12 g, F3 = 18 g.

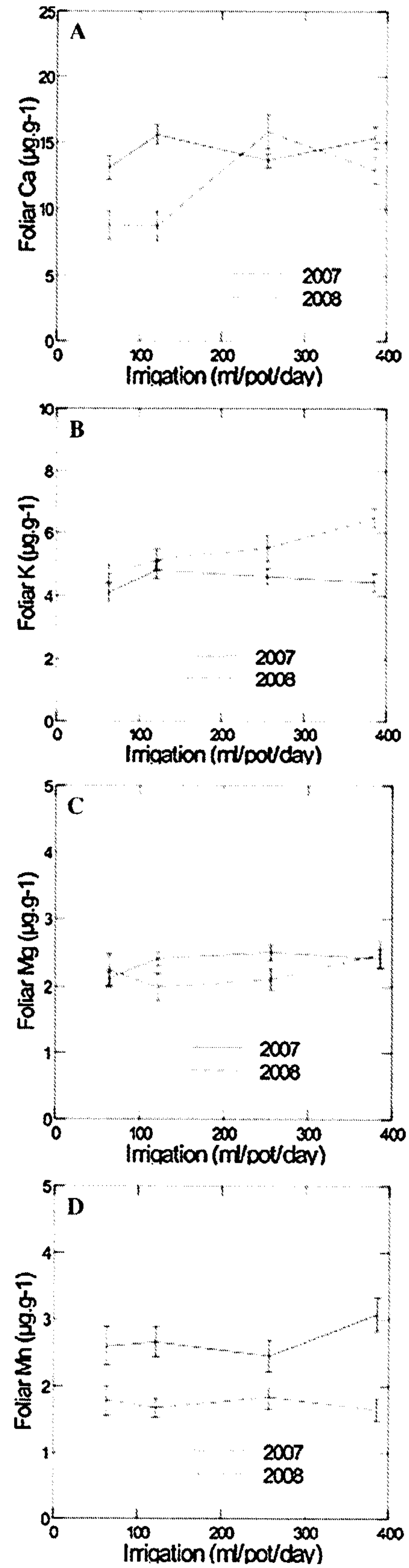

Fig. 2. Change in foliar calcium (Ca) (**A**), potassium (K) (**B**), magnesium (Mg) (**C**), and manganese (Mn) (**D**) as affected by irrigation treatment in 2007 (continuous lines) and 2008 (discontinued lines). Ca was the only element significantly affected by irrigation treatments.

Table 2. Plant nitrogen (N) content partitioning in response to irrigation and fertilization (mg of N).

Treatments	Organ nitrogen content			
	Needles (mg)	Stems (mg)	Roots (mg)	Total (mg)
Irrigation[z]				
Level 1	3.52 (0.84)	5.81 (1.24)	5.48 (1.54)	14.81 (3.54)
Level 2	4.86 (0.32)	4.24 (0.31)	5.77 (1.01)	14.86 (2.40)
Level 3	2.80 (0.28)	2.73 (0.51)	4.24 (0.50)	9.77 (1.11)
Level 4	1.96 (0.46)	1.59 (0.51)	2.31 (0.30)	5.86 (1.21)
Significance	NS	$^{**}r^2 = 0.75$	$^{*}r^2 = 0.60$	$^{*}r^2 = 0.69$
Nitrogen[y]				
Level 1	2.81 (0.51)	2.22 (0.43)	2.92 (0.42)	7.9 (1.06)
Level 2	2.89 (0.79)	4.08 (1.45)	4.66 (0.88)	11.63 (3.02)
Level 3	4.14 (0.64)	4.47 (1.07)	5.76 (1.19)	14.38 (2.75)
Significance	NS	NS	$^{*}r^2 = 0.60$	NS

[z]Irrigation levels 1, 2, 3, and 4 = 386, 257, 122, and 63 mL per pot per week, respectively.
[y]Nitrogen levels 1, 2, and 3 = 6, 12, and 18 g per pot, respectively.
[x]Numbers in parentheses are SEs of the arithmetic mean
Nitrogen content data were analyzed for main effect by simple regression analysis and analysis of variance at $P \leq 0.05$.
NS, *, **, ***Nonsignificant, or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Table 3. Water leaching fractions and percentage nitrogen (N) leached in response to irrigation and fertilization.

Treatments	2007			2008		
	Water applied (l)	Water leached (%)	N leached[z] (%)	Water applied (l)	Water leached (%)	N leached[z] (%)
I1F1	19.3	23.8	1.6	23.1	11.4	2.2
I1F2	19.3	20.2	5.1	23.1	11.3	5.4
I1F3	19.3	21.1	6.8	23.1	10.5	4.3
Average I1	19.3	21.7	4.5	23.1	11.0	4.0
I2F1	12.9	3.0	ND[y]	15.4	9.9	1.2
I2F2	12.8	8.6	2.6	15.4	10.5	1.9
I2F3	12.8	8.2	3.6	15.4	8.3	3.0
Average I2	12.8	6.6	3.1	15.4	9.6	2.0
I3F1	6.1	0.0	0.0	7.3	0.0	0.0
I3F2	6.1	0.0	0.0	7.3	0.0	0.0
I3F3	6.1	0.0	0.0	7.3	0.0	0.0
Average I3	6.1	0.0	0.0	7.3	0.0	0.0
I4F1	3.1	0.0	0.0	3.7	0.0	0.0
I4F2	3.1	0.0	0.0	3.7	0.0	0.0
I4F3	3.1	0.0	0.0	3.7	0.0	0.0
Average I4	3.1	0.0	0.0	3.7	0.0	0.0

Irrigation: I1 = 386 mL, I2 = 257 mL, I3 = 122 mL, I4 = 63 mL; fertilization F1 = 6 g, F2 = 12 g, F3 = 18 g.
[z]The effect of irrigation on the N concentration in leachates was analyzed by the repeated-measures analysis of variance procedures. The N concentration in leachates was not significant in 2007 ($P = 0.5$) and highly significant in 2008 ($P = 0.00$).
[y]ND = no data.

Resource use efficiency. Assimilatory nitrogen use efficiency (ANUE), and N use efficiency generally increased with irrigation amounts (Table 3). The index of N availability per unit foliage (N/RW) was the lowest at the highest irrigation treatment and highest at the lowest treatment. Root weight values were similar for all irrigation treatments (Table 3).

Discussion

Growth. Both water and N were limiting for height growth, but there was no significant interaction between the two (Table 1). Stem diameter growth responded positively to irrigation but not fertilization. Biomass accumulation also increased with irrigation. These conclusions agree with previous studies related to growth, volume, and biomass production as related to fertilization and irrigation in various conifer species under field conditions (Nilsson and Orlander, 2003; Snowdon and Benson, 1992; Trichet et al., 2008). Maintaining a wet growing medium in highly irrigated plots allows stomata to remain opened longer resulting in more volume growth (Albaugh et al., 2008). This physiological process leads to increased production of carbohydrates as a result of enhanced photosynthesis and explains the strong height, radial, and biomass growth response observed in this study. Increases in accumulated biomass were the result of positive changes in stem and root growth. This explains why there was no clear increase in shoot/root ration as a response to fertilization treatments. We hypothesized that this was the result of a resource partitioning process favoring establishment.

Foliar nutrient concentrations. The foliar N and P concentrations found in this study (Fig. 1) were generally within the range of nutrient sufficiency for containerized conifers (Landis, 1989). High water treatments negatively affected foliar N concentration, but increased fertilization positively affected foliar N. Lower growth and biomass accumulations obtained with low water treatments should normally result in lower demand for nutrient elements (Clarkson, 1985), which were possibly met by lower nutrient availability and uptake under low fertilization and moisture treatments. This can explain why sufficiency levels were observed even in low fertility and low moisture treatments. The marginal effect of irrigation and lack of interaction between foliar N and P and irrigation may have been caused by the elevated volumes of leaching in high irrigation treatments. Increased resource availability also positively affected foliar Ca content but not foliar K, Mg, or Mn contents (Fig. 2). The reason for the significant effect on foliar Ca needs to be further investigated because Berger (1994) did not observe any change in Ca, K, or Mg concentration in xylem sap after mild or severe drought cycles.

The response to the addition of water and nutrients can be variable and depends on seasonal site water balance and initial soil fertility (Trichet et al., 2008). Therefore, increased water addition through irrigation is likely to leach mobile nutrients such as nitrates below the root zone. The strong foliar nutrient concentration response to fertilization suggests that N addition is a strong determining factor for early development of this species.

Plant nitrogen accumulation and resource use efficiency. The lower foliar N concentration in higher water treatments was opposite the increased growth response, indicating higher N use efficiency (NUE) and ANUE in high irrigation treatments (Table 4). This is the result of higher efficiency in carbon assimilation that caused an increase in the net primary productivity in plants under high irrigation treatment. For the lowest fertilizer and irrigation treatments, low assimilation levels resulted in reduced biomass production. However, because foliar concentration was used in the calculation of ANUE, it is necessary to take into account the resource partitioning between assimilatory and non-assimilatory activities such as biochemical processes, structure, and storage (Margolis and Brand, 1990; Sheriff et al., 1995).

Evaluation of the partitioning efficiency did not show a clear improvement of the root weight ratio in plants receiving high irrigation and water treatments (Table 4). However, the index of N availability in the foliage per unit of root (N/RW) to supply suggests enhanced N availability for plants receiving lower irrigation treatments. This implies that under water stress conditions, the decrease in assimilation in plants is somewhat buffered by the increase in the relative ability of plants to allocate resources to roots development. This is in agreement with previous studies suggesting that efficiencies of use water and foliar N in assimilating carbon

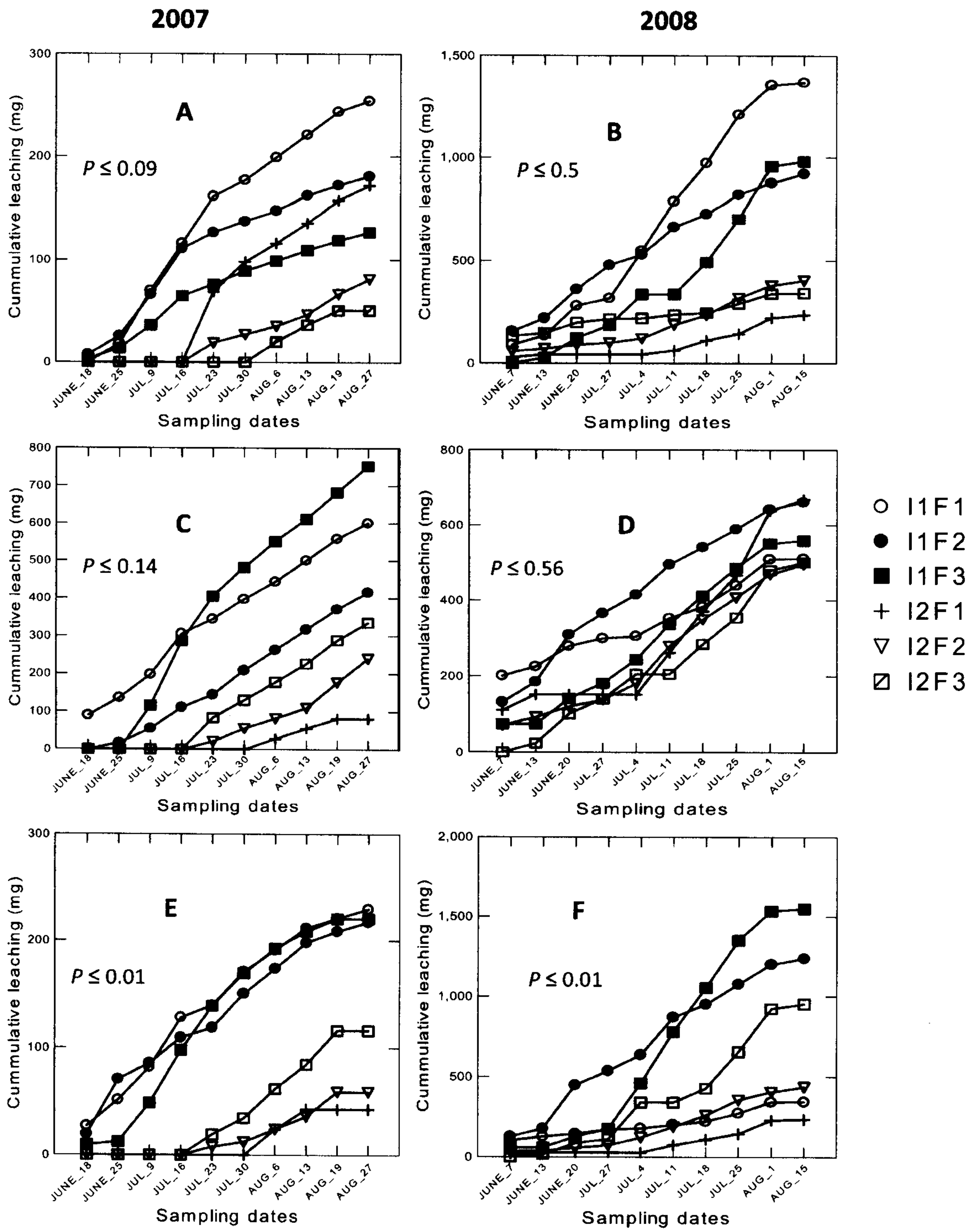

Fig. 3. Cumulative calcium (**A–B**), potassium (**C–D**), and magnesium (**E–F**) leached in response to irrigation treatments in 2007 (left panels) and 2008 (right panels).

have opposing constraints such that if they vary with experimental treatments or species, they are often negatively correlated (Farquhar and Kirschbqum, 1985).

Conclusion

This study investigated the growth, nutrient concentration and content, and NUE of plants under varying irrigation and fertilization treatments. Height and stem diameter growth were increased by irrigation treatments, possibly as a result of increased photosynthesis and subsequent carbohydrate production resulting from improved stomatal response in low water stress conditions in trees under high irrigation. Increases in biomass were caused by a resource partitioning process favoring root growth.

The resource use efficiency analysis suggests that under low water stress, *Abies fraseri* had a higher efficiency in carbon accumulation that caused an increased in net primary productivity. Under water stress conditions, the decrease in assimilation can be buffered by an increase in the plant's abilities to provide N and other nutrients to various organs. The improved resource use efficiency resulting from irrigation can be attributed to one or any combination of factors, including improvements in the photosynthetic ability; decrease in stomatal limitations; changes in resource allocation in favor of the stem; or

Table 4. Resource use efficiency parameters of fraser fir transplants grown in containers as affected by irrigation and fertilization.

	ANUE (g/μg/g)	NUE (g/g/yr)	N/RW (mg/g)	RWR (g/g)
I1F1	0.15 ± 0.1	32.4 ± 0.5	84.0 ± 2.1	0.38 ± 0.01
I1F2	0.14 ± 0.1	48.7 ± 1.4	81.1 ± 2.5	0.29 ± 0.03
I1F3	0.16 ± 0.1	36.7 ± 1.6	118.5 ± 2.0	0.34 ± 0.01
Average I1	0.15 ± 0.1	39.3 ± 1.2	94.5 ± 2.2	0.34 ± 0.02
I2F1	0.20 ± 0.1	31.8 ± 0.9	140.2 ± 3.6	0.38 ± 0.02
I2F2	0.22 ± 0.2	45.8 ± 1.5	129.4 ± 1.9	0.29 ± 0.06
I2F3	0.16 ± 0.1	25.5 ± 0.8	143.0 ± 1.2	0.40 ± 0.05
Average I2	0.19 ± 0.1	34.4 ± 1.1	137.5 ± 2.2	0.36 ± 0.04
I3F1	0.12 ± 0.1	26.7 ± 1.0	99.2 ± 1.6	0.43 ± 0.05
I3F2	0.09 ± 0.1	21.4 ± 0.7	88.5 ± 1.5	0.41 ± 0.03
I3F3	0.08 ± 0.1	22.0 ± 0.8	114.4 ± 1.8	0.39 ± 0.02
Average I3	0.10 ± 0.1	23.3 ± 0.8	100.7 ± 1.6	0.41 ± 0.03
I4F1	0.07 ± 0.1	15.5 ± 0.9	121.5 ± 1.7	0.38 ± 0.04
I4F2	0.05 ± 0.1	7.8 ± 0.8	127.1 ± 2.1	0.39 ± 0.03
I4F3	0.07 ± 0.1	12.8 ± 1.9	195.4 ± 1.7	0.31 ± 0.06
Average I4	0.06 ± 0.1	12.0 ± 1.2	148.0 ± 1.8	0.36 ± 0.04

Irrigation: I1 = 386 mL, I2 = 257 mL, I3 = 122 mL, I4 = 63 mL; fertilization F1 = 6 g, F2 = 12 g, F3 = 18 g. ANUE = assimilatory nutrient use efficiency (rate of carbon assimilation, or foliar biomass production per unit of foliar nitrogen): NUE = whole plant nutrient use efficiency in gram of biomass per gram of nitrogen per year; N/RW = index of nitrogen availability (foliar nitrogen per unit root weight); RWR = root weight ratio (grams of root per gram of total biomass).

increases in the ratio of photosynthesis to respiration. Further physiological studies are underway to confirm these hypotheses.

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