Effects of variable nitrogen fertilization on growth, gas exchange, and biomass partitioning in black spruce and tamarack seedlings

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Abstract: In order to compare the ability of black spruce (*Picea mariana* (Mill.) BSP) and tamarack (*Larix laricina* (Du Roi) K. Koch) to adjust to variable edaphic conditions, as found in natural peatlands, we varied nitrogen (N) fertilization of seedlings in a growth chamber experiment over two growing seasons and examined growth, biomass partitioning, and gas exchange. Seedlings from both species received either high-N (100 µg L^{-1}) or low-N (10 µg L^{-1}) in consecutive growing seasons as follows: a) low-N + low-N (LL); b) low-N + high-N (LH); c) high-N + low-N (HL); and d) high-N + high-N (HH). Both species had greater shoot and total dry weight after one year in the high-N treatment, as compared to seedlings grown for one year under low-N. For tamarack these differences were larger and they also exhibited a positive effect of fertilization on net assimilation and water-use efficiency. Only black spruce exhibited a positive growth response following the move to higher nitrogen fertilization in the second year (LL vs. LH), whereas only tamarack exhibited a negative growth response following the move to lower nitrogen fertilization (HH vs. HL). Still, tamarack had greater total biomass at the end of two years than did black spruce, irrespective of fertilizer treatment. Both species had greater total biomass in the HL treatment than in the LH treatment. Tamarack seems able to take advantage of favorable nutrient conditions, but it also experiences more dramatic growth declines under poor or deteriorating conditions. While black spruce grows more slowly than tamarack it is somewhat buffered from declines in growth under poor or deteriorating conditions. Each species appears to be adapted in its own way to the edaphic heterogeneity that exists in natural boreal peatlands.

Key words: Biomass accumulation, black spruce, gas exchange, nitrogen fertilization, plasticity, tamarack.

Introduction

Nitrogen (N) is the most limiting nutrient in the boreal forest (Wollum and Davey 1975). Nitrogen deficiency often inhibits plant productivity (Cetiom-Inra 1983) by reducing the number of leaves, leaf area, and leaf nitrogen content (Osman et al. 1977), ultimately reducing maximum rates of photosynthesis (Mooney and Gulmon 1979). The dominance of evergreen trees in the boreal forest has been attributed to their greater annual net carbon gain and more efficient use of nutrients as compared to deciduous species (Mooney 1972; Chapin 1980). The greater leaf longevity of evergreens reduces the annual carbon and nutrient requirement to produce new foliage (Chabot and Hicks 1982). Thus, absolute differences in net photosynthesis between evergreen and deciduous species are likely less under infertile conditions (Givnish 2002). With increasing soil fertility, however, dominance shifts from evergreen to deciduous species (Aerts et al. 1991; Fox 1992; Nams et al. 1993; Givnish 2002).

In peatlands, the low nutrient requirement and conservative use of available nutrients by evergreens are thought to be particularly important because nutrient availability is low due to anaerobic conditions caused by high water table (Campbell 1980) and the effect of low soil temperature on decomposition, mineralization, and nutrient uptake (Van Cleve and Alexander 1981). Thus, it is somewhat incongruous that a deciduous conifer, tamarack, occurs along with evergreen conifers such as black spruce throughout the boreal forest, often dominating wetter peatland sites (Tilton 1977; Kenkel 1987; Jeglum and He 1996).

Tamarack not only survives on nutrient poor peatland sites, but it exhibits greater height growth than black spruce, even on crowded sites and under very limiting conditions (Mead 1978; Bares and Wali 1979; Montague and Givnish 1996). It has several attributes that might explain this: 1) efficient resorption of nitrogen (Tyrrell and Boerner 1987); 2) low leaf weight per unit area and correspondingly high rate of total carbon gain (Mugasha 1992) and photosynthesis [per unit area or per unit N concentration (Macdonald and Lieffers 1990)] as compared to black spruce; 3) low carbon allocation to respiration and root maintenance during the adverse season due to the absence of foliar transpiration or respiration (Givnish 2002); 4) a lighter-weight canopy that may allow for greater carbon allocation to height growth (Matyssek 1986; Tyrrell and Boerner 1987; Gower and Richards 1990; Montague and Givnish 1996).

As with most evergreen conifers black spruce exhibits fixed growth (i.e., preformed growth in which growth during a given growing season is constrained by the preset number of cells and needles that were formed in the previous fall). Tamarack, in contrast, exhibits heterophyllous growth. Its short shoots have fixed growth, whereas its long shoots display indeterminate growth (i.e., buds preset in the prior fall expand and then new apical growth occurs prior to bud set). Thus, tamarack may exhibit a greater degree of variation of annual growth in response to conditions during the current growing season (Clausen and Kozlowski 1967).

Edaphic conditions in boreal peatlands are generally poor because of low nutrient availability, cold soils, and high water table. However, microtopography and fluctuations in water table can lead to high spatial and temporal variability in soil moisture and nutrient availability among microsites. We hypothesized that the growth flexibility (deciduous habit and heterophyllous growth) of tamarack enables it to adjust to changing edaphic conditions, thus conferring a greater total carbon gain and explaining its ability to thrive in peatland conditions, where evergreen conifers are thought to have an advantage.

We examined this hypothesis in a growth chamber experiment in which tamarack and black spruce were treated with different regimes of nitrogen fertilization.

Materials and methods

Black spruce and tamarack seeds were obtained from the Alberta Tree Improvement and Seed Center (ATISC acc #4042); seed of both species had been collected from the same region (latitude 55° 03' and longitude 113° 14'). Seeds were stratified for three weeks at 4^{o}C and then germinated in Petri-dishes. One week after germination, seedlings were transplanted to Spencer-Lemaire (300 mL) containers (Spencer-Lemaire Industries Ltd. Edmonton, AB. Canada) containing (1:1:1; peat:moss:vermiculite) planting medium (Pro-Mix BX; Premier Horticulture Inc., Riviere-du-Loup, Que. Canada) (both black spruce and tamarack grow well in this planting medium, which provides adequate drainage) and placed in a controlled growth chamber with 21^{o}C/18^{o}C day/night temperature, 65% relative humidity and 16-h photoperiod with photosynthetically active radiation (PAR) of 400 μmol m^{-2} s^{-1} at the seedling height being provided by fluorescent lamps (GE -F96T8/SPX35/HO; General Electric Company, USA). Seedlings were watered to run off every other day. Application of treatments began when seedlings were eight weeks old.

A 2 x 2 x 4 factorial design was used in this experiment. Seedlings were randomly assigned to one of four possible experimental treatments: (a) high-N (100 µg L^{-1}) in the form of NH_4NO_3 in two consecutive growing seasons (HH); (b) low-N (10 µg L^{-1}) in two consecutive growing seasons (LL); (c) high-N in the first and low-N in the second growing season (HL); and (d) low-N in the first and high-N in the second growing season

(LH). Fertilizer treatments were applied once per week. NH_4NO_3 was the main source of nitrogen. The other sources of macronutrients included KCl (0.06 g L^{-1}), $MgSO_4$ (0.15 g/L), KH_2PO_4 (0.06 g/L), $CaCl_2$ (0.134 g/L), and $FeCl_3$ (2.508 x 10^{-2} g/L). The micronutrients included H_3BO_3 (8.58 x 10^{-4} g/L), $ZnSO_4$ (1.43 x 10^{-4} g/L), Na_2MO_4 (5.72 x 10^{-4} g/L), $MnSO_4$ (3.34 x 10^{-4} g/L), $CaCl_2$ (5.72 x 10^{-4} g/L), and $CuSO_4$ (5.72 x 10^{-4} g/L).

The first sets of measurements (including net photosynthesis, stomatal conductance, water use efficiency, total plant dry weight, root: shoot ratio) were taken after the seedlings grew for twenty weeks. Six seedlings of each species were measured in each treatment. The remaining forty-eight seedlings were then subjected to a simulated winter period as follows: a cold room with 10^0C temperature and a 10-h photoperiod for six weeks, followed by eight weeks at 4^0C and a 8-h photoperiod. Seedlings from both species set buds during this time. After that, seedlings were brought back to 15^oC temperature and a 10-h photoperiod for two weeks. During this overwintering period seedlings were not fertilized. Thereafter, seedlings were transplanted to 12.7 cm pots with Pro-Mix BX (as above) and returned to the original growing conditions ($21^oC/18^oC$ day/night temperature, 65% relative humidity and 16-h photoperiod) and grown under the experimental treatment condition for the second growing season for 24 weeks. Final measurements of the same physiological and morphological parameters were taken after the second growing season.

Net assimilation (A_{net}), stomatal conductance (g_s) and water use efficiency (WUE; net carbon assimilation rate divided by transpiration rate) of the black spruce and tamarack seedlings were measured using an open-system infrared gas analyzer (IRGA) (LCA-3: Analytical Development Company Ltd. Hoddesdon, U.K.) equipped with a conifer cuvette. Gas exchange was measured under the growth chamber conditions except that an artificial light source was used to supplement the PAR to 1050 μmol m^{-2} s^{-1} (which was previously determined to be above the light saturation point). The uppermost shoots of a randomly selected seedling from each species and treatment combination were placed in the cuvette for gas exchange measurements. Needles were carefully detached from the stem and their surface areas measured by digitizing the scanned images (Sigma Scan 3.0, Jandel Scientific, San Rafael, CA, USA). Net assimilation and stomatal conductance rates were calculated as described by von Caemmerer and Farquhar (1981) and expressed on a leaf area basis. Gas exchange measurements were taken before mid-day to avoid the possibility of a mid-afternoon decline in gas exchange rates.

After completing gas exchange measurements, plants were destructively harvested, dried in an oven at 68°C for 48 h and weighed. Oven dried shoot samples then were ground in a Willey mill to pass a 20-mesh screen. Samples were digested in concentrated sulphuric acid, followed by oxidation with hydrogen peroxide (Lowther 1980). Total N digests were determined with an autoanalyzer (Technicon Instruments 1977) and expressed as a concentration (percent dry weight).

Data were evaluated by analysis of variance using SAS version 8.1 software (1996; SAS Institute Inc., Cary, NC). When main effects of species or treatment or their interactions were significant ($P< 0.05$), means were further compared by Tukey's test.

Results

As measured after 20 weeks of growth during the first growing season, shoot, root, total dry weight, shoot:root ratio, A_{net} and WUE were, overall, higher under the high nitrogen (H) compared to low nitrogen (L) treatment but the effect was greater for tamarack than for black spruce (Table 1, Figs. 1 and 2). Tamarack showed greater A_{net}, WUE, and root dry weight in response to the fertilization treatment whereas black spruce was unaffected (Table 1, Figs. 1 and 2). Tamarack also exhibited a greater increase in shoot, root, and total plant dry weight in response to the fertilizer treatment than did black spruce (e.g. for total dry weight: 40 % vs. 23 %). By contrast, the shoot:root dry weight ratio of tamarack did not differ with fertilizer treatment, whereas for black spruce the shoot:root ratio was 25 % higher under the high-N (vs. low-N) treatment.

Tamarack had higher A_{net} (per unit leaf area) under high-N than black spruce, but there were no differences between the two species in A_{net} under low-N (Table 1, Fig. 1). There were no differences in g_s between black spruce and tamarack in either low or high nitrogen fertilization. WUE was greater for tamarack than black spruce under high-N. Shoot dry weight, root dry weight, total plant dry weight and shoot: root ratio were higher in tamarack than in black spruce, irrespective of fertilizer treatment (Fig. 2).

There were many differences between the species in the way they responded to the four treatment combinations applied over the two growing seasons for all variables except A_{net} (species by treatment interactions; Table 1). For A_{net} there were effects of both species and fertilizer treatment (Table 1).

There were no differences in A_{net} between tamarack and black spruce in the LL, LH or HL treatments. However, under the HH treatment tamarack had higher A_{net} than black spruce (Table 1; Fig. 3). Stomatal conductance of black spruce was higher than in tamarack under the LL treatment, but lower in the LH treatment (Fig. 3). There were no differences in stomatal conductance between black spruce and tamarack in the HL or HH treatments. Water use efficiency was lower in black spruce than tamarack in the LL treated plants, but higher in the LH treatment. There were no differences in WUE between black spruce and tamarack in the HL and HH treatments (Fig. 3).

Similar to the results from the first growing season shoot, root, and total plant dry weight after two growing seasons were, overall, higher in tamarack than in black spruce irrespective of fertilization treatment (Table 1, Fig. 4). In contrast to the first year results, however, shoot:root ratio was generally lower for tamarack than black spruce, although the reverse was true for the LH treatment. Shoot dry weight, root dry weight and total plant dry weight of both black spruce and tamarack increased progressively from the LL, to the LH, HL and the HH treatments (Fig. 4). The effects were more pronounced in tamarack than black spruce (91 % increase in total dry weight from LL to HH in tamarack as compared to only 66 % increase for black spruce). For tamarack shoot: root was lower in the HL and HH treatments than in LL or LH, whereas for black spruce shoot: root ratio was lower in LH and higher in LL compared with the other treatments (Fig. 4).

Both species responded similarly to the transfer from low to high nitrogen in the second growing season (LL compared to LH) with a substantial increase in A_{net}, but only black spruce exhibited a simultaneous increase in plant mass (Table 1, Fig. 4). For black spruce there was no change in g_s following the transfer to higher nitrogen (LH vs. LL) but WUE increased. In tamarack, on the other hand, g_s increased with the transfer to H nitrogen in parallel to the increase in A_{net} such that WUE was similar for the LL and LH treatments. With the transfer from high to low nitrogen (HL vs. HH), both species exhibited lower A_{net}, g_s and WUE, although the differences were generally larger for tamarack. Tamarack had lower shoot, root and total dry weights in HL as compared to

HH, whereas black spruce was unaffected. The shoot:root ratio in each species was similar in HL and HH treatments.

Application of the high nitrogen treatment (H) in the first growing season did not produce any substantial difference in needle nitrogen concentration in either species, as compared to the low-N treatment (Table 2). There were no differences between the two species in their leaf nitrogen concentration at the end of two growing seasons, for any treatment (HH, HL, LH, and LL). However, there were effects of nitrogen treatment on needle tissue N concentration and species differed in their response to the fertilization treatment (species x fertilization interaction, Table 1). Tamarack was more responsive to HH and LL treatments in terms of needle tissue N concentration (Table 2).

Discussion

We hypothesized that the deciduous habit and heterophyllous growth of tamarack would enable it to adjust to variable edaphic conditions found in natural peatlands. While our results supported the idea that tamarack can take advantage of favourable conditions, the specifics of responses to changing nutrient availability did not conform to our hypothesis. Tamarack generally grew faster and had higher rates of net assimilation than black spruce, irrespective of treatment. Treatments effects were greater for tamarack than for black spruce such that differences between the two species were exaggerated under more favorable conditions and diminished under poorer conditions. For example, total dry weight was 70 % higher in tamarack than in black spruce after one year of high-N, but only 19 % higher after a second year of low-N (“H” after one year vs. HL treatment).

Tamarack seedlings were always larger than black spruce in every treatment and this may be partially due to their larger seed size (~ 70 %; 1.68 vs. 0.99 mg $seed^{-1}$, Macdonald S.E. unpublished data).Variation in the magnitude of the difference, however, suggests that tamarack has a growth advantage only under more favorable conditions. For example, after one year in low-N total dry weight of tamarack seedlings was 59 % higher than in black spruce but 80 % higher after one year in high-N. Likewise, the difference in total seedling weight between the species was greater following two years of high-N than for the treatments with one low nitrogen year [tamarack was 47 % greater than black spruce under LL, 20 % for LH, 19 % for HL vs. 70 % for HH]. The greater size of tamarack was mirrored by greater A_{net} and WUE efficiency; this conformed to previous studies of trees in natural peatlands (Macdonald and Lieffers 1990; Dang et al. 1991). As for growth, the differences in gas exchange between the species were greater under more favorable nitrogen conditions (e.g., one or two years of high-N); under some less favorable treatments the species did not differ (e.g., LL, LH).

The high nitrogen treatment in the first year resulted in higher foliar nitrogen concentration for both black spruce (2.59 vs. 2.44 % dry weight) and tamarack (2.66 vs. 2.53 % dry weight), but only tamarack exhibited a corresponding increase in A_{net} (39 % higher than for low-N). This agrees with previous work in drained peatlands where fertilization increased foliar nitrogen of both species, but increased A_{net} only in tamarack (Mugasha 1992; Mugasha et al. 1993). WUE was lower under low-N, but stomatal conductance was not lower under low-N for tamarack and was actually higher under low-N for black spruce; this suggests that the observed differences in A_{net} between fertilizer treatments were due largely to non-stomatal limitations to photosynthesis.

We predicted that tamarack would respond more dramatically to the transfer from low-N to high-N, but only black spruce exhibited greater total biomass in the LH vs. the LL treatment. This contrasts with previous studies in which tamarack responded more dramatically than black spruce to improved edaphic conditions following peatland drainage and/or fertilization (Macdonald and Lieffers 1990; Mugasha 1992; Macdonald and Yin 1999). Proportionally allocation to root biomass is expected to be lower under better nutrient availability, but black spruce exhibited increased proportional root biomass when nutrient availability improved in the second year. This may reflect a rebalancing of shoot:root ratio as resources become available to direct towards root growth, which might have been severely limited in the first (low-N) growing season.

Both species had higher foliar nitrogen concentration and higher A_{net} in the LH vs. the LL treatment. This was not associated with a positive growth response in tamarack, perhaps reflecting a lag as tissue N accumulated and shoot and root biomass re-balanced after the first low-N growing season. In tamarack, changes in g_s mirrored those in A_{net} suggesting stomatal limitations to photosynthesis were predominant; the net effect was no difference in WUE between the LL and LH treatments. In black spruce, however, stomatal conductance did not change when A_{net} increased with high-N in the second year; thus, WUE increased along with A_{net}. This suggests predominantly non-stomatal limitations to photosynthesis (Farquhar and Sharkey 1982).

When nutrient conditions became less favorable in the second year (HL vs. HH treatments) only tamarack exhibited lower growth (total biomass). This suggests a disadvantage for tamarack under deteriorating edaphic conditions, but also demonstrates the dramatic ability of this species to take advantage of favourable conditions. For tamarack a second year of high-N resulted in 30 % more plant biomass as compared to seedlings that were transferred to the low-N treatment. In contrast, a second year of high-N made no difference for black spruce (total biomass in HH vs. HL). Under improving nutrient conditions (HL vs. HH) both species had higher A_{net} , g_s , WUE and foliar nitrogen. Again, the differences were greater for tamarack than for black spruce.

Application of high-N in the first year resulted in greater total biomass for both species than when high-N was applied in the second year (HL vs. LH). This reflects the long-term benefit of an early growth advantage. Tamarack increased its allocation to roots when N availability declined (HL vs. LH), but black spruce exhibited the opposite response, suggesting an overriding influence of the nutrient conditions in the first year on black spruce shoot:root ratio.

In terms of gas exchange, a high-N treatment in the second year had much more effect on A_{net} for both species than did any persistent effect of high-N applied in the first year (LH vs. HL treatment). In black spruce g_s did not mirror the higher A_{net} seen in plants receiving the high-N treatment in the second year; thus, WUE increased along with A_{net}, again suggesting the importance of non-stomatal (mesophyll) control of A_{net} in black spruce (as for the LL vs. LH comparison). In contrast, tamarack exhibited higher g_s along with A_{net} when N availability increased (vs. declined) in the second year. Thus, WUE remained the same suggesting, again, the predominance of stomatal limitations on net assimilation in tamarack.

Nutrient availability (total availability and relative availability of nitrate vs. ammonium) and root zone conditions vary with microtopography at a fine scale within boreal peatlands (Astridge 1996). For example, in a single peatland in central Alberta Astridge (1996) found black spruce and tamarack rooted in microsites, which varied six-fold in NO_3 availability, 12-fold in NH_4 availability, from 3.21 to 7.92 in pH, and from -5 (standing water) to 39 cm in depth of the aerated zone. Similarly, nutrient availability and soil conditions in peatlands are expected to vary within and between years as climate influences water table and soil aeration and temperature (Dang et al. 1991). It has been shown that nutrient availability, soil temperature and depth to water table exert a major influence on growth and gas exchange of both black spruce and tamarack in peatlands (Lieffers and Macdonald 1990; Macdonald and Lieffers 1990; Dang et al. 1991; Astridge 1996; Macdonald and Yin 1999). Thus, the ability of a species to adjust and respond quickly to variation in these conditions is expected to prove advantageous for survival and growth in peatlands.

Overall, our results suggest that tamarack can readily take advantage of favorable edaphic conditions. Under one year of high nitrogen availability it grew much better than black spruce and two years of high-N provided a substantial growth advantage as compared to a single year of high-N followed by a year of low-N. Black spruce, on the other hand, exhibited only a minor growth response to a single year of high vs. low nitrogen and it grew exactly the same when given a second year of high-N as when nitrogen declined in the second year. This suggests that black spruce has little ability to take advantage of favorable conditions, but also that it is buffered from the effects of poor or deteriorating conditions. We conclude that black spruce has a more “conservative” strategy of generally slower growth than tamarack, but that this provides a buffer from dramatic changes in growth as edaphic conditions vary. Tamarack, on the other hand responds dramatically to favorable conditions, but it did not react as quickly to improving conditions as we had predicted and it experiences dramatic growth declines when conditions deteriorate. Black spruce and tamarack each appear to be adapted in a different way to the temporally and spatially variable edaphic conditions found in natural peatlands.

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Table 1. Results of Analysis of Variance (P values) testing for the effect of fertilizer treatment (Fert; high vs. low nitrogen) and species (spp; black spruce and tamarack) and their interaction (Fert*spp) on several growth and physiological response variables after the first growing season (a) and the effect of the four fertilizer treatment combinations after the second growing season (b).

Source	Response Variable						
	A_{net}[1]	g_s	WUE	Shoot dw	Root dw	Total plant dw	Shoot: root ratio
a) after one growing season							
Fertilizer	0.0009	0.5805	0.0001	0.0001	0.0033	0.0001	0.0001
Species	0.0001	0.4461	0.0001	0.0001	0.0001	0.0001	0.0001
Fert*spp	0.0257	0.3357	0.0013	0.0301	0.0055	0.0150	0.0032
a) after two growing seasons							
Fertilizer	0.0001	0.0056	0.0001	0.0001	0.0001	0.0001	0.0001
Species	0.0300	0.7163	0.9234	0.0001	0.0001	0.0001	0.0001
Fert*spp	0.0961	0.0025	0.0008	0.0001	0.0001	0.0001	0.0001

[1] A_{net}: net assimilation; g_s: stomatal conductance; WUE: water use efficiency; dw: dry weight

Table 2. Needle nitrogen concentrations (percent dry weight) of black spruce and tamarack seedlings after the first growing season treated with either high (H) or low (L) nitrogen (a) and after the second growing season in response to four fertilizer treatment combinations (HH, HL, LH, LL) (b). Values are the mean (SE) of six seedlings.

Species	**Treatment**	**%N**
(a)[1]		
Black spruce	H	2.59 (0.11)
Black spruce	L	2.44 (0.22)
Tamarack	H	2.66 (0.11)
Tamarack	L	2.53 (0.18)
(b)[2]		
Black spruce	HH	2.39 (0.08)
Black spruce	HL	2.36 (0.16)
Black spruce	LH	2.45 (0.07)
Black spruce	LL	2.22 (0.19)
Tamarack	HH	2.73 (0.09)
Tamarack	HL	1.99 (0.12)
Tamarack	LH	2.21 (0.09)
Tamarack	LL	1.84 (0.09)

[1] There was no significant effect of species or treatment

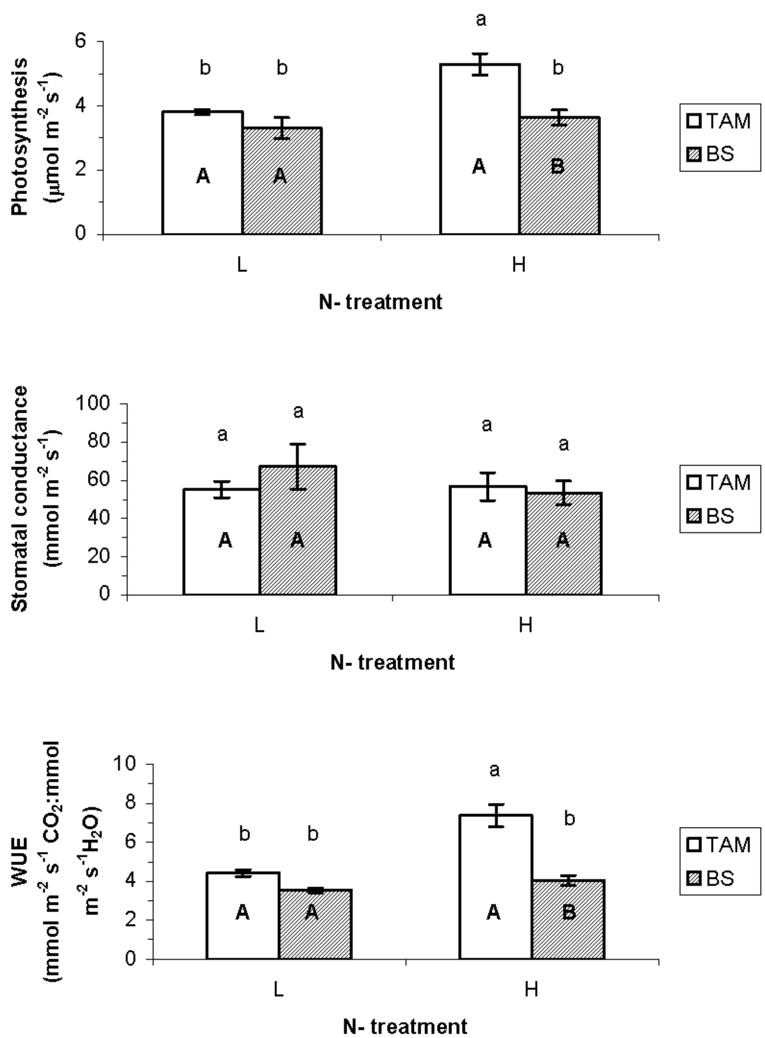
[2] There was no significant effect of species, effect of treatment $P = 0.001$; species X treatment interaction $P = 0.017$

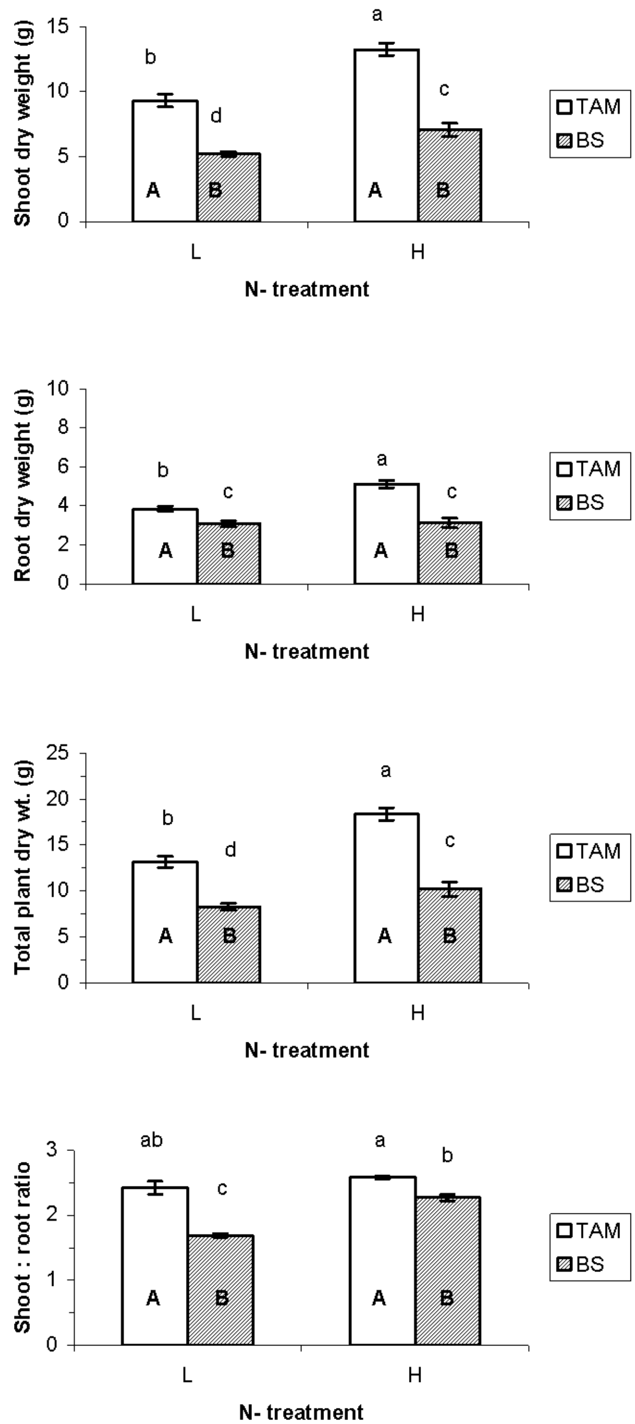
Fig. 1. Effects of high and low nitrogen fertilizer on several physiological response variables in black spruce and tamarack seedlings after the first growing season. TAM = tamarack and BS = black spruce. Values are means (±SE) of six seedlings. Means with different upper case letters are significantly different between species within treatment, whereas means with different lower case letters are significantly different among all four species by treatment combinations.

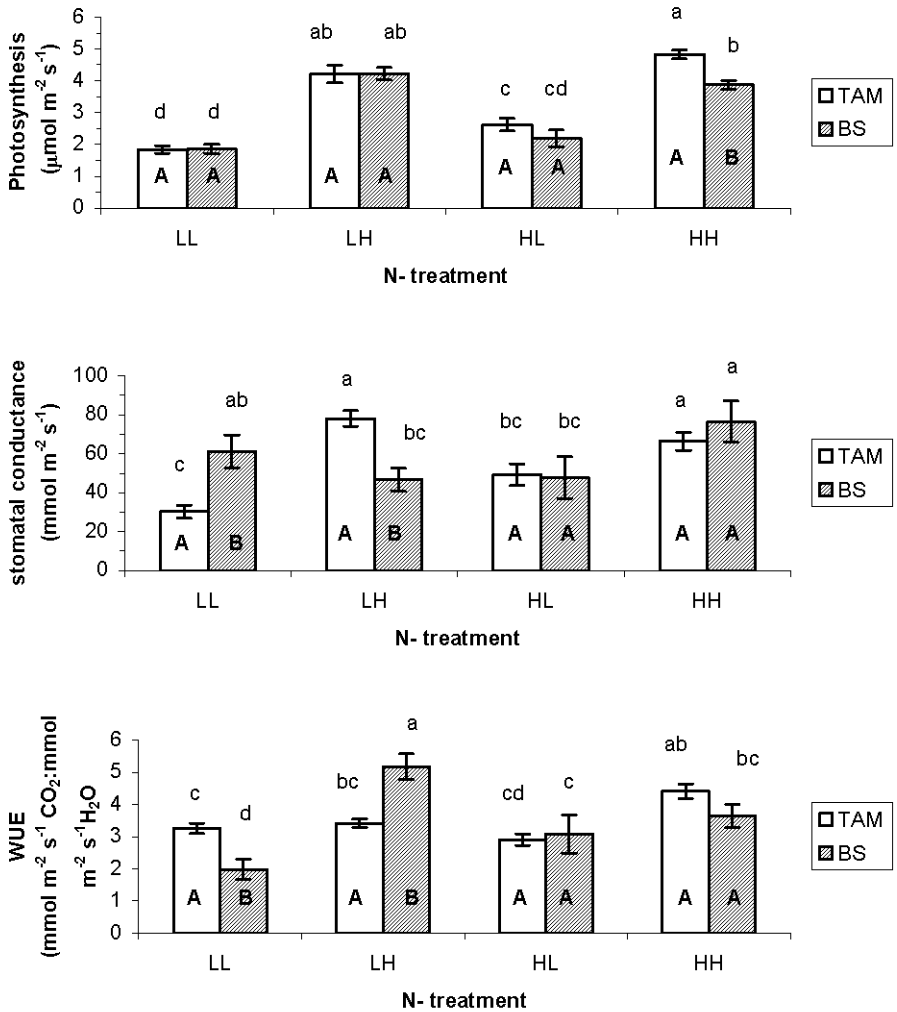
Fig. 2. Effects of high and low nitrogen fertilizer on several growth response variables in black spruce and tamarack seedlings after the first growing season. TAM = tamarack and BS = black spruce. Values are means (±SE) of six seedlings. Means with different upper case letters are significantly different between species within treatment, whereas means with different lower case letters are significantly different among all four species by treatment combinations.

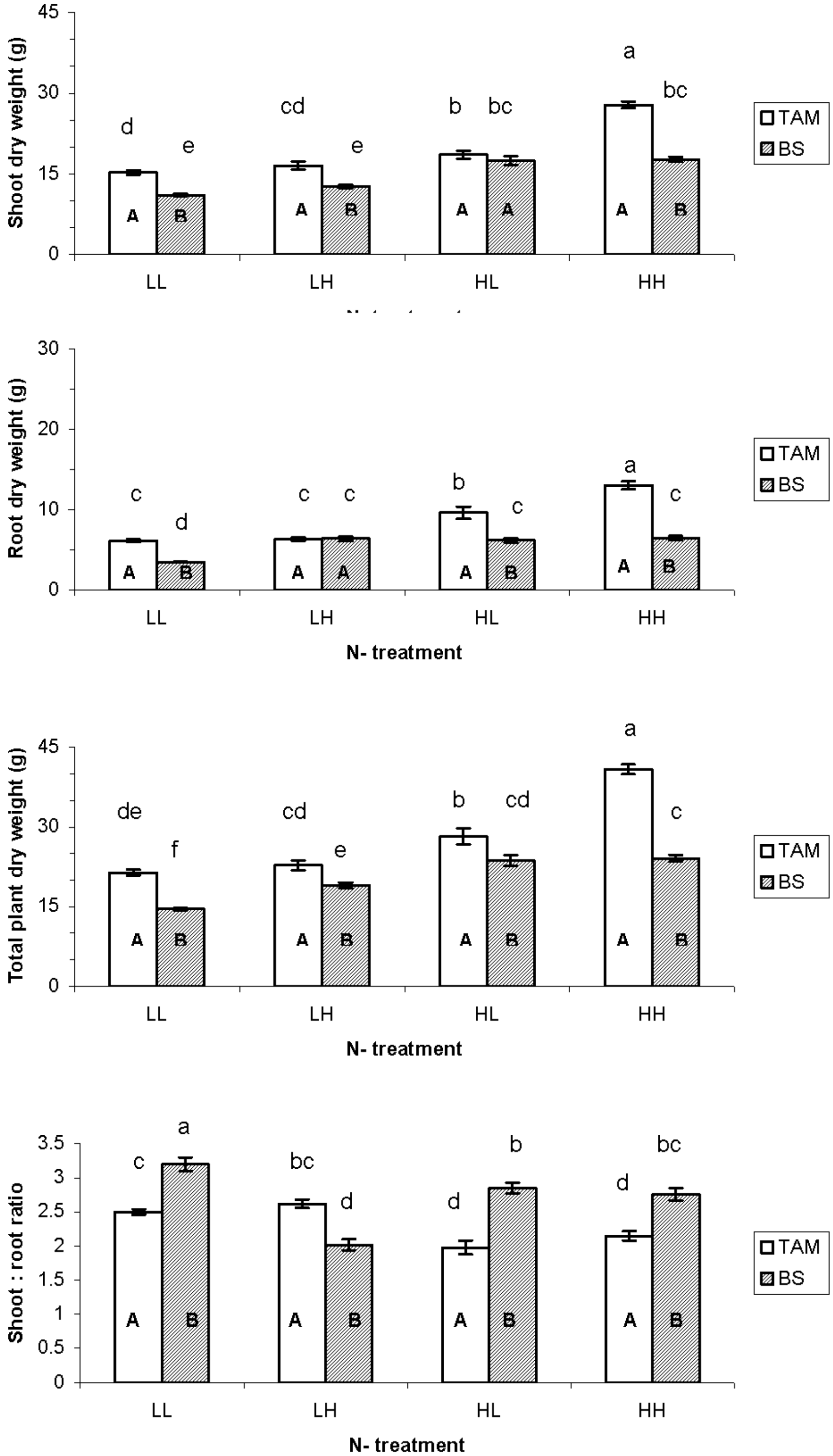
Fig. 3. Effects of four different nitrogen fertilizer treatments on several physiological response variables in black spruce and tamarack seedlings after the second growing season. TAM = tamarack and BS = black spruce. Values are means (±SE) of six seedlings. Means with different upper case letters are significantly different between species within treatment, whereas means with different lower case letters are significantly different among all eight species by treatment combinations.

Fig. 4. Effects of four different nitrogen fertilizer treatments on several growth response variables in black spruce and tamarack seedlings after the second growing season. TAM = tamarack and BS = black spruce. Values are means (±SE) of six seedlings. Means with different upper case letters are significantly different between species within treatment, whereas means with different lower case letters are significantly different among all eight species by treatment combinations.


Photosynthesis (µmol m-2 s-1)
N- treatment
L
H
TAM
BS
Stomatal conductance (mmol m-2 s-1)
N- treatment
L
H
TAM
BS
WUE (mmol m-2 s-1 CO2:mmol m-2 s-1H2O)
N- treatment
L
H
TAM
BS


Shoot dry weight (g)
15
10
5
0
b
d
a
c
A
B
A
B
L
H
N- treatment
TAM
BS
Root dry weight (g)
10
8
6
4
2
0
b
c
a
c
A
B
A
B
L
H
N- treatment
TAM
BS
Total plant dry wt. (g)
25
20
15
10
5
0
b
d
a
c
A
B
A
B
L
H
N- treatment
TAM
BS
Shoot : root ratio
3
2
1
0
ab
c
a
b
A
B
A
B
L
H
N- treatment
TAM
BS


Photosynthesis
(μmol m-2 s-1)
6
5
4
3
2
1
0
d
d
ab
ab
c
cd
a
b
A
A
A
A
A
A
A
B
LL
LH
HL
HH
N- treatment
TAM
BS
stomatal conductance
(mmol m-2 s-1)
100
80
60
40
20
0
c
ab
a
bc
bc
bc
a
a
A
B
A
B
A
A
A
A
LL
LH
HL
HH
N- treatment
TAM
BS
WUE
(mmol m-2 s-1 CO2:mmol
m-2 s-1 H2O
6
5
4
3
2
1
0
c
d
bc
a
cd
c
ab
bc
A
B
A
B
A
A
A
A
LL
LH
HL
HH
N- treatment
TAM
BS


Shoot dry weight (g)
45
30
15
0
LL
LH
HL
HH
d
e
cd
e
b
bc
a
bc
A
B
A
B
A
A
A
B
TAM
BS
Root dry weight (g)
30
20
10
0
c
d
c
c
b
c
a
c
A
B
A
A
A
B
A
B
LL
LH
HL
HH
N- treatment
TAM
BS
Total plant dry weight (g)
45
30
15
0
de
f
cd
e
b
cd
a
c
A
B
A
B
A
B
A
B
LL
LH
HL
HH
N- treatment
TAM
BS
Shoot : root ratio
3.5
3
2.5
2
1.5
1
0.5
0
c
a
bc
d
d
b
d
bc
A
B
A
B
A
B
A
B
LL
LH
HL
HH
N- treatment
TAM
BS