

ARTICLE

Northward migration of trembling aspen will increase growth but reduce resistance to drought-induced xylem cavitation

Sahari Inoue, Qing-Lai Dang, Rongzhou Man, and Binyam Tedla

Abstract: Tree migration to higher latitudes may occur in response to future changes in climate, exposing the trees to higher concentrations of carbon dioxide ($[CO_2]$), new photoperiods, different levels of soil moisture, and other new conditions. These new conditions can influence the physiology, survival, and growth of trees. This study examined the interactive effects of $[CO_2]$, photoperiod, and soil moisture on the morphology and resistance to xylem cavitation in trembling aspen (*Populus tremuloides* Michx.). One-year-old seedlings, in greenhouses, were exposed to two $[CO_2]$ (ambient $[CO_2]$ 400 µmol·mol⁻¹ or an elevated $[CO_2]$ 1000 µmol·mol⁻¹), four photoperiod regimes corresponding to latitudes 48°N (seed origin), 52°N, 55°N, and 58°N, and two levels of soil moisture (60%–75% and 13%–20% of field capacity) for one growing season. Seedling growth, leaf size, specific leaf area, biomass allocation, and xylem resistance to cavitation (water potentials for 20%, 50%, and 80% loss of hydraulic conductivity) were assessed. The seedlings under the longest photoperiod regime (58°N latitude) had greatest height and biomass but smallest specific leaf area. Under the elevated $[CO_2]$, however, the longest photoperiod corresponding to 48°N. These results suggest that when migrating to higher latitudes, trembling aspen may grow faster but could become less resistant to drought and more prone to hydraulic failure during a drought spell.

Key words: climate change, tree migration, morphology, cavitation resistance.

Résumé : Un jour, les arbres pourraient migrer à des latitudes plus élevées en réponse aux changements climatiques, les exposant des concentrations plus élevées de CO₂ ([CO₂]), à de nouvelles photopériodes, à une humidité du sol différente et à d'autres conditions nouvelles. Les nouvelles conditions peuvent influencer la physiologie, la survie et la croissance des arbres. Cette étude s'est penchée sur les effets interactifs de la [CO₂], de la photopériode et de l'humidité du sol sur la morphologie et la résistance à la cavitation du peuplier faux-tremble aspen (Populus tremuloides Michx.). Des plants âgés d'un an ont été exposés à deux $[CO_3]$ ($[CO_3]$ ambiante de 400 μ mol·mol⁻¹ et $[CO_3]$ élevée de 1000 μmol·mol⁻¹), quatre régimes de photopériodes correspondant à des latitudes de 48° (origine de la semence), 52°N, 55°N et 58°N, et deux conditions d'humidité du sol (60-75 % et 13-20 % de la capacité du champ) pendant une saison de croissance en serres. La croissance des plants, la taille des feuilles, la surface spécifique des feuilles, les répartitions de la biomasse et la résistance du xylème à la cavitation (potentiels hydriques pour 20, 50 et 80 % de perte de conductivité hydraulique) ont été évaluées. Les plants soumis à la plus longue photopériode (latitude 58°N) présentaient la hauteur et la biomasse les plus élevées, mais la surface foliaire spécifique la plus petite. À une [CO₂] élevée, cependant, la photopériode la plus longue réduisait significativement la résistance du xylème à la cavitation induite par la sécheresse comparativement à la photopériode correspondant à une latitude de 48°N. Les résultats suggèrent que lors de sa migration vers des latitudes plus élevées, le peuplier faux-tremble pourrait croître plus rapidement, mais devenir moins résistant à la sécheresse et plus enclin à une insuffisance hydraulique durant un épisode de sécheresse. [Traduit par la Rédaction]

Mots-clés : changement climatique, migration des arbres, morphologie, résistance à la cavitation.

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Introduction

The projected increases in global temperatures and changes in precipitation patterns will likely induce a northward migration of boreal trees by the end of this century (McKenney et al. 2007, 2011). As a consequence, trees will be exposed to new environments with different photoperiod regimes and higher concentrations of carbon dioxide ([CO₂]). The effects of photoperiod and [CO₂] alone on trees have been studied (Oleksyn et al. 1992; Norby et al. 2010), but it is unknown how these factors interact to affect trees in the context of this predicted northward migration. It is also predicted that the frequency and severity of water stress will increase in many regions of North America (Pachauri et al. 2014). Increased water stresses will likely hinder the northward migration of boreal trees, e.g., trembling aspen (Populus tremuloides Michx.). Trembling aspen is widely distributed in the boreal region and has high economic and ecological values, but is very sensitive to water stress (Perala 1990; Peterson and Peterson 1992). Under severe drought conditions, a good understanding of how trembling aspen may respond to drought stress under such new environmental conditions may be essential for planning latitudinal seed transfer and predicting dieback and mortality (Hogg et al. 2008; Michaelian et al. 2011), thus future tree distribution in response to climate change.

Hydraulic failure due to xylem cavitation is a major mechanism of drought-induced tree mortality (McDowell et al. 2008; Allen et al. 2010; Adams et al. 2017). Trees can undergo physiological and (or) morphological acclimation to maintain xylem water potential above the threshold for hydraulic failure, e.g., to increase root:shoot ratio (Kozlowski and Pallardy 2002; Klein et al. 2011) and (or) stomatal sensitivity to changes in water status, or to have smaller and thicker leaves (Kozlowski 1968; Rigling et al. 2010). Increasing xylem resistance to cavitation can also help trees to survive severe drought stress (Vilagrosa et al. 2012). In deciduous trees, cavitation resistance is inversely related to the total area of the pits in conduit vessels, which increases with vessel diameter (Hacke and Sperry 2001; Tyree and Zimmermann 2002; Cai and Tyree 2010). However, there is a trade-off between hydraulic efficiency and cavitation resistance (Fichot et al. 2010). For instance, trees grown under mild drought stress have more resistant xylem, i.e., conduit vessels with a smaller diameter and smaller pit area, which lead to a reduction in hydraulic conductance and the risk of cavitation at the expense of lowering hydraulic efficiency (Tyree and Zimmermann 2002). The interactions among [CO₂], photoperiod, and water availability can influence the physiological and morphological characteristics of trees and have a significant impact on the northward migration or assisted seed transfer of boreal trees. For instance, elevated [CO₂] increase tree growth and improve water use efficiency (WUE) (Norby et al. 1999; Centritto et al. 2002)

and thus mitigate the negative effects of drought stress on growth. Longer photoperiods during the growing season increase the shoot:root ratio and enhance leaf development (Oleksyn et al. 1992; Gestel et al. 2005; Abeli et al. 2015), resulting in improved hydraulic efficiency but increased water loss. Further, higher [CO₂] increases vessel diameter in aspen (Kostiainen et al. 2014), and longer photoperiods increase the diameter of xylem tracheid in Pinus resinosa (Larson 1962), which may improve hydraulic efficiency but also reduce cavitation resistance. However, there is generally a paucity of information on the interactive effects of [CO₂], photoperiod, and soil moisture on the morphological and hydraulic characteristics of boreal trees. For example, Newaz et al. (2018) examined the interactive effect of [CO₂], photoperiod, and soil moisture on the hydraulic characteristics of jack pine in the context of northward migration, and found significant increases in hydraulic conductivity with higher $[CO_2]$, and cavitation resistance decreased with increasing photoperiod under elevated [CO2]. This study investigated the fore-mentioned three-way interaction on the morphology and resistance to cavitation in trembling aspen in the context of climate-change-induced northward migration. We hypothesized that elevated [CO₂] and longer photoperiod would increase tree growth, and that the increase would be reduced by water stress. We further hypothesized that water stress would increase xylem cavitation resistance, whereas elevated [CO₂] and longer photoperiods would have the opposite effect.

Materials and methods

Plant materials

Trembling aspen catkins were collected in June 2016 from 10 free-pollinated trees in the Thunder Bay region, Ontario, Canada (48.38°N, 89.25°W). The catkins were air-dried for five days at room temperature, and the seeds were extracted. All of the seeds were mixed and stored in a sealed glass bottle at -4 °C. The seeds were sown in germination trays filled with a mixture of peat moss and vermiculite (1:1 v/v) in a greenhouse at the Thunder Bay Campus of Lakehead University. The greenhouse was maintained at 24-14 (±2) °C (day/night) temperature, and the natural photoperiod was prolonged to 16 h by using high-pressure sodium lamps (P.L. Systems, Beamsville, Ont.), which amounted to about 600 µmol·m⁻¹·s⁻¹ photosynthetically active radiation (PAR) at the canopy level. All of the trays were kept under ambient $[CO_2]$ and well-watered. The seedlings (N = 96) were individually transplanted to circular pots (12 cm in height, and 12.5 cm, and 9.5 cm top and bottom diameter, respectively) filled with a mixture of peat moss and vermiculite (7:3 v/v) 18 days after germination.

Experimental design

The experiment was conducted in the Forest Ecology Complex of Lakehead University, Thunder Bay campus. The treatments consisted of two $[CO_2]$ {ambient $[CO_2]$ (AC) 400 µmol·mol⁻¹ or an elevated $[CO_2]$ (EC) of 1000 µmol·mol⁻¹}, four photoperiod regimes corresponding to latitudes of 48°N (seed origin), 52°N, 55°N, and 58°N, and two soil moisture regimes (high vs. low). The experiment was a split–split plot design with $[CO_2]$ as the main plots, photoperiods as the subplots, and soil moisture level as the sub-subplots. Each concentration of CO_2 was tested using two independent replicates and the test was randomly assigned to two of the four greenhouses. We used a total of 96 seedlings: three seedlings per treatment combination (two levels of CO_2 , four photoperiods, and two soil moisture levels), and two replicates per combination: $3 \times 2 \times 4 \times 2 \times 2 = 96$.

Treatments and environmental controls

The environmental conditions in each greenhouse were independently monitored and controlled using an Argus Titan Environment Control System (Argus Controls Systems Ltd., Surrey, British Columbia, Canada). $[CO_2]$ was elevated using the model GEN2E gas CO_2 generators made by Custom Automated Products Inc. (Riverside, California, USA). The photoperiod in each greenhouse was set to the longest of the four treatment levels by supplementing natural light (on cloudy days, and in early mornings and late evenings) using highpressure sodium lamps (model LR48877; P.L. Systems). The shorter photoperiods were obtained by manual shading. A wooden frame was installed for each photoperiod treatment, and light was blocked with neutral density shading cloth. The light intensity inside the shaded-frame was 0 µmol·s⁻¹·m⁻² as measured with a light meter (LI-250; LI-COR Inc.) with a quantum sensor (LI-190; LI-COR Inc.). The photoperiod setting was adjusted weekly, according to the calculated photoperiod for each of the four latitudes. The volumetric water content of the soil was monitored using a Delta-T ML2x probe and HH2 moisture meter (Delta-T Devices, Cambridge, UK) and kept between 60% and 75% of the field capacity for the high moisture treatment, and between 13% and 20% of the field capacity for the low soil moisture treatment.

The experiment was run from 1 November 2016 to 4 February 2017, and we emulated the natural growing season of June 7th to September 10th. The temperature and photoperiod were adjusted weekly based on the weekly averages from the past 10 years (2006–2015) for each of the four latitudes (Environment Canada Weather Records). The daily temperature in each greenhouse was ramped at six-hour set points (averages from the past 10 years). We fertilized seedlings in three phases with different fertilizer formulations: (*i*) the seedlings in the rapid growth phase (emulated June 7th to June 21st) received 100 mg N·L⁻¹, 60 mg P·L⁻¹, 150 mg K·L⁻¹, 80 mg Ca·L⁻¹, 40 mg Mg·L⁻¹ and 60 mg S·L⁻¹; (*ii*) the seedlings in the establishment phase (emulated June 22nd to August 30th) received 33 mg N·L⁻¹, 73 mg P·L⁻¹ and 55 mg K·L⁻¹; the seedlings in the hardening phase (emulated September 1st to the end of the experiment) received 33 mg $N\cdot L^{-1}$, 44 mg $P\cdot L^{-1}$ and 83 mg $K\cdot L^{-1}$ (Landis 1989).

Growth measurements

Three seedlings were randomly selected from each treatment combination (two [CO₂], four photoperiods, and two levels of soil moisture) and two replicates per combination $(3 \times 2 \times 4 \times 2 \times 2 = 96$ seedlings in total). The randomization was carried out when measurements were taken. The selected seedlings were harvested after height and root collar diameter (RCD) were measured and were separated into leaves, stem, and roots. The leaves from each seedling were scanned to determine total leaf area (LA) and the number of leaves was using the WinFolia software (Regent Instruments Inc., Quebec City, Quebec, Canada). The root system was washed individually. Dry mass components were weighed separately after oven-drying for 48 h at 80 °C and used for calculations of biomass allocation, specific leaf area (SLA = total leaf area/total leaf dry mass), leaf area ratio (LAR = leaf area/total dry mass leaf mass ratio), leaf mass ratio (LMR leaf dry mass/total dry mass), stem mass ratio (SMR = stem dry mass/total dry mass), root mass ratio (RMR = root dry mass/total dry mass), and root to shoot mass ratio (RSR = root dry mass/shoot dry mass).

Xylem conductivity and cavitation resistance

Three seedlings were randomly selected from each treatment combination, as described previously. The randomization was carried out at the time of measurement. The air-injection method (Sperry and Saliendra 1994) using a double-ended pressure chamber (1505D-EXP Pressure Chamber; PMS Instrument Company, Albany, Oregon, USA) was used to create cavitation in the xylem. Stems were cut into 15 cm segments to accommodate long maximum vessel lengths (mean vessel length 1.9 cm, between 8 and 15 cm of stems; Sperry and Saliendra 1994; Sperry et al. 1994) at 5 cm from the root collar under water to avoid embolism in the xylem conduits (Wheeler et al. 2013). The bark at the end of stem segment was removed with a razor blade, and the xylem was covered with parafilm, which was attached to a flexible tube connected to a solution tank filled with distilled water and 20 mmol·L⁻¹ of potassium chloride. The bark in the middle of the segment (5 cm) was removed to ensure air entry into the xylem (Ennajeh et al. 2011). The tank was installed at a height of 0.5 m. The segment was then installed in the doubled-ended pressure chamber. To make the sample segments fully functional (no embolism in the xylem conduits), the segments were flushed at 175 kPa pressure for 20 min to remove any air bubbles. After full saturation, the maximum conductivity of the xylem segment was measured (K_{max}), which was divided by the functional xylem area of each segment to obtain maximum specific hydraulic conductivity (K_{smax}). The hydraulic conductivity was measured according to

Table 1. Summary of ANOVA for the effects of *C*, P, SM, and their interactions on plant height, RCD, leaf size, SLA, total DM, leaf DM, stem DM, root DM, LMR, SMR, RMR, and RSR.

Variable	C (DF = 1)	P (DF = 3)	SM (DF = 1)	$C \times P (DF = 3)$	$C \times SM (DF = 1)$	$P \times SM (DF = 3)$	$C \times P \times SM (DF = 3)$
Height							
F	0.427	13.761	8.875	0.528	0.070	2.314	3.001
р	0.581	0.004	0.018	0.679	0.798	0.152	0.095
RĈD							
F	0.605	0.796	28.739	1.213	0.059	0.909	1.203
р	0.518	0.539	0.001	0.383	0.815	0.479	0.369
Leaf size							
F	0.736	0.553	7.940	1.013	0.044	0.117	0.419
p	0.481	0.665	0.023	0.450	0.838	0.948	0.744
SLA							
F	0.964	4.933	2.749	1.304	0.518	0.794	1.106
р	0.430	0.047	0.136	0.357	0.492	0.531	0.402
Total DM							
F	0.966	6.889	37.817	3.115	0.081	1.606	3.332
p	0.429	0.023	<0.001	0.110	0.783	0.263	0.077
Leaf DM							
F	0.485	10.542	38.056	3.627	0.164	2.139	1.699
p	0.558	0.008	<0.001	0.084	0.696	0.173	0.244
Stem DM							
F	1.211	4.440	42.117	1.257	0.157	1.459	3.347
р	0.386	0.057	<0.001	0.370	0.703	0.297	0.076
Root DM							
F	2.273	4.380	22.737	3.956	0.266	1.021	4.607
p	0.271	0.059	0.001	0.072	0.620	0.433	0.037
LMR							
F	0.480	1.544	12.290	0.685	0.103	0.249	2.547
p	0.560	0.297	0.008	0.593	0.757	0.860	0.129
SMR							
F	0.160	2.032	8.893	0.245	0.017	0.204	5.557
<i>p</i>	0.728	0.211	0.018	0.862	0.899	0.891	0.023
RMR							
F	0.450	5.339	4.332	2.066	0.043	0.805	4.179
<i>p</i>	0.571	0.040	0.071	0.206	0.841	0.525	0.047
RSR							
F	0.615	5.278	4.221	2.102	0.021	0.784	4.298
p	0.515	0.040	0.074	0.202	0.890	0.536	0.044

Note: C, $[CO_2]$; P, photoperiod; SM, soil moisture; RCD, root collar diameter; SLA, specific leaf area; DM, dry mass; LMR, leaf mass ratio; SMR, stem mass ratio; RMR, root mass ratio; RSR, root:shoot mass ratio. The seedlings were exposed to two $[CO_2]$ (400 or 1000 μ mol·mol⁻¹), four photoperiod regimes [corresponding to latitudes of 48.38°N (seed origin), 51.68°N, 54.98°N, and 58.28°N], and two soil moisture regimes [high (60%–75%) or low (13%–20%)]. The numbers in bold font are considered to be statistically significant differences (p < 0.05).

Sperry et al. (1988). A gravity-induced flow rate (5 min) and 10 kPa-pressure-induced flow rate (5 min) were measured, and the gravity-induced flow rate was subtracted from 10 kPa-induced flow rate. The hydraulic conductivity (K_h) = K_{max} through the segment was calculated as follows:

$$(K_{\rm h}) = \frac{\text{Mass flow rate (mg \cdot s^{-1})}}{\text{Pressure difference (MPa)/Segment length (m)}}$$

After measuring K_{max} , the segment was pressurized to create cavitation in the xylem. The segment was exposed to different pressures (0.5, 1.0, 1.5, 1.8, 2.0, 2.5, 3.0, 3.5, and 4.5 kPa) for 10 min. The K_{h} measurement was initiated after the stem stopped releasing air, and continued until the percentage loss of conductivity (PLC) was >95%. PLC was calculated as follows:

$$PLC = 100 \times \left(1 - \frac{K_{\rm h}}{K_{\rm max}}\right)$$

The relationship between hydraulic conductance and decreasing water potential (–MPa) for each seedling was fitted with a Weibull curve using the "fitplc" function in the fitplc package (Duursma and Choat 2017) in R software (version 3.5.0; R Development Core Team 2018). From these curves, the water potential corresponding to 20%, 50%, and 80% loss of K_h (P_{20} , P_{50} , and P_{80}) and bootstrapped confidence intervals (CIs; 95%) were calculated. Differences in vulnerability between treatments were deemed significant only if CIs did not overlap.

Data analysis

All of the data were examined graphically for the normality of distribution (probability plots of residuals) and

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Fig. 1. Total height (mean + SE) for the seedlings of trembling aspen grown under (*a*) four different photoperiods [emulating 48°N (seed origin), 52°N, 55°N, and 58°N], and (*b*) two different soil moisture levels (high and low). (*b*) The mean root collar diameter (RCD) for the seedlings grown in each of the two soil moisture levels. The data in (*a*) were pooled for the two [CO₂] and two levels of soil moisture because the three-way interaction was not statistically significant ($N = 3 \times 2 \times 2 \times 2 = 24$). The sample size for (*b*) was 48 because the data were pooled for the two [CO₂] and four different photoperiods because the interaction was not statistically significant (p > 0.05; 3 seedlings × 2 replicates × 2 [CO₂] × 4 photoperiods = 48). Different letters above the error bars indicate significant differences as determined using Fisher's Least Significant Difference post-hoc test (p < 0.05); *, p < 0.05; **, p < 0.01;



homogeneity of variance (scatter plots) with the R software (version 3.5.0) before being subjected to analysis of variance (ANOVA). ANOVA was used to test the effects of [CO₂], photoperiod, soil moisture regimes, and their interactions. When the ANOVA showed a significant $(p \le 0.05)$ photoperiod effect or a significant interaction, Fisher's Least Significant Difference (LSD) post-hoc test was used to examine differences among treatment means. There were limitations in pair-wise comparisons in the split-split plot experimental design we used in this study because lower level plots were nested within a higher level plot. Furthermore, the sample size in this study was very small, increasing the likelihood of real treatment effects being undetected (type II error). Fisher's LSD offers a reasonable control of type II error without compromising the power of the statistical test for split plot and split-split plot designs. All of the analyses were performed using R software (version 3.5.0).

Results

Growth and biomass allocation

The seedlings in the longest photoperiod (58°N) treatment grew significantly taller (110 ± 17.55 cm) and had smaller specific leaf area (SLA) (363.49 ± 90.81 cm²·g⁻¹) than all of the other photoperiod treatments (92.19 ± 17.16 cm, 432.63 ± 104.18 cm²·g⁻¹) (Table 1; Figs. 1*a* and 2*b*). Seedlings grown with low soil moisture were significantly shorter (92.74 ± 17.70 cm), RCD (7.03 ± 1.14 mm), and leaf size (56.84 ± 13.87 cm²) than that of high soil moisture treatment (100.30 ± 19.19 cm, 7.98 ± 1.32 mm, 65.33 ± 14.24 cm²) (Table 1; Figs. 1*a*, 1*b*, and 2*a*).

The seedlings in the longest photoperiod had significantly greater total biomass (18.93 \pm 6.68 g) and leaf biomass (6.49 \pm 1.97 g) than those in the shorter photoperiods (15.04 \pm 7.28 g, 5.07 \pm 2.09 g) (Table 1; Figs. 3*a* and 3*b*). Similarly, the seedlings at low soil moisture were lower in total biomass $(13.20 \pm 5.35 \text{ g})$, leaf biomass $(4.67 \pm 1.53 \text{ g})$, stem biomass $(5.61 \pm 2.44 \text{ g})$, and root biomass $(2.39 \pm 1.47 \text{ g})$ compared with seedlings grown with a high soil moisture content $(18.82 \pm 7.94 \text{ g},$ $6.18 \pm 2.40 \text{ g}, 8.24 \pm 3.47 \text{ g}, 3.74 \pm 2.20 \text{ g})$ (Figs. 3*a*-3*c*). The difference in root biomass between seedlings grown with low and high soil moisture content was significantly greater at the combinations of AC and the photoperiod for 58°N (high moisture = 4.87 ± 1.71 g; low moisture = 2.00 ± 0.97 g), and EC and the photoperiod for 52° N (high moisture = 5.06 ± 3.21 g; low moisture = $1.43 \pm$ 0.97 g) (Fig. 3*d*; significant three-way interaction).

Longer photoperiods tended to reduce the root:shoot mass ratio (RSR) and root mass ratio (RMR) under elevated [CO₂], although the trend seemed slightly different when comparing the seedlings grown with low or high soil moisture (significant three-way interactions) (Table 1; Figs. 4*a* and 4*d*). Low soil moisture levels generally resulted in an increase in leaf mass ratio (LMR) (high moisture = 0.34 ± 0.05 ; low moisture = 0.37 ± 0.06) (Fig. 4*b*), but a decrease in RMR (high moisture = 0.19 ± 0.04 ; low moisture = 0.17 ± 0.05), RSR (high moisture = 0.23 ± 0.07 ; low moisture = 0.46 ± 0.04 ; low moisture = 0.44 ± 0.05) (Figs. 4*a*, 4*c*, and 4*d*).

Xylem cavitation

The effects of $[CO_2]$, photoperiod, and soil moisture on xylem resistance to cavitation varied with loss of conductivity (Table 2). Under the EC, the seedlings exposed to long photoperiods lost 20%, 50%, and 80% of conductivity (P_{20} , P_{50} , and P_{80}) at less negative water potentials (less cavitation resistant) than those at the seed origin (Figs. 5 and 6). Particularly, there was no overlap of the CIs for P_{20} , P_{50} , and P_{80} between 48°N [$P_{20} = -1.51$ MPa (CI = 1.11–1.83); $P_{50} = -2.22$ MPa (CI = 1.75–2.32); $P_{80} = -2.75$ MPa (CI = 2.43–3.20)] and 58°N [$P_{20} = -0.86$ MPa (CI = 0.62–1.12);

Fig. 2. (*a*) Mean leaf size of the trembling aspen seedlings grown in two different soil moisture levels (high or low). (*b*) Specific leaf area (mean + SE) for the seedlings grown in four different photoperiods [emulating 48°N (seed origin), 52°N, 55°N, and 58°N]. The data for (*a*) were pooled for $[CO_2]$ and photoperiod because the three-way interaction was not statistically significant (*p* > 0.05; 3 seedlings per treatment combination × 2 replications per combination × 2 $[CO_2]$ × 4 photoperiods = 48). The data for (*b*) were pooled for the two $[CO_2]$ treatments and the two soil moisture treatments ($N = 3 \times 2 \times 2 \times 2 = 24$); *, *p* < 0.05.



Fig. 3. Total biomass (*a*) and leaf biomass (*b*) of the trembling aspen seedlings grown in four different photoperiods [emulating 48°N (seed origin), 52°N, and 58°N] and in two different soil moisture levels (high or low). (*c*) Stem biomass for the seedlings grown under high or low soil moisture regimes. (*d*) Root biomass for the seedlings grown under the combination of two different [CO₂] (400 or 1000 μ mol·mol⁻¹), four different photoperiods [emulating 48°N (seed origin), 52°N, 55°N, and 58°N], and high or low soil moisture levels. Data (mean + SE) were pooled for effects that were not statistically significant (*p* > 0.05): the data for (*a*) and (*b*) were pooled for the two levels of [CO₂] and two soil moisture levels (*N* = 3 × 2 × 2 × 2 = 24). The data for (*c*) were pooled for the two levels of [CO₂] and the four photoperiods (*N* = 3 × 2 × 2 × 4 = 48). (*d*) *N* = 6 (3 × 2). Different letters above the error bars in (*a*) and (*b*) indicate significant differences as determined using Fisher's Least Significant Difference post-hoc test (LSD; *p* < 0.05). Different lowercase letters in (*d*) indicate significant differences among photoperiods within the same [CO₂] and soil moisture level (LSD, *p* < 0.05). Different uppercase letters in (*d*) indicate significant differences with soil moisture within the same [CO₂] and photoperiod (LSD, *p* < 0.05). The asterisk above the error bars in (*d*) indicate the significant differences with [CO₂] within the same photoperiod and soil moisture treatment (LSD, *p* < 0.05); *, *p* < 0.05; **, *p* < 0.01; ***, *p* < 0.001.



 P_{50} = -1.33 MPa (CI = 1.09–1.53); P_{80} = -1.89 MPa (CI = 1.62–2.22)] under EC, which indicates significant differences in conductivity loss between the shortest and longest photoperiod treatments (Table 3; Figs. 5*e* and 5*h*). Under the AC, however, the threshold water potentials for conductivity

loss appeared to be more negative (more resistant to cavitation) at the photoperiod corresponding to the highest latitude, but the differences were generally not significant (Table 3; Figs. 6a-6d). The seedlings in low soil moisture reached P_{80} at less negative water potential;

Fig. 4. (*a*) Root:shoot mass ratio (RSR), (*c*) stem mass ratio (SMR), and (*d*) root mass ratio (RMR) for seedlings of trembling aspen grown in a combination of two different concentrations of CO₂ (400 or 1000 μ mol·mol⁻¹), four different photoperiods [emulating 48°N (seed origin), 52°N, 55°N, and 58°N], and two different levels of soil moisture (high vs. low). (*b*) Leaf mass ratio (LMR) for the seedlings grown in high or low levels of soil moisture. *N* = 6 for (*a*), (*c*), and (*d*) (3 seedlings per treatment combination × 2 replicates); *N* = 48 for (*b*) because the data (mean + SE) were pooled for the two levels of [CO₂] and four photoperiods because the interactions were not statistically significant (*p* > 0.05; *N* = 3 seedlings per treatment combination × 2 replications per combination × 2 [CO₂] × 4 photoperiods = 48). Different lowercase letters in (*a*), (*c*), and (*d*) indicate significant differences with photoperiod within the same [CO₂] and soil moisture levels (LSD, *p* < 0.05). Different uppercase letters in (*a*), (*c*), and (*d*) indicate significant differences with soil moisture level within the same [CO₂] and photoperiod (LSD, *p* < 0.05). The asterisks above the error bars in (*c*) and (*d*) indicate significant differences with [CO₂] within the same photoperiod and soil moisture level (LSD, *p* < 0.05); *, *p* < 0.05; **, *p* < 0.01; ***, *p* < 0.001.



Table 2. Summary of ANOVA results for water potentials associated with 20%, 50%, and 80% loss of conductivity (P_{20} , P_{50} , and P_{80} , respectively), and maximum specific hydraulic conductivity (K_{smax}).

Variable	C (DF = 1)	P(DF = 3)	SM (DF = 1)	$C \times P (DF = 3)$	$C \times SM (DF = 1)$	$P \times SM (DF = 3)$	$C \times P \times SM (DF = 3)$
P ₂₀							
F	433	1.503	0.286	5.929	1.607	1.073	0.669
p	0.002	0.307	0.607	0.032	0.241	0.413	0.594
P ₅₀							
F	17.360	1.022	1.648	7.488	2.387	0.891	0.697
р	0.053	0.447	0.235	0.019	0.161	0.486	0.580
P ₈₀							
F	2.628	1.048	9.836	7.201	5.078	1.234	1.155
р	0.246	0.437	0.014	0.021	0.054	0.359	0.385
K _{smax}							
F	0.248	0.789	5.441	2.116	0.076	0.115	0.365
р	0.668	0.543	0.048	0.200	0.790	0.949	0.780

Note: The seedlings were exposed to two $[CO_2]$ (400 or 1000 μ mol·mol·1), four photoperiod regimes [corresponding to latitudes of 48.38°N (seed origin), 51.68°N, 54.98°N, and 58.28°N], and two soil moisture regimes [high (60%–75%) or low (13%–20%)]. The numbers in bold font are considered to be statistically significant differences (p < 0.05).

however, the CIs overlapped for the seedlings grown with high and low soil moisture [high moisture = -2.3 MPa (CI = 2.03–2.69); low moisture = -2.08 MPa (CI = 1.80–2.42)] (Fig. 3). Seedlings grown with low soil moisture had significantly lower maximum specific hydraulic conductivity (K_{smax}) (0.0020 ± 0.0013 mg·mm⁻¹·s⁻¹·MPa⁻¹)

than the seedlings grown with high soil moisture levels $(0.0014 \pm 0.0013 \text{ mg} \cdot \text{mm}^{-1} \cdot \text{s}^{-1} \cdot \text{MPa}^{-1})$ (Fig. 6).

Discussion

The first hypothesis was fully supported by our findings that the seedlings grown under the longest photo**Fig. 5.** Hydraulic vulnerability curves showing the response (loss of stem hydraulic conductivity, %) to decreasing water potential (–MPa) in trembling aspen seedlings under the interactive effects of two different [CO₂] [ambient (AC, 400 μ mol·mol⁻¹) or elevated (EC, 1000 μ mol·mol⁻¹)] and four different photoperiods [emulating 48°N (seed origin), 52°N, 55°N, and 58°N]. Each data point shows the loss of conductivity (%; mean + SE) at each different water potential. (*a*–*h*) *N* = 12, three seedlings per treatment combination and two replicates per combination; the data were pooled for the two levels of soil moisture because the three-way interaction was not statistically significant (*p* > 0.05; 3 × 2 × 2 = 12). Vertical dotted/dashed lines indicate the 95% confidence interval for *P*₂₀ (gray with dotted line), *P*₅₀ (dark-gray with short-dash), and *P*₈₀ (black with medium-dash), as estimated from the bootstrap.



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period (corresponding to 58°N latitude) grew the tallest and had the greatest biomasses among all of the photoperiod regimes. The results are in general agreement with the findings of Oleksyn et al. (1992) on Scots pine (*Pinus sylvestris* L.). Specific leaf area (SLA), however, was the lowest for seedlings grown under the longest photoperiod. While growth rates are generally positively related to SLA, the opposite is occasionally reported (Wright et al. 1994; Thumma et al. 2001). The negative relationship between SLA and growth can be explained in that thicker leaves associated with low SLA may have more mesophyll cells per unit leaf area, which will increase photosynthesis and therefore biomass production (Thumma et al. 2001; Anyia and Herzog 2004). A low SLA should reduce transpirational water loss, increase water use efficiency, and ameliorate the risk of desiccation, particularly for seedlings with high leaf biomass, which is the case in this study.

Our results suggest that trembling aspen can physiologically acclimate to drought. The seedlings in the low soil moisture treatment had lower hydraulic conductivity. Low soil moisture reduces vessel diameter (Awad Inoue et al.

Fig. 6. Maximum specific hydraulic conductivity (K_{smax}) of trembling aspen seedlings grown in two different soil moisture levels (high or low), two different concentrations of CO₂] [ambient (400 µmol·mol⁻¹) or elevated (1000 µmol·mol⁻¹)] and four different photoperiods [emulating 48°N (seed origin), 52°N, 55°N, and 58°N]. Data are the mean + SE (N = 48, three seedlings per treatment combination and two replicates per combination; $3 \times 2 \times 2 \times 4 = 48$). The data were pooled for the two [CO₂] and four photoperiods because the three-way interaction was not statistically significant (p > 0.05); *, p < 0.05.



et al. 2010), resulting in lower water transport capacity or hydraulic efficiency (Tyree and Zimmermann 2002). While a high hydraulic conductivity generally promotes higher growth rates (Hacke and Sperry 2001; Tyree 2003), as demonstrated by the growth and biomass data in this study, the smaller vessel diameter associated with a low hydraulic conductivity can increase xylem resistance to cavitation, particularly freeze-thaw induced cavitation (Davis et al. 1999; Venturas et al. 2017). Fast-growing and short-lived pioneer species, such as trembling aspen, generally have high phenotypic xylem plasticity and acclimate to different soil moisture conditions (Plavcová and Hacke 2012; Schreiber et al. 2015). The results from this study are generally consistent with the findings of other studies (Tyree and Zimmermann 2002; Nobel 2009; Hacke et al. 2016).

The results do not support the hypothesis that drought would increase xylem resistance to droughtinduced cavitation. Although the specific hydraulic conductivity of the stem was lower in the low soil moisture treatment, there were no significant differences between the two soil moisture treatments in the water potentials for 20%, 50%, and 80% loss of hydraulic conductivity. This result is contrary to the expectation that high hydraulic conductivity is associated with large xylem vessels and poor resistance to cavitation (Wheeler et al. 2005; Markesteijn et al. 2011; Hacke et al. 2016; Pratt and Jacobsen 2017). However, resistance to cavitation is more closely related to the characteristics of the pit membrane (Wheeler et al. 2005). It is possible that the results may vary with seedling age (Sperry et al. 1991). Because the size of the largest membrane pore and the average size of pits in a vessel affect the tree's resistance to cavitation

(Wheeler et al. 2005), the difference in cavitation resistance in different soil moisture treatments would be more apparent in larger trees.

Our hypothesis on the effects of elevated [CO₂] and longer photoperiod on cavitation resistance was only partially supported: cavitation resistance decreased with longer photoperiods under elevated [CO₂]. The seedlings grown photoperiod simulated for 58°N reached a 50% loss of conductivity at high water potential (-1.33 MPa) under elevated [CO₂] compared with the photoperiod simulated for 48°N (-2.21 MPa). While the reasons for this result cannot be entirely explained, there are studies of the effect of $[CO_2]$ and photoperiod on the anatomical structure of xylem suggesting that they affect a tree's resistance to cavitation (Hacke and Sperry 2001; Tyree and Zimmermann 2002; Cai and Tyree 2010). Elevated [CO₂] has been reported to increase xylem cell size in several Populus spp. (Luo et al. 2005; Kostiainen et al. 2014), which is not linked to changes in cavitation resistance. In P. tremula, elevated [CO2] did not affect cavitation resistance (Tognetti et al. 1999). However, elevated [CO₂] and longer photoperiods have been shown to increase the diameter of xylem conduits (Larson 1962; Handa et al. 2006; Kostiainen et al. 2014) but the effects of elevated [CO₂] vary greatly with changes in other environmental factors (Saxe et al. 1998; Norby et al. 1999, 2010; Curtis et al. 2000; Oren et al. 2001). In the present study, we did not characterize anatomical changes to xylem in response to our experimental treatments, but we feel that the response of xylem anatomy to the interactions between elevated [CO₂] and longer photoperiods should be investigated to further elucidate the physiological responses of trembling aspen in the context of northward migration. Nonetheless, our results indicate that xylem resistance to cavitation in trembling aspen could decline if and when the species migrates northward to higher latitudes due to predicted future climate conditions, which could impact the success of its migration or seeds.

In summary, our results suggest that trembling aspen would have greater growth and biomass under a longer photoperiod when migrating northwards, but the growth enhancement may be offset by low soil moisture levels. However, the resistance of xylem to cavitation decreases with increasing photoperiod regimes, associated with higher latitudes under elevated [CO₂]. This, along with reduced hydraulic conductivity under low soil moisture conditions, suggests that aspen could have lower resistance to water stress when migrating northward if drought becomes more frequent and severe in the northern regions (Pachauri et al. 2014). Our results indicate that although temperature and precipitation patterns are often considered as main factors influencing future tree distribution, other factors that are part of species' niche such as photoperiod, [CO₂], and moisture variability likely influence the shift of species distribu-

Table 3. Water potentials (average MPa) plus 95% confidence intervals (CI) for 20% (P_{20}), 50% (P_{50}), or 80% (P_{80}) loss in hydraulic conductivity in seedlings of trembling aspen subjected to different conditions of soil moisture or [CO₂] × photoperiod.

	<i>P</i> ²⁰ (MPa; 95% CI)	<i>P</i> ₅₀ (MPa; 95% CI)	<i>P</i> ₈₀ (MPa; 95% CI)
Soil moisture			
High	1.13 (0.82-1.40)	1.37 (1.39–1.87)	2.30 (2.03-2.69)
Low	1.04 (0.74-1.31)	1.52 (1.24-1.72)	2.08 (1.80-2.42)
[CO ₂] × photope	riod		
Ambient × 48°N	0.78 (0.55-1.07)	1.27 (1.03–1.50)	1.92 (1.65-2.30)
Ambient × 52°N	1.08 (0.84-1.24)	1.44 (1.25–1.63)	1.87 (1.70-2.20)
Ambient × 55°N	0.88 (0.61–1.17)	1.38 (1.12-1.56)	1.97 (1.72-2.26)
Ambient × 58°N	1.17 (0.81-1.58)	1.81 (1.45-2.03)	2.55 (2.17-3.02)
Elevated \times 48°N	1.51 (1.11-1.83)	2.21 (1.75-2.32)	2.75 (2.43-3.20)
Elevated \times 52°N	1.30 (0.96–1.51)	1.83 (1.55-2.00)	2.42 (2.13-2.77)
Elevated \times 55°N	1.07 (0.75-1.36)	1.57 (1.28-1.79)	2.15 (1.86-2.48)
Elevated \times 58°N	0.86 (0.62-1.12)	1.33 (1.09-1.53)	1.89 (1.62-2.22)

Note: Ambient, concentration of 400 µmol·mol⁻¹; Elevated, concentration of 1000 µmol·mol⁻¹. Curves were fit for each individual seedling and the 95% CIs for P_{20} , P_{50} , and P_{80} were calculated.

tion. As our results were obtained from one-year-old seedlings under controlled greenhouse conditions, the results may not be directly applicable to large trees grown in the field. However, the value we found in the present study (i.e., -1.27 MPa at P_{50} for AC × 48°N) is similar to the values reported for other Populus species from both field and controlled environment studies (Cai and Tyree 2010; Hacke et al. 2010; Hillabrand et al. 2016). The consistency in results from different studies, particularly between this study and field research by other researchers, suggests that the use of manipulative experiments to investigate the interactive effects of multiple factors on xylem vulnerability can be a powerful tool for examining how trees may respond to the novel environmental conditions of the future, and (or) at new locations. Our results indicate the need to consider the interactive effects of [CO₂], photoperiod, and soil moisture for planning assisted migration and for projecting the future distribution of boreal forests.

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