Effects of early thinning and fertilization on soil temperature and soil respiration in a poplar plantation

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ABSTRACT

The main goal of this study was to determine the short-term effects of forest management practices (precommercial thinning and fertilization) on soil CO₂ efflux of a young black cottonwood (*Populus trichocarpa*) plantation in southern Iceland. Changes in leaf area index, tree growth, soil and air temperatures were also monitored during the first year following the management period. Traditional precommercial thinning (50%) had little effect on soil temperature, but heavy thinning (80%) led to higher soil temperatures in spring and summer. Thinning did not change foliage nutrient content or tree growth in the first treatment year. Effects on soil CO₂ efflux were surprising; even if soil temperature was slightly higher and all organic material was left at site after precommercial thinning, soil CO₂ efflux in the thinned stands was significantly lowered. Fertilization increased foliage nutrient content but did not significantly change tree growth during the first growing season following spring application. It did however significantly increase soil CO₂ efflux rate in the first treatment year. These results are important when the effects of early forest management on carbon fluxes are modelled.

Keywords: Soil CO₂ efflux, nitrogen, thinning intensity, Populus trichocarpa, fertilisation

YFIRLIT

Áhrif snemmgrisjunar og áburðargjafar á jarðvegshita og jarðvegsöndun í asparskógi

Meginmarkmið rannsóknarinnar var að kanna skammtímaáhrif skógræktaraðgerða, nánar tiltekið grisjunar og áburðargjafar, á jarðvegsöndun í íslenskum asparskógi. Einnig var fylgst með trjávexti, laufflatarmáli og breytingum á loft- og jarðvegshita. Hefðbundin snemmgrisjun (50%) hafði lítil áhrif á jarðvegshita. Mikil grisjun (80%) jók jarðvegshita að vori og sumarlagi en hafði lítil áhrif yfir veturinn. Grisjun hafði engin áhrif á magn næringarefna í laufi eða trjávöxt fyrsta árið. Áhrif grisjunar á jarðvegsöndun voru nokkuð óvænt: hún minnkaði marktækt í kjölfar grisjunar, þrátt fyrir að hitastig hafi hækkað og allt lífrænt efni sem féll til við grisjun hafi verið skilið eftir á skógarbotni. Einu áhrif áburðargjafar á trjávöxt fyrsta árið komu fram í auknu magni næringarefna í laufi. Jarðvegsöndun jókst hins vegar marktækt í kjölfar áburðargjafar. Þessar niðurstöður geta komið að gagni við gerð hermilíkana af áhrifum skógræktaraðgerða á kolefnishringrás og kolefnisbindingu.

INTRODUCTION

Anthropogenic activities have increased greenhouse gas emissions, especially carbon dioxide (CO₂), yielding an annual accumulation of carbon (C) in the atmosphere at the rate of 2.8 Pg C y⁻¹ (Fan et al. 1998) or 1.9 ppm per year during 1995-2005 (IPCC 2007). As a result, the surface air temperature has been rising steadily and it has been suggested that even more drastic changes will occur in the future (IPCC 2007). Soil CO₂ efflux is of particular importance as it is the largest terrestrial source of C to the atmosphere, contributing 80.4 Pg C y⁻¹ (Raich et al. 2002). Hence, small changes in terrestrial soil CO₂ efflux could have significant effects on atmospheric CO₂ concentration. Furthermore, a positive correlation has been demonstrated between temperature and soil CO₂ efflux (Knorr et al. 2005b). Higher temperatures could therefore increase soil CO, efflux to the atmosphere and thus further exacerbating global warming (e.g. Kirschbaum 1995, Knorr et al. 2005b). However, it has been pointed out that this effect could be reduced through an increase in primary production in nutrient limited ecosystems, as nutrient turnover (availability) is expected to increase with higher temperatures (e.g. Liski et al. 1999, Jarvis & Linder 2000). On a hectare scale, similar changes occur when managed forests are thinned. The decreased leaf area changes the microclimate at the forest floor which in turn affects soil processes, such as decomposition and CO₂ efflux (Siira-Pietikäinen et al. 2001, Hyvönen et al. 2007).

Soil CO_2 efflux (respiration) can be partitioned into two processes, metabolic activity of plant roots (autotrophic respiration) and the decomposition of dead organic material (heterotrophic respiration) (Ryan & Law 2005). Autotrophic and heterotrophic respiration can respond independently to a number of factors, such as climate, soil type, forest type and human disturbances (Boone et al. 1998, Hanson et al. 2000, Knorr et al. 2005b, Olsson et al. 2005, Luo & Zhou 2006). Probably because of the diverse and complex nature of these interactions, studies focusing on the

effect of forest management practices on soil CO_2 efflux have given ambiguous results. For instance, soil CO_2 efflux was found to have increased (Selmants et al. 2008), decreased (Tang et al. 2005, Sullivan et al. 2008) or stayed unchanged (Toland & Zak 1994) following thinning. Fertilizer applications to forest soils have also yielded variable responses, with reduction (Bowden et al. 2004, Olsson et al. 2005), increase (Cleveland & Townsend 2006) or no change (Castro et al. 1994) in soil CO_2 efflux. Therefore, more work is needed to fully understand what are the general responses to such management practices.

It is of special interest to study the impact of forest management on soil organic matter (SOM) in Iceland. Previous research has indicated that Icelandic forest soils can store twice the amount of C as aboveground woody biomass (Snorrason et al. 2002) and that the rate of C sequestration in SOM, fine roots and litter can be as high as or higher than accumulation in woody biomass during the establishment phase after afforestation (Bjarnadóttir 2009).

The aim of this study was to determine the short-term effects of precommercial thinning and fertilization on CO₂ efflux of a young black cottonwood (Populus trichocarpa Torr. & Gray) plantation in southern Iceland. Black cottonwood is the second most used broadleaved tree species in afforestation in Iceland, following the native mountain birch (Betula pubescens Ehrh.). It was expected that precommercial thinning of a young broadleaved plantation would lead to higher soil CO, efflux due to higher soil temperatures and increased litter input and that the size of the response would depend on the thinning intensity. Fertilization was expected to further increase the soil CO, efflux.

MATERIAL AND METHODS

Site description

The experimental site is located in Gunnarsholt in southern Iceland (63° 51' N and 20° 13' W, 78 m a.s.l.). In 1990, cuttings of a single clone of black cottonwood (*Populus trichocarpa*; Clone Idunn) were planted in an abandoned hayfield from which the sod had been removed in 1989. A total of 145,000 propagated cuttings were planted in 14.5 ha with 1 m spacing (stand density of 10,000 trees ha⁻¹). The Idunn clone originates from the Copper River Delta region, Alaska (Lat 60-61°), an area with climate similar to that of Gunnarsholt (Sigurdsson 2001).

A microclimate station was installed at the centre of the site in 1989, where a range of climatic parameters, including air temperature, soil temperature and global radiation, were monitored (Aradottir et al. 1997). The soil is an Andosol (found only in volcanic areas) and silty loam in texture. The soil water potential is permanently close to field capacity, and water availability was therefore not considered to limit tree growth at the site (Strachan et al. 1998). Organic carbon content of the A1 soil layer ranged from 1.8 to 2.4%, pH was 5.8, cation exchange capacity (CEC) was 19 meq 100 g⁻¹ and no peat was found in the soil profile (Strachan et al. 1998).

The most limiting environmental factor for tree growth at the site has been found to be nitrogen availability (Sigurdsson 2001). The stand development was slow in the beginning, but after the saplings had overgrown the competing vegetation and the most active frost layer in 1997, the average annual height increment has been 33 cm. In the autumn of 2003 the average tree height, diameter at breast height and basal area were 3.1 m, 2.7 cm and 5.9 m² ha⁻¹, respectively, across the whole plantation. Prior to the thinning treatments, the forest floor was mainly covered by grasses (40%), with Agrostis capillaris L. and Poa pratensis L. as dominant species, mosses (34%) and litter (23%) (Jónsson et al. 2006). More information about the climate, soil and other physical conditions at the site can be found in Aradottir et al. (1997), Strachan et al. (1998) and Sigurdsson (2001).

Experimental design

In early June 2004, 24 plots were established in the experimental plantation, each 0.06 ha (25x25 m) in size. The plots were arranged in a

randomized block design with thinning intensity and fertilization as the main factors. Treatments consisted of unthinned control (10,000 trees ha⁻¹), 50% thinned (5,000 trees ha⁻¹) and 80% thinned (2,000 trees ha⁻¹). The planting density of black cottonwood is normally ca. 3,000 trees ha⁻¹ in Iceland (Sigurdsson 2001), considerably less than was used when the experimental forest was established. Therefore the 80% thinned stands were of traditional stand density after first thinning, even though the relative thinning intensity was far above the recommended practice. The thinning treatments were repeated on either unfertilized soil or where all macro- and micronutrients were applied in early June as 80 kg N ha⁻¹ and with other elements in optimum proportions for black cottonwood. The optimum N ratios were determined in an earlier laboratory study with cuttings from the Gunnarsholt plantation (Sigurdsson 2001), where the nutrient requirements were studied with the Ingestad method (Linder 1995, Ingestad 1991). The treatments were entitled C-00, F-00, C-50, F-50, C-80 and F-80 for the two nutrient treatments (C = Controland F = Fertilized) and the three thinning intensities (00%, 50%, 80%), respectively. All thinned trees (stems, branches and leaves) were left on the forest floor to decompose, as is customary following precommercial thinning of forest stands not much used for recreation in Iceland. The total amount of thinning residues added to the forest floor contained 4.8 Mg C ha⁻¹ and 7.7 Mg C ha⁻¹ for the 50% and 80% thinning treatments, respectively (Jónsson 2007).

Leaf morphology and chemical analysis

To check if trees had increased their nutrient uptake following the spring fertilization, the youngest fully expanded leaves on the top shoots were excised from 20 trees in each nutrient treatment in late August 2004. The leaves were placed directly on ice and thereafter stored at -18 °C for eight months before further processing took place. Six leaves from each treatment were randomly chosen for morphological analysis, scanned on a pre-calibrated scanner and analysed for area, length and width with the WinFOLIA image analysis program (WinSeedle, Regent Inc., Canada). Thereafter the leaves were dried at 85 °C for 48 hours and weighed. Specific Leaf Area (SLA; cm² g⁻¹) was then calculated for each leaf. The other leaves were used for chemical analysis. They were dried in the same way, ground and sent to the Centre for Chemical Analyses (Efnagreiningar Keldnaholti), ICETEC, Reykjavik, Iceland, where their total nitrogen (N) was measured by Kjeldahl wet combustion on Tecator Kjeltec Auto 1030 Analyzer.

Growth

At the start of the experiment diameter at breast height (DBH) was measured for all trees in all treatment plots. The results were used to randomly choose five trees from the mean diameter class in each plot for further measurements of both stem diameter and height increment.

Leaf area index

Leaf area index (LAI) of trees (projected leaf area) was measured with a pair of LAI-2000 Plant Canopy Analyzers (LI-COR Inc., Lincoln, Nebraska) on an overcast day (only diffused light) in early August 2004. One instrument was placed outside the forest and the other was used to take readings of sky brightness at nine fixed points within each treatment plot. The sensor heads always faced north, a 180° lens cap was used and the calculations of LAI were limited to the hemispherical area above 23°, due to the relatively small plot size.

Soil CO, efflux

Eight 5 cm deep PVC collars with 100 mm inner diameter were randomly inserted ca. 3 cm into the soil surface in each treatment plot in early June 2004, before thinning took place. The soil and vegetation growing inside the collars got three weeks to recover from the disturbance before the first flux measurements started. The collars also contained the thinning residues (leaves and small branches) that fell

into them during and after thinning. Soil respiration and aboveground respiration of ground vegetation growing inside the collars (termed here as soil CO₂ efflux) were measured from each collar with a SRC-1 dark chamber with 100 mm diameter and a CIRAS-2 gas analyser (PP-Systems, Hitchin, Hertfordshire, UK). Each measurement started ca. 30 sec. after inserting the chamber on the collar and lasted for 1.5 minutes. The CO₂ efflux rate was calculated by applying a linear function to the rise in CO₂ concentration that was measured once per 1.6 seconds. The 1.5 min. duration was selected after having first tested how different waiting and measurement times fit the linear assumption. Measurement campaigns were carried out between 9:00 AM and 17:00 PM during 22-30 June, 28 July, 16 August and 22 September. Measurements were only made during the daytime to minimize any systematic variation in fluxes. During the first campaign all 8 replicate PVC collars were measured in each plot (192 measurements in total) to establish how spatially variable the soil CO, efflux was. Four collars with median efflux rates were chosen per plot (96 collars in total) for the consequent measurement campaigns that could then be terminated in one full day. This was important to minimize the effect of changes in temperature between consequent days. Soil temperatures at 5 and 10 cm depth were also simultaneously measured at each collar. On 28 July, only 3 out of 4 blocks could be measured due to instrument failure.

Climate and soil temperature

Air and soil temperatures were continuously monitored in the three thinning treatments (C-00, C-50 and C-80) by six HOBO dataloggers (Onset Computer Corporation, Pocasset, MA, USA) and sensors made out of copperconstantan thermocouples. Two sensors were placed in each treatment. Soil temperature was measured at 10 cm depth and air temperature at 50 cm height and both were stored as 30min averages. Other climatic variables, including global radiation above the forest canopy, air temperature at 2 m height and precipitation at 1.5 m height, were measured continuously and stored as 30-min averages at the central microclimatic station.

Data analysis

The effects of thinning and fertilization different on treatments were analysed using the SAS statistical program (SAS system 9.1, SAS Institute Inc., Cary, NC, USA). Two-way ANOVA and ad-hoc pairwise Fisher's Least Significant Difference tests were used to test for treatment differences. When the average difference in soil CO₂ efflux was analysed, soil



Figure 1. Mean N concentration per g leaf in the youngest fully developed leaves of *Populus trichocarpa* canopy in August 2004 in unfertilized (C) or fertilized (F) treatments with different thinning intensities (0%, 50%, 80%). Each bar represents an average \pm SE of n = 14.

temperature at 10 cm depth was used as a covariate to adjust for any systematic temperature differences between and within treatments. This method makes a linear correction for small temperature differences (< 3 °C) that indeed existed between, for example, thinned and unthinned treatments at each measurement campaign. Regression analysis was used to study the effects of thinning intensity on measured seasonal average air and soil temperatures.

RESULTS

Leaf Area Index

Leaf area index (LAI) was, on average, 3.2 in the unthinned treatments in August 2004 (Table 1). The LAI was significantly reduced by 53% and 85% in the 50% and 80% thinned treatments, respectively (Table 1). No significant fertilization effects were noted on the LAI at the end of the first growing season following spring fertilizer application (Table 1; P=0.49).

Nutrient status and leaf morphology

Nitrogen (N) concentration in leaves ranged from 18.5 to 32.8 mg N per gram leaf between treatments (Figure 1). The spring fertilization led to significantly increased N concentrations in August (P<0.001). Effects of thinning on nutrient status were more subtle and not significant across unfertilized treatments. However, when compared across fertilized treatments thinning had a negative effect on N concentration (P=0.01).

Mean leader shoot leaf size ranged from 8.5 to 19.9 cm² between treatments in the autumn (Table 1). Fertilization significantly increased leaf size (P<0.001) while thinning had a significant negative effect on leaf size (P=0.002). Specific leaf area (SLA) ranged from 74 to 85 cm² g⁻¹, but no statistical difference was noted between fertilization treatments, while thinning significantly decreased the SLA (Table 1; P=0.02).

Growth

Diameter at breast height ranged from 3.4 to 3.8 cm and average tree height ranged from 3.5 to 3.8 m at the end of the first growing season (Table 1). Neither fertilization nor thinning affected diameter or height growth in the first growing season (Table 1).

Climate and soil temperature

Total annual global radiation, mean annual temperature and total annual precipitation in 2004 were 2487 MJ m⁻², 4.9 °C and 991 mm,

Table 1. Mean leaf area index (LAI), mean diameter at breast height (DBH), mean tree height (H), mean top shoot leaf size (leaf size) and mean specific leaf area (SLA) of top shoot leaves in unfertilized (C) or fertilized (F) treatments with different thinning intensities (0%, 50%, 80%) and statistical outcome of a Two-Way ANOVA analysis.

Treament	LAI	DBH (mm)	H (m)	Leaf size (cm²)	SLA (cm ² g ⁻¹)
C-00	3.23±0.50	36.2±3.3	3.8±0.2	11.2±0.4	81.5±1.8
C-50	1.51±0.11	33.9±2.6	3.6±0.1	8.5±0.3	79.8±2.6
C-80	0.48±0.08	33.7±2.0	3.6±0.2	8.7±0.5	80.2±1.3
F-00	2.77±0.71	37.7±2.4	3.8±0.2	19.9±1.2	85.3±2.7
F-50	1.41±0.11	34.7±1.0	3.5±0.1	15.0±1.5	80.6±1.2
F-80	0.46±0.05	35.7±2.8	3.7±0.2	14.9±1.4	74.2±0.9
Effect of fertilization (P-value)	0.49	0.32	0.80	<0.001	0.79
Effect of thinning (P-value)	<0.001	0.27	0.15	0.002	0.02
Interaction (P-value)	0.80	0.94	0.80	0.43	0.06



Figure 2. Daily global radiation above canopy (top panel, W m⁻²), mean daily air temperature at 2 m height (middle panel, °C) and daily precipitation (bottom panel, mm day⁻¹) measured in the *Populus trichocarpa* experimental plantation in 2004.

respectively (Figure 2). Mean monthly temperature ranged from -2.1 °C (December) to 12.1 °C (July). Monthly precipitation ranged from 13.7 mm (October) to 158.2 mm (March), but remained relatively stable throughout the growing season (Figure 2). Air temperature at 50 cm height rose by 7% and 13% in the 50% and 80% thinned treatments, respectively (data not shown). This means that on a warm summer day with a temperature of 18 °C in the unthinned treatments, the air temperature was 19.3 °C and 20.3 °C in the thinned treatments.

Thinning also increased soil temperature over the summer period, but the effects were more subtle than on air temperature (Figure 3). The 50% and 80% thinned treatments had, on average, 1% and 7% higher soil temperatures, respectively, than the unthinned treatments (Figure 3). The soil temperature measured between 9:00-17:00 each day showed a 2.8 °C average daily variation for both the control and 50% thinned treatments during the study period, but the average daily variation rose to 3.3 °C in the 80% thinned treatment (data not shown).

Soil CO, efflux

Soil CO₂ efflux in the treatments generally followed the average soil temperature as it rose from spring until the middle of August and declined thereafter, while the unthinned fertilized treatment had maximum efflux rates in July (Figure 4).

When individual measurements of soil CO₂ efflux were plotted against soil temperature across all treatments (n=429), a clear temperature response appeared (Figure 5). A linear temperature model fitted to the data across all treatments explained 34% of the total variability in the seasonal CO₂ efflux (R_s , mmol CO₂ m⁻² s⁻¹):



$$R_s = 0.344 \times T_s - 0.829 , \quad (1)$$

Figure 3. Soil temperature (°C) at 10 cm depth in different thinning treatments over one year period from establishment. The measurements are averages of n=2.

where T_s is soil temperature in °C. This relationship was

highly significant (ANOVA, P<0.001, R²=0.34). A more commonly used exponential model explained 42% of the total variability:

$$R_{z} = 0.542 \times \exp^{0.145 \times T_{s}}$$
(2)

This relationship was also highly significant (ANOVA, P<0.001, R²=0.42). The variability in CO₂ efflux that could possibly be attributed

to treatment differences at a given soil temperature was therefore 58%. It should be noted that even if the exponential model better fitted the total variation found in the whole dataset, both models performed similarly when looked at across a narrower temperature range (Figure 5; the two lines).

Seasonal average soil CO_2 efflux ranged from 2.04 to 3.18 µmol CO_2 m⁻² s⁻¹ between



Figure 4. Seasonal changes in soil CO₂ efflux rates of *Populus trichocarpa* plots in unfertilized (no fill) or fertilized (grey fill) treatments with unthinned (no pattern), 50% thinned (diagonally hatched) and 80% thinned (crosshatched) along with average soil temperature in all treatments at 10 cm depth (line) during the growing season in 2004 (22 June to 22 September). Each bar represents an average \pm SE of n = 4.

treatments (Figure 6). Statistical analysis (Two-way ANOVA), where respiration rates were first normalized to a given temperature between treatments with a linear covariate



Figure 5. Soil CO₂ efflux rates as a function of soil temperature at 10 cm depth in a *Populus trichocarpa* forest in southern Iceland (n=429). Different symbols indicate unfertilized (open) or fertilized (filled), unthinned (squares), 50% thinned (triangles) and 80% thinned (diamonds) stands. Also shown are two regression lines; exponential and linear response of respiration to changes in soil temperature.



Figure 6. Average soil CO₂ efflux of *Populus trichocarpa* plots at 10.4 °C soil temperature (as estimated by a covariate analysis) in unfertilized (C) or fertilized (F) treatments with different thinning intensities (0%, 50%, 80%) during the growing season in 2004. Each bar represents an average of n = 4.

analysis, revealed that thinning significantly lowered the soil CO_2 efflux rate (P=0.004), when compared across fertilization treatments. The reduction in soil CO₂ efflux with thinning

> intensity was more pronounced in the unfertilized treatment (Figure 6), even if the interaction between thinning and fertilization was not significant.

> Two-Way ANOVA with soil temperature as a covariate also showed that fertilization significantly increased soil CO₂ efflux (P=0.007), when compared across all three thinning treatments (Figure 6). This was a valid observation for all thinning intensities, since the interaction term was not significant. When the thinning treatments were compared individually, the positive fertilization response increased with thinning intensity.

DISCUSSION

Physical factors

The precommercial thinning increased average soil and air temperatures within the stand and increased the daily fluctuations in temperature. Such responses were to be expected as leaf area and shading within the stand decreased (Aussenac 2000, Thibodeau et al. 2000). The increases in soil temperatures followed the thinning intensity during the frost-free (April-September), season while temperature differences were much smaller during autumn and winter. The slightly higher soil temperature in 80% thinned stands during December-April could have been caused either by more insulation from thinning residues or by more snow being accumulated on the ground in the more open stands.

Responses of trees

Leaf N concentration in unfertilized plots (ca. 20 mg N g⁻¹ dry weight in the youngest fully expanded leaf) revealed that the natural N supply was low and N was a limiting factor in tree growth. Sigurdsson (2001) found that N limited tree growth at the site when dry weight leaf N concentration was below 30 mg g⁻¹.

No effects were noted on tree height and diameter growth in the first year of fertilization treatments. This slow growth response is in accordance with previous Icelandic forest management experiments (e.g. Oskarsson & Sigurgeirsson 2001, Sigurdsson 2001), where lag in fertilization response was observed. The only tree growth response in the first year was observed in the mean leaf size, which was significantly increased with fertilization. The average leaf size, however, did not increase as much in F-50 and F-80 compared to F-00. When *Populus* trees grow in an environment where competition for light is high they often respond by growing larger and thinner leaves (Sigurdsson 2001, Curtis et al. 1995). The smaller leaf size observed in thinned fertilized treatments may show that competition for light was considerable in the unthinned plots and thinning was needed.

The negative response of leaf N to thinning intensity in the fertilization treatments was noteworthy, and perhaps indicated more competitive understory N uptake with higher forest floor global radiation when tree LAI decreased. Alternatively it could have been caused by more immobilization of N by previously more temperature-limited soil microorganisms. The latter was observed in a study by Thibodeau et al. (2000).

Soil CO, efflux

In the present analysis a linear temperature function (covariate) was used to remove the effect of different soil temperatures between treatments when their soil CO_2 efflux was compared. When analysing CO_2 efflux data that are measured across a wider temperature range, an exponential temperature function (e.g. Q10 function) would be more appropriate for such temperature correction (Tuomi et al. 2008). This was not so important in the present study, since both linear and exponential relationships were close to each other over most of the temperature range encountered (Figure 5).

Seasonal average soil CO₂ efflux at ca. 10 °C ranged from 2.04 to 3.18 µmol CO₂ m⁻² s⁻¹ between treatments or 323 to 503 mg CO₂ m⁻² hour⁻¹. These CO₂ efflux rates are in the higher range compared to several studies on coniferous forest soils in the boreal zone (Bowden et al. 2004, Tang et al. 2005, Selmants et al. 2008, Sullivan et al. 2008), but still lower than reported for N American aspen (Populus tremuloides Michx.) forests (e.g. Tang et al. 2009). The difference can probably be attributed to Iceland having lower soil temperatures than found in the N American aspen forests. It has, however, to be noted that several older studies from northern broadleaved forests report lower fluxes than the present study (e.g. Toland & Zak 1994), but most of those measurements were done by the sodalime technique. This technique does not yield correct absolute values found by direct IRGA flux measurements and normally underestimates high fluxes (Sigurdsson 2009). Similar or higher fluxes have also been observed in other afforestation areas in Iceland (Bjarnadóttir 2009), fertile natural grasslands (Sigurdsson & Magnusson 2010) and drained pastures (Oskarsson 1998). The CO₂ efflux rates measured in the Icelandic black cottonwood forest seem therefore to represent fluxes in similar ecosystems beyond the local Icelandic context.

The results of the present experiment only partly supported the hypothesis that was being tested. We hypothesized that soil CO_2 efflux would increase with thinning intensity, due to higher soil temperatures and increased litter input. Thinning was, however, found to reduce soil CO_2 efflux significantly during the first summer after treatments, and the reduction

increased with thinning intensity. How can this be explained? Olsson et al. (2005) found that 63% of total soil CO₂ efflux can be attributed to living tree roots in a Norway spruce stand in Sweden and similar results were recently reported by Korhonen et al. (2009) for Scots pine forest in Finland. Högberg et al. (2001) demonstrated that in northern forest ecosystems an unexpectedly large proportion of the soil CO₂ efflux consists of recently fixed CO₂ by canopy photosynthesis that has been translocated belowground and used by roots, mycorrhizae and exudation. The thinning in the present study reduced tree density by approximately 50% and 80%, leading to similar relative reductions in LAI. This should have reduced photosynthesis per area and the amount of respiring roots per area in similar proportions. Therefore we believe the negative effect of thinning on the soil CO₂ efflux in the present study to be the result of a reduction in the autotrophic root respiration and this effect was greater than the likely increase in heterotrophic respiration and understory respiration. That the reduction of soil CO, efflux increased with thinning intensity in the present study strongly supports this hypothesis.

An alternative explanation for reduced soil CO₂ efflux following thinning could be that ground water level rose in the thinned stands because of lower evapotranspiration, thereby decreasing the aerated soil volume contributing to the CO₂ efflux. Such a rise in ground water level will normally lead to increased runoff (Sørensen et al. 2009), and this frequently occurs when forests on poorly drained wetland soils are harvested. The thinned plots were small (0.06 ha) in the present study, which makes such a thinning-level dependent change in ground water level unlikely to occur. Furthermore, no peat layer was found in the site's soil profiles, which indicated that ground water was not close to the surface prior to afforestation, which further decreases the likelihood that it would occur at the present time. The present study therefore probably gives an example of strong autotrophic control of soil CO₂ efflux for northern deciduous forest; this result should be compared to the fact that most other studies that have shown similar results have been done in coniferous stands (Högberg et al. 2001, Olsson et al. 2005, Tang et al. 2005, Korhonen et al. 2009).

Our initial hypothesis that fertilization would increase soil CO₂ efflux was supported by our findings. A meta-analysis by Knorr et al. (2005a) indicates that fertilization initially stimulates litter decomposition at sites with low ambient N deposition (<5 kg ha⁻¹ y⁻¹) and for high quality (low-lignin) litters, whereas decomposition rates are generally reduced at sites with moderate levels of N deposition (5-10 kg ha⁻¹ y⁻¹). The rate of N decomposition in Iceland is low, or generally <1.5 kg N ha⁻¹ y⁻¹ (Gíslason et al. 1996). Litter decomposition only contributes to the heterotrophic soil respiration, while our soil CO₂ efflux values included both heterotrophic and autotrophic respiration fluxes. Our results are, however, also in accordance with previous findings on the initial fertilization response of soil CO₂ efflux at higher latitudes where the N supply is a limiting factor in forest ecosystems (Hyvönen et al. 2007). It should, however, be stated that some recent studies have shown that long-term fertilization in northern forests may decrease the rate of decomposition and soil CO₂ efflux (e.g. Bowden et al. 2004, Hyvönen et al. 2007).

Temperature and moisture have been found to play an important role in seasonal patterns of soil CO_2 efflux (Ma et al. 2005). As was previously mentioned, the soil water potential has been found to be permanently close to field capacity at the present site (Strachan et al. 1998), and water availability was therefore not considered a limiting factor in tree growth or ecosystem processes. Therefore, temperature is likely the key determinant of seasonality in soil CO_2 efflux at the site, as was indeed indicated by the fact that exponential temperature function explained 42% of the seasonal variation across all thinning and fertilization treatments.

The present study only reports the shortterm responses of soil respiration, while both thinning and fertilization management will also have long-term implications on soil respiration and other processes. The fertilization treatments have been continued annually at the sites and it is planned to repeat the study ca. ten years after the thinning. The long-term responses to both fertilization and thinning may be expected to differ in some aspects, as has been explained earlier.

CONCLUSIONS

It was expected that precommercial thinning and fertilization would have an immediate additive effect on soil CO₂ efflux due to higher soil temperatures and increased litter input. The data showed that in the first treatment year fertilization indeed increased soil CO₂ efflux, but thinning intensity decreased it. This occurred even though soil temperatures rose with thinning and all organic material was left on site, both of which were expected to increase the heterotrophic respiration. This response was interpreted as a signal from decreased autotrophic root respiration in the thinned stands, which was then relatively stronger than the expected effect on the heterotrophic respiration, a response not always well represented in simulation models of the carbon cycle in managed forests. Hence, these results may be important when the effects of early forest management on carbon fluxes are modelled.

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