Chapter 3

Short-term effects of clearfelling on soil CO_2 effluxes

3. 1 Introduction

An important component of ecosystem C exchange with the atmosphere is soil CO_2 efflux, which is commonly referred to as soil respiration. The net change in terrestrial carbon or the net efflux of carbon between land and the atmosphere depends on the rates at which carbon is lost to the atmosphere from decomposition of dead plant material and from oxidation of soil organic matter and the rates at which carbon is removed from the atmosphere through growth of live vegetation and accumulation of organic matter (Houghton *et al*., 1987) in both standing biomass and the soil.

The total soil CO_2 efflux is a combination of biotic, chemical and physical processes. The two main sources of soil respiration are the heterotrophic (decomposition of organic compounds by soil microorganisms) and the autotrophic (respiration of plant roots and rhizomes) respiration where carbon sequestered by photosynthesis returns to the atmosphere, both resulting from different soil depths (Buchmann, 2000). Soil respiration may also derive from abiotic reactions among carbonate species (Rochette *et al*., 1997). The literature reviewing the processes involved in soil respiration and its main biophysical controlling factors has been presented in Chapter 1 and will not be repeated here.

Instead, an analysis of the ecological effects of clearfelling will be presented here, particularly with regard to its effects on soil CO_2 efflux. Forest clearfelling is one of the management practices used most frequently for the harvesting of timber. It can have a significant effect on soil CO_2 efflux by altering the biogeochemical cycles of a forest ecosystem. The ecological impacts of clearfelling were summarised by Keenan and Kimmins (1993). They argued that while generally the impacts are minor and short lived, clearfelling might also cause severe long-term effects in some instances. The effects of clearfelling on the forest ecosystem depend on site conditions such climate, geology and topography, on the structure and composition of the forest, the method used for tree harvesting and the length of the rotation. Clearfelling alters the microclimate at the forest floor, resulting in higher soil surface temperatures during the day and lower ones during the night. It also causes an increase in soil water content and a rise of the water table due to reduced evapotranspiration rates and an increased amounts of precipitation reaching the ground because of the absence of trees. These changes of the soil temperature and water balance are generally short-lived and re-establishment of vegetation lowers the water table and prevents extreme changes in soil temperature (Keenan and Kimmins, 1993).

The removal of a large proportion of the total biomass by clearfelling can lead to a loss of nutrients (Smethurst and Nambiar, 1990) because of higher rates of decomposition of the forest floor, nitrification and leaching. The mechanical disturbance from machines used for tree harvesting and site preparation causes changes in the physical properties of the soil. Compaction of the soil by heavy equipment decreases the soil macroporosity and causes a reduction in air diffusion and water infiltration rates (Pritchett, 1979), thus increasing the soil water content and consequently causing the soil environment to become more anaerobic.

Tree harvesting results in large amounts of residues, litter and dying tree roots, which are easily decomposed. Rates of decomposition may be increased because of the warmer and wetter conditions in the forest floor and mineral soil, which could accelerate microbial activity (Binkley, 1986; Hendrickson *et al.*, 1989). Some evidence also shows that litterfall from re-established vegetation, following the first few years after clearfelling, is more easily decomposed and thus, decomposition of surface litter exceeds litter input (Covington, 1981).

There are a number of studies comparing soil CO_2 efflux under different forest management practices including clearfelling. These studies have been reviewed in Chapter 1 and will not be repeated here. Suffice to say that it is difficult to decide on a pattern of soil CO_2 efflux, following clearfelling of a forest. The magnitude of change in soil CO_2 efflux depends on whether or not litter and organic layers are removed, roots are disturbed and mineral soil horizons are exposed or mixed (Buchmann, 2000), the rates of C input to soil from the logging residues and the response of soil microbial biomass to microclimatic conditions created after the removal of trees. All these responses may differ among ecosystems. Also the different types of harvesting machines used in each occasion cause different degrees of disturbance to the soil. Tractors, used in earlier times, cause more disturbance to the soil compared to rubber-tyred skidders (Yanai *et al*., 2000). Hence, the response of soil CO_2 efflux to clearfelling may vary among different locations.

Despite this large site-to-site variability in the ecosystem responses to clearfelling, measurements of soil respiration remain invaluable to understand the main interactions and processes occurring at any one site. This is particularly true if these measurements are coupled, as was the case at Harwood thanks to the CARBO-AGE project, to measurements of whole ecosystem respiration from eddy covariance. An additional point of interest is represented by the fact that short-term measurements of soil carbon losses after clearfelling can help understand some of the patterns emerged by the study of the long-term changes in soil C stocks using a chronosequence approach.

The specific objectives of this study were:

a) To determine the soil CO_2 effluxes immediately following forest clearfelling.
b) To measure the environmental factors (soil temperature, moisture and water table depth) affecting the emissions of soil CO_2.
c) To examine possible relationships of the soil CO_2 efflux with soil temperature, moisture and water table depth.

3. 2 Materials and Methods

3.2.1 Site description

A full site description of the site is provided in Chapter 1.

Two mature stands, both 40 years old (in 2001), of Sitka spruce on peaty gley soil were chosen. In each stand and a 30 × 30 m plot was established. Measurements took place from June 2001 till December 2002. One of the stands was kept intact throughout the study period, as the control (from now on 40-yr) whereas the other was clearfelled in February 2002 (CF_{before} and CF, before and after clearfelling, respectively, from now on). The stands were about 1000 m apart. The most important features of the two stands are given in Table 1. There was no understorey vegetation in either of the two stands at the start of the project.

Table 1: Characteristics of the CF_{before}, 40-yr and CF sites. Numbers in brackets indicate the standard error of the mean.

	CF_{before}	40-yr	CF
Area (ha)	28	19	28
Trees ha^{-1}	1600	1600	0
Average tree height (m)	18.6 (1.3)	17.5 (1.2)	n.a.*
Average soil pH	3.5 (0.02)	3.3 (0.02)	4.9 (0.05)
Soil C stocks (t C ha^{-1})	101.4 (7.2)	120.5 (15.4)	n.d.**

* not applicable, **not determined

In January 2002, just prior to clearfelling, a strong windstorm blew down many of the trees within the CF_{before}. Then the remained were felled with mechanised harvesters. These machines have a mechanically operated harvesting head that fells a tree, de-limbs it, and transfers the logs to a special extended rear frame. The machine then carries them out of the forest. After felling a tree, the harvester places all the limbs directly in front of it, so when the machine moves forward, it rides on these limbs, helping to reduce soil compaction. Based on visual observations, clearfelling at our sites created a surface layer of mixed organic material, logging slash, twigs and roots. Prior to replanting, additional operations are carried out. They consist of the re-digging of the original ditches to improve drainage and on the mounding of the soil to create suitable microsites for planting. This results in the formation of mounds and of pools of almost stagnant water after heavy rainfall events.

3.2.2 Soil CO_2 efflux measurements

Soil CO_2 efflux was measured *in situ* using two methods, a closed dynamic chamber (EGM-3, SCR-1, PP-Systems, Hitchin, UK) and a closed static chamber method (from now on referred as CC) (Smith *et al*., 1995). Measurements of soil CO_2 efflux were made with no attempt to distinguish between the two main kinds of respiration (heterotrophic and autotrophic). Measurements were taken from 23 June 2001 through to 18 December 2002, weekly or biweekly during the summer and biweekly or once a month during winter.

All measurements were taken between 9.30 and 14.30 to minimise changes in soil CO_2 effluxes associated with diurnal cycles (Davidson *et al*., 1998). However in a comparison study, where diurnal cycles of measurements were taken at the same forest in a 30-year old stand and another clearfelled site, no significant differences were found in soil CO_2 efflux throughout the day (T. Ball, unpublished data).

3.2.2.1 Soil CO_2 measurements with a closed dynamic system

In both mature stands (CF_{before} and 40-yr) ten collars were randomly positioned in the 30 × 30 m plots. The collars were permanently inserted in the soil to about 3 cm depth and the exact height above ground was recorded for correcting the values of soil CO_2 efflux. A visual examination showed that no fine roots were cut. The CO_2 efflux measurements were taken with a portable, dynamic closed chamber system (from now on referred as DC) (EGM-3 with SCR-1, PP-Systems, Hitchin, UK), equipped with a portable infra-red gas analyser (IRGA) with a chamber slightly modified to fit the soil collar with a gas-tight seal. A small, low-speed fan ensured mixing of the air within the chamber during the measurements and a metal mesh was fit in the bottom of the chamber in order to minimise pressure effects at the soil surface. Pressure measurements with a precision micro-manometer in the laboratory across the chamber base showed very small pressure differentials of ± 0.1 Pa.

The chamber was placed on the collar for two minutes and measurements of CO_2 concentration were taken every 8 s. Soil CO_2 efflux was calculated by the software provided by the PP-Systems. Later the values were corrected in order to account for the efflux in the volume of the collar above the ground with the equation:

$$F_S = F \times \frac{V_c}{V_{Ch}} + F \qquad (1)$$

where: F_S is the corrected soil CO_2 efflux, F is the soil CO_2 efflux measured from the PP-Systems, V_c (cm^3) is the volume of the collar above the soil, and V_{Ch} is the volume (cm^3) of the PP-Systems chamber.

After clearfelling, 13 collars were randomly inserted on the ground and left there till the end of the study. However, we could not determine the exact position of the previous collars, although the exact location of the plot was determined.

3.2.2.2 Soil CO_2 measurements with closed static chambers

The closed static chamber (SC) technique (Smith *et al*., 1995) was also used for the determination of soil CO_2 efflux. Twelve chambers, each consisting of a PVC cylinder, inside diameter 40 cm and height 20 cm open at the top and the bottom, were inserted into the soil to a depth of about 5 cm to make a gas-tight seal. A removable aluminium sheet, with a rubber seal and sampling port fitted with a three-way stopcock, acted as a lid at the top of the chamber. The chambers were left permanently in the field in order to minimise the effects of disturbance caused by their insertion in the soil.

At each site the 12 chambers were inserted in a stratified design (four chambers in each of three strata: plain, ridge and furrow) at both mature stands. After clearfelling of the CF_{before} stand, the chambers were placed as closely as possible to their old positions.

After having kept the chambers sealed with a lid for an hour, air samples from inside the chambers were taken with 60 ml syringes. External air samples were also taken, close to the chamber, at the same time in order to determine the ambient CO_2 concentration in the field. Also, the linearity of CO_2 concentration increase over time was occasionally checked (see Chapter 6). The samples were transferred to the laboratory and analysed with a gas chromatograph (Perkin Elmer, instrument fitted with a thermal conductivity detector) within 24 hours of their collection.

In the static closed chamber, the concentration of gas starts to increase with closure of the chamber. The exchange rate of a trace gas across the soil-atmosphere boundary is largely a function of its diffusion coefficient and the concentration gradient between sites of production (or consumption) and the soil surface (Hutchinson and Livingston, 1993):

$$F_s = d \times \frac{V}{A} \times \frac{(C_t - C_0)}{t} \tag{2}$$

where: F_s is the CO_2 efflux (g m^{-2} d^{-1}), d (g m^{-3}) is the gas density calculated on the assumption that 1 mole of gas (1 mole of CO_2 is 44 g) occupies 22.4 x 10^{-3} m^3 of volume at 273 K, V is the volume of the chamber (m^3), C_t is the concentration of the gas (µmol mol^{-1}) chamber after closure time t (d), C_0 is the initial concentration of the gas (µmol mol^{-1}), A is the area of the chamber (m^2) and t is the time of chamber closure.

3.3.3 Measurement of environmental parameters

Soil temperature was measured with a digital temperature probe (Fisher Scientific) adjacent to each collar and chamber, at depths of 1, 5 and 10 cm (from now on T_1, T_5, and T_{10}, respectively) every time a measurement of soil CO_2 efflux was taken. Continuous soil temperature measurements were also taken at 5 cm depth with a data logger (Campbell Scientific Inc.) at the clearfelled site. A datalogger was not available at the 40 yr stand, but another mature stand in the same forest (30 years old) was monitored as part of the CARBO-AGE project. Although the age was different, both stands had a closed canopy and similar LAI and those data were used for comparison with the data from the clearfelled site. Air temperature was also measured at about 1. 5 m height.

Volumetric soil water content (cm^3 water cm^{-3} soil) was measured with a Theta probe (TK1- Basic, Delta-T Devices LTD, Cambridge, UK) at 5 cm depth, next to each collar and chamber. In order to minimise disturbance of the soil from frequent insertion of the probe, an effort was made to place the theta probe in the same position each time.

Water table depth (cm from the soil surface) was also measured in six wells at both sites. The wells were randomly dug with a soil auger in both sites and plastic tubes of 5 cm diameter with small apertures (~ 0.5 cm diameter) along the tube, were inserted to a depth of about one metre.

3.3.4 Statistical analysis

3.3.4.1 Treatment comparisons

Monthly differences in soil CO_2 efflux and environmental factors between the two sites, before and after clearfelling, were analysed by repeated-measures ANOVA in SAS (SAS Institute, 1999), using the individual measurements as replicates.
For all other statistical analyses the average value of each measurement day was used. The significance level of all analyses was set at 0.05.

3.3.4.2 Comparison of a closed dynamic chamber versus a closed static chamber system

To assess the statistical significance of the differences between the two methods used (DC and SC), a two samples t-test was used with the individual measurements of both methods as replicates. The analysis was performed in SAS.

3.3.4.3 Modelling the effects of soil temperature and soil water content on soil CO_2 efflux

The soil temperature and soil water content were used as independent or combined predictors of soil CO_2 efflux. In order to describe the dependence of soil CO_2 efflux on soil temperature, the following exponential function was used:

$$R = R_0 e^{bT} \qquad (3)$$

where: R is the measured soil CO_2 efflux (g m^{-2} d^{-1}), R_0 is the basal CO_2 efflux at a temperature of 0 °C, T is the soil temperature at 1, 5 or 10 cm depth (°C) and b is the temperature coefficient, which is related to the Q_{10} as follows:

$$Q_{10} = e^{10b} \qquad (4)$$

For the description of the relationship between soil CO_2 efflux and soil water content alone, an empirical function with the best fit to the data was applied each time.

In order to account for both temperature and water content effects on soil CO_2 efflux two models were used: a Multiple Linear Regression (M.L.R.) model (Gordon *et al*., 1987; Raich and Schlesinger, 1992; Rey *et al*., 2002) and a non linear model where soil CO_2 efflux was described as being multiplicatively dependent on soil temperature and soil water content, adapted from Reichstein *et al*. (2002):

$$R = R_{ref} \cdot f(T_{soil})\, g(W) \qquad (5)$$

Where: R_{ref} is the soil CO_2 efflux at 10 ºC and $f(T_{soil})$ is the function of Lloyd and Taylor (1994), which provides better estimates at low temperatures than the first order exponential function:

$$f(T_{soil}) = e^{E_0\left(\frac{1}{T_{ref}-T_0}-\frac{1}{T_{soil}-T_0}\right)} \quad (6)$$

where T_{ref} and T_0 are fixed at 10 and –46 °C, respectively. E_0 was considered to be a free parameter and was fitted to each data set.

The water content function used was the commonly applied saturation function:

$$g(W) = \frac{W}{W_{1/2} + W} \quad (7)$$

Where: $W_{1/2}$ is the soil water content (expressed as cm^3 of water per cm^3 total soil volume) at which half maximal respiration occurs (Bunell *et al*. 1977; Hanson *et al*., 1993).

Multiple linear regression modelling was performed in SAS, while the nonlinear model was performed in SPSS.

3.4 Results

3.4.1 General comparison of the two mature stands before clearfelling

The monthly averages for soil CO_2 efflux and environmental factors in the two mature stands (CF_{before} and 40-yr) are shown in Table 2. Soil CO_2 efflux in the two mature stands in the second half of 2001 varied between 1.09 g m^{-2} d^{-1} in February 2002 at the 40-yr stand and 11.57 g m^{-2} d^{-1} in July 2001 again at the 40-yr stand. The highest values were reached in the summer months (June to August 2001) and the lowest values in the subsequent winter months (December 2001 to February 2002). While the month–to-month variability was found to be highly significant ($P<0.0001$, Table 3), no significant differences were found between the two sites ($P=0.7$). Similar results were obtained when data were not grouped by month and individual weeks were analysed separately ($P>0.05$).

Similar seasonal trends were observed for daytime soil temperatures measured at 1 and 5 cm depth, whereas the data measured at 10 cm depth were only compared for the period after December 2001 and prevented an analysis of seasonal variability. As expected, temperatures at the soil surface (T_1) varied more than deeper in the soil (T_5 and T_{10}), with higher values in the summer and lower values in the winter. Again significant differences were found among months ($P<0.001$, Table 3), but not between sites ($P>0.05$), although when the weekly temperature data were compared a significant difference ($P<0.0001$) also appeared between the two sites. The most likely explanation for this discrepancy is the sampling of stands during some unusually warm/cold weather during the summer/winter of 2002.

Table 2: Monthly values of soil CO_2 flux and soil environmental variables (temperature, water content and water table depth) for the CF_{before} and 40-yr stands. Each monthly value is the average of two and four weekly campaigns. T_1, T_5 and T_{10} are soil temperatures (°C) measured at 1, 5 and 10 cm depth, W is the water content (cm^3 water in cm^3 soil). Measurements of soil CO_2 flux were obtained with the DC method.

	CF_{before}						40-yr (control)					
Month	**CO_2 ($g\ m^{-2}\ d^{-1}$)**	**T_1 (°C)**	**T_5 (°C)**	**T_{10} (°C)**	**W ($cm^3\ cm^{-3}$)**	**Water table depth (cm)**	**CO_2 ($g\ m^{-2}\ d^{-1}$)**	**T_1 (°C)**	**T_5 (°C)**	**T_{10} (°C)**	**W ($cm^3\ cm^{-3}$)**	**Water table depth (cm)**
June 01	9.54 (0.43)	12.1 (0.17)	10.3 (0.11)	n. m.	0.379 (0.01)	n. m.	n. m.	n. m.	n. m.	n. m.	n. m.	n. m.
July 01	10.79 (0.5)	13.7 (0.14)	12.6 (0.11)	n. m.	0.289 (0.01)	n. m.	11.57 (0.84)	11.6 (0.06)	11.2 (0.06)	n. m.	0.246 (0.02)	n. m.
August 01	9.57 (0.55)	13.1 (0.07)	12.1 (0.05)	n. m.	0.315 (0.01)	n. m.	7.37 (0.56)	12.0 (0.05)	11.9 (0.07)	n. m.	0.399 (0.01)	n. m.
September 01	6.59 (0.39)	11 (0.15)	10.5 (0.10)	n. m.	0.379 (0.01)	-44.3 (3.90)	7.51 (0.61)	11.3 (0.06)	10.9 (0.08)	n. m	0.223 (0.02)	n. m.
November 01	4.13 (0.27)	8.3 (0.05)	8.5 (0.04)	n. m.	0.284 (0.04)	-29.5 (4.20)	4.63 (0.30)	8.0 (0.02)	8.2 (0.05)	8.4 (0.05)	0.193 (0.02)	-64.5 (2.8)
December 01	1.69 (0.29)	3.3 (0.39)	3.9 (0.31)	4.2 (0.28)	0.246 (0.04)	-17.5 (3.30)	2.02 (0.28)	3.3 (0.47)	4.2 (0.36)	4.9 (0.27)	0.208 (0.02)	-35.5 (2.3)
January 02	1.63 (0.21)	4.5 (0.09)	4.6 (0.07)	4.6 (0.08)	0.324 (0.02)	-21.90 (1.80)	2.27 (0.26)	4.6 (0.06)	4.9 (0.07)	5.1 (0.10)	0.260 (0.01)	-60 (3.5)
February 02	n. m.	n. m.	n. m.	n. m.	n. m.	n. m.	1.09 (0.25)	3.9 (0.16)	4.6 (0.11)	5.2 (0.07)	0.365 (0.02)	-45.3 (3.80)

Table 3: Results from repeated-measures ANOVA for soil CO_2 efflux and environmental parameters (soil temperature, soil water content and water table depth). Repeated-measures ANOVA tested the significance of the differences across different sampling intervals (months and weeks nested within months) and across the two study sites. It also tested the interaction between sampling interval and site.

Statistical differences, before clearfelling (P-values)						
	Soil CO_2 flux ($g\ m^{-2}\ d^{-1}$)	**T_1 (°C)**	**T_5 (°C)**	**T_{10} (°C)**	**W ($cm^3\ cm^{-3}$)**	**Water table depth (cm)**
Month	< 0.0001	< 0.001	< 0.001	n. a.	< 0.0001	< 0.0001
Site	0.7	0.3	0.06	n. a.	< 0.0001	< 0.0001
Week	0.2	< 0.0001	< 0.0001	n. a.	< 0.0001	< 0.0001
Site*Month	0.1	<0.0001	<0.0001	n. a.	<0.0001	<0.0001

Soil water content also varied from month to month ($P<0.0001$), with maximum values in the period November-December 2001. Significant differences were found between sites, with the CF_{before} stand having a generally higher soil water content than the 40-yr stand. The water content in the CF_{before} stand varied between 0.236 and 0.442 cm cm^{-3}, while in the 40-yr stand varied between 0.193 and 0.399 cm cm^{-3} (11 to 22% difference, based on weekly measurements data). The same trend was found also for the depth of the water table, which also exhibited month-to-month variability ($P<0.0001$) and significant differences between the two stands ($P<0.0001$), with the water table being at greater depths in the 40-yr stand (35.5 and 64.5 cm depth) than in the CF_{before} stand (range 17 to 44 cm depth).

3.4.2 Comparison of a closed dynamic versus a closed static system

The closed dynamic system (DC, PP-System) generally gave higher values than the closed static chamber system SC. Figure 1 shows soil CO_2 efflux measured by both methods for the 40-yr stand. The discrepancy between the two methods, in all sites, ranged between 0.3 and 6.8 (ratio DC/SC), with the two methods not being significantly different when the DC measured effluxes between 0.5 and 3.4 g m^{-2} d^{-1} (P=0.09, ratios from 0.3 to 1.2). The two methods were significantly different when effluxes measured with the DC method were larger than 4 g m^{-2} d^{-2} (P< 0.0001, ratios from 1.3 to 6.8). Further investigations were conducted to evaluate the causes of this discrepancy (see Chapter 6 for more details). Further analyses pointed to a likely underestimation of the soil CO_2 efflux by the closed static method. All subsequent analyses of the effects of clearfelling on soil CO_2 efflux are presented by using data obtained with the closed dynamic method, unless otherwise stated.

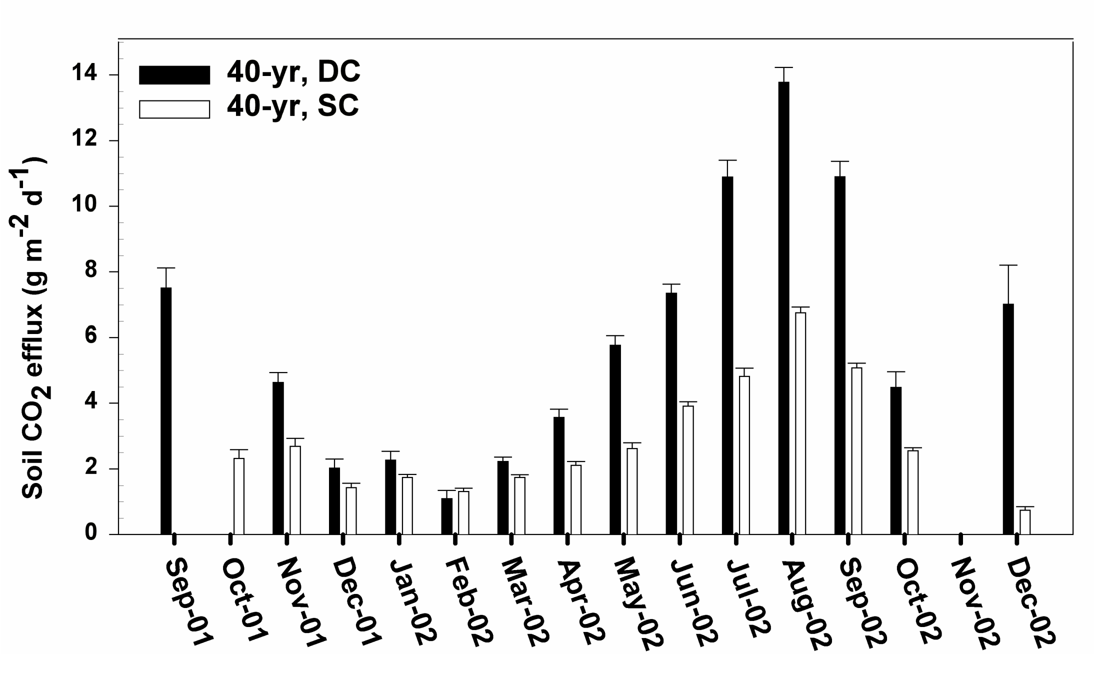

Figure 1: Monthly averages of soil CO_2 efflux measured with the closed dynamic (DC) and the closed static method (SC), for the 40-yr stand. The two methods were statistically different when the DC was measuring soil CO_2 efflux larger than 4 g m^{-2} d^{-1} (P<0.0001). The vertical bars indicate the standard error of the mean.

3.4.3 Effects of clearfelling on soil temperature, water content and water table depth

Monthly averages of soil temperature are shown in Table 4. Clearfelling caused a significant increase in soil temperatures at all depths (at least P<0.001, Table 5).

Table 5: Results from repeated-measures ANOVA for soil CO_2 efflux and environmental parameters (soil temperature, soil water content and water table depth). Repeated-measures ANOVA tested the significance of the differences across different sampling intervals (months and weeks nested within months) and across the two study sites. It also tested the interaction between sampling interval and site.

Statistical differences, after clearfelling (P-values)						
	Soil CO_2 flux ($g\ m^{-2}\ d^{-1}$)	**T_1 (°C)**	**T_5 (°C)**	**T_{10} (°C)**	**W ($cm^3\ cm^{-3}$)**	**Water table depth (cm)**
Month	< 0.001	< 0.001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Site	< 0.001	0.008	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Week	0.8	<0.0001	<0.0001	<0.0001	< 0.0001	< 0.0001
Site*Month	< 0.001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

On a weekly basis, soil temperature and air temperature in the CF were always higher than in the 40-yr stand (Figures 2 and 3). With the only exception of a spell of cold weather in October 2002, higher fluctuations of soil temperature at 5 cm depth were observed in the CF than in the closed canopy stand of the 30-yr (Figure 4).

Soil temperature followed the pattern of air temperature at both sites, particularly at the surface (Figure 2). Clearfelling increased soil temperature during daytime, in comparison with the control stand (P<0.0001). The temperature at the soil surface (1 cm depth) averaged 4.8 ºC higher in the clearfelled site than the mature stand (the increase varied from 2.1 to 7.6 °C higher than the values of the 40-yr stand) throughout the growing season. The temperature at 5 cm depth averaged about 3.6 ºC higher (the increase varied from 2.0 to 6.0 °C higher than the values of the 40-yr stand) and the one at the 10 cm depth averaged 2.8 ºC higher (the increase varied from 2.0 to 4.8 ºC higher than the values of the 40-yr stand). Clearly, clearfelling also increased the vertical gradients in soil temperature, particularly during the summer months (Figure 3) due to absence of a canopy allowing solar radiation to warm directly the surface of the exposed soil. Clearfelling also increased daily amplitude of the temperature fluctuations at each depth (Figure 4), particularly during the warmer months of August and September. During October however, when temperatures started to drop (Figures 2 and 3), the differences in daily amplitude between sites were reduced.

Table 4: Monthly values of soil CO_2 flux and soil environmental variables (temperature, water content and water table depth) for the CF and 40-yr stands. Each monthly value is the average of two and four weekly campaigns. T_1, T_5 and T_{10} are soil temperatures (°C) measured at 1, 5 and 10 cm depth, W is the water content (cm^3 water in cm^3 soil) . Measurements of soil CO_2 flux were obtained with the DC approach.

Month	CF						40-yr (control)					
	CO_2 (g m^{-2} d^{-1})	T_1 (°C)	T_5 (°C)	T_{10} (°C)	W (cm^3 cm^{-3})	Water table depth (cm)	CO_2 (g m^{-2} d^{-1})	T_1 (°C)	T_5 (°C)	T_{10} (°C)	W (cm^3 cm^{-3})	Water table depth (cm)
March 02	2.92 (0.49)	9.3 (0.42)	8.2 (0.36)	7.2 (0.29)	0.411 (0.02)	-17.5 (4.50)	2.22 (0.14)	5.0 (0.16)	5.0 (0.13)	5.1 (0.10)	0.347 (0.01)	-42.0 (3.8)
April 02	5.29 (0.67)	12.5 (0.35)	9.5 (0.28)	8.1 (0.24)	0.351 (0.02)	-25 (3.90)	3.57 (0.25)	6.5 (0.31)	6.3 (0.23)	6.3 (0.17)	0.160 (0.02)	-84.60 (1.80)
May 02	4.85 (0.67)	14.6 (0.39)	13.1 (0.30)	11.5 (0.24)	0.386 (0.02)	-17.20 (1.2)	5.77 (0.29)	9.2 (0.26)	8.7 (0.17)	8.4 (0.11)	0.179 (0.02)	-90
June 02	4.26 (0.66)	14.9 (0.37)	13.7 (0.29)	12.8 (0.24)	0.371 (0.02)	-14.10 (3.70)	7.35 (0.28)	9.9 (0.08)	9.6 (0.08)	9.4 (0.08)	0.257 (0.02)	-49.5 (3.9)
July 02	7.52 (1.40)	15.5 (0.46)	13.9 (0.36)	13.1 (0.36)	0.350 (0.02)	-16.40 (3.30)	10.89 (0.51)	10.2 (0.17)	9.9 (0.13)	9.6 (0.14)	0.185 (0.02)	-66.3
August 02	7.66 (0.77)	17.7 (0.48)	16.0 (0.34)	14.9 (0.23)	0.363 (0.02)	-15.30 (2.5)	13.78 (0.45)	13.1 (0.09)	12.7 (0.09)	12.2 (0.11)	0.230 (0.02)	-55.5 (4.20)
September 02	6.12 (0.56)	15.7 (0.38)	14.2 (0.22)	13.4 (0.18)	0.337 (0.02)	-19.90 (3.60)	10.90 (0.47)	11.9 (0.19)	11.4 (0.15)	11.2 (0.14)	0.159 (0.02)	-60.5 (8.3)
October 02	3.41 (1.37)	7.7 (0.18)	7.1 (0.14)	7.0 (0.16)	0.414 (0.01)	-9.5 (3.60)	4.48 (0.48)	6.1 (0.04)	6.5 (0.05)	6.7 (0.11)	0.263 (0.03)	-46.25 (4.69)
December 02	2.41 (1.09)	0.9 (0.36)	1.8 (0.31)	2.6 (0.19)	0.468 (0.01)	-10.60 (3.14)	5.60 (1.35)	0.8 (0.23)	2.8 (0.10)	3.6 (0.21)	0.311 (0.05)	-46.75 (7.15)

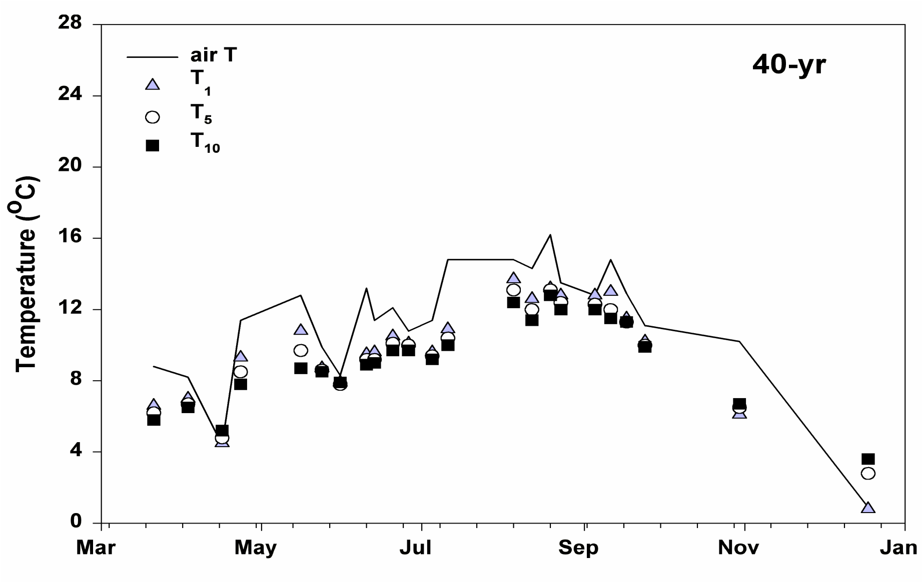

Figure 2: Air and soil temperatures (°C) for the period March to December 2002, in the 40-yr stand (during daytime). The points refer to the weekly soil T measurements, while the line to weekly air temperature.

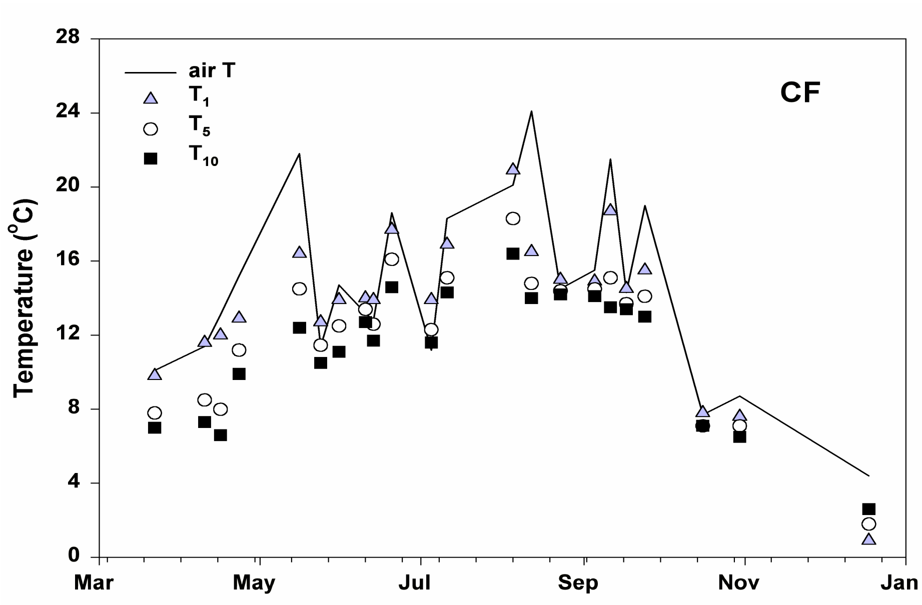

Figure 3: Air and soil temperatures at 1 cm (T_1), 5 cm (T_5) and 10 cm (T_{10}) depth in the clearfelled site (CF) for the period March to December 2002 (during daytime). The points refer to the weekly soil T measurements, while the line to weekly air temperature.

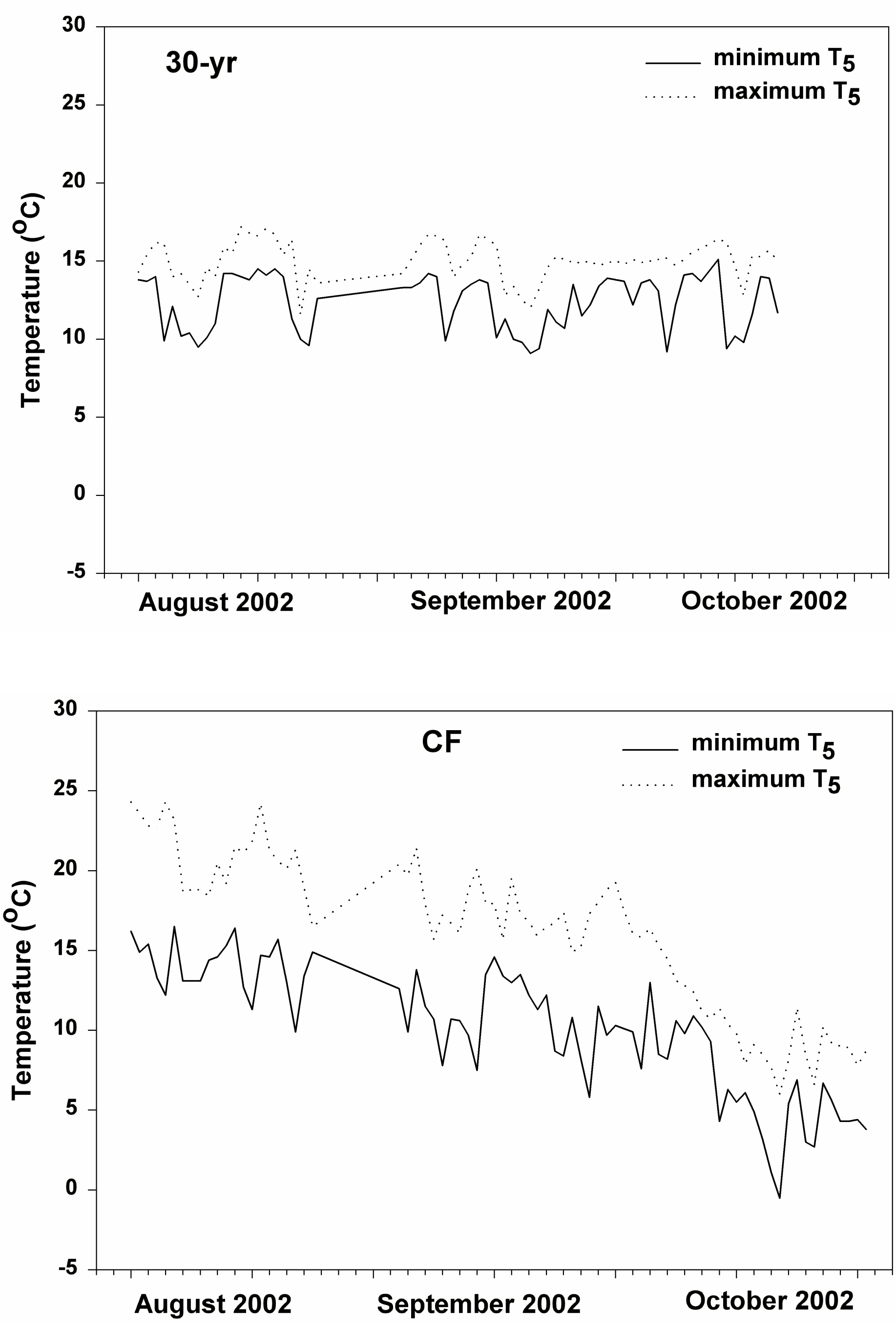

Figure 4: Minimum and maximum daily soil temperatures at 5 cm depth in the CF site and a 30-yr stand. Temperatures were recorded every 15 minutes with a datalogger, from 5 August to 29 October 2002. The fluctuations in soil temperature in the CF site were larger compared to the 30-yr stand, with the exception of a period of cold weather in October.

Soil water content in the CF site was still significantly higher than in the 40-yr stand ($P<0.0001$). Soil water content during March to December 2002, varied between 0.308 and 0.468 $cm^3\ cm^{-3}$ at the clearfelled site compared to a range between 0.114 and 0.310 $cm^3\ cm^{-3}$ at the 40-yr stand (15 to 253% difference) (Figure 5).

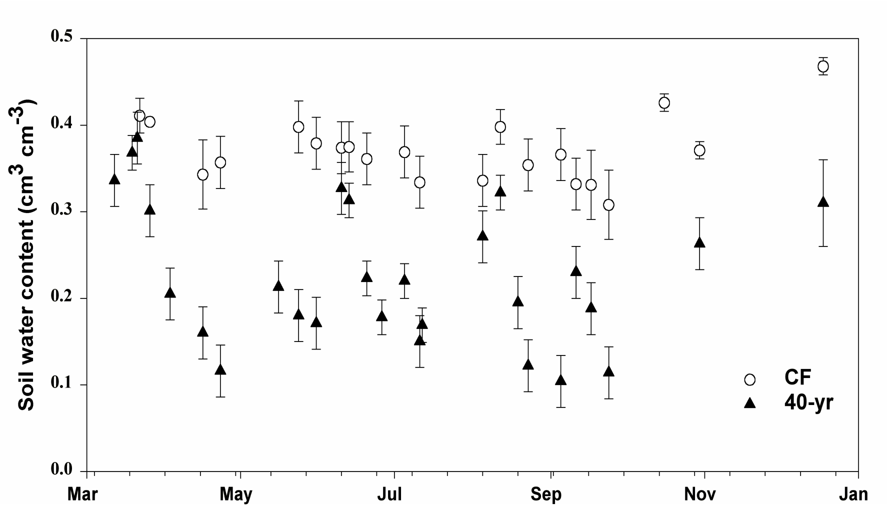

Figure 5: Weekly averages of soil water content in the CF and the 40-yr stand. The vertical bars indicate the standard error of the mean.

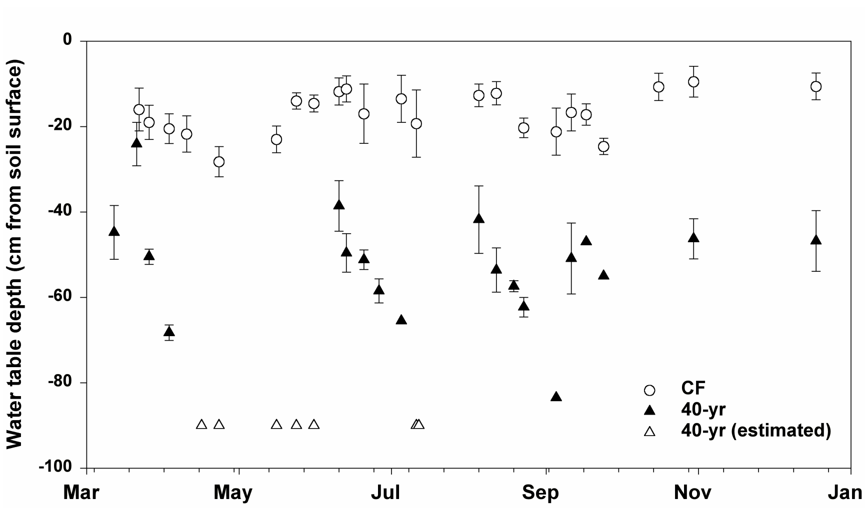

Figure 6: Weekly averages of water table depth (cm) in the CF and the 40-yr stand. The white triangle symbol indicates an assumed water table depth in the 40-yr stand, when the water table level dropped below the well depth. The vertical bars indicate the standard error of the mean.

Water table depth at the CF site was significantly higher than in the 40-yr stand ($P<0.0001$). The water table depth at the CF site varied between 10.7 and 24.7 cm from the soil surface, while in the 40-yr stand it varied from 24.1 to below 90 cm depth for the period March to December 2002 (Figure 6).

3.4.4 Effects of clearfelling on soil CO_2 efflux

Soil CO_2 efflux showed a marked seasonal pattern, with values falling between 1.65 and 15.18 g CO_2 m^{-2} d^{-1} in the 40-yr stand and between 2.33 and 9.15 g CO_2 m^{-2} d^{-1} in the CF (Figure 7). Soil CO_2 efflux in the 40-yr increased steadily from spring to summer 2002, reaching a maximum value in August (15.18 g m^{-2} d^{-1}), and then effluxes started to decline during the autumn-winter period. In the CF the highest soil CO_2 efflux occurred in August 2002 (9.15 CO_2 m^{-2} d^{-1}) and the lowest in December 2002 (2.41 g CO_2 m^{-2} d^{-1}), when the water table was close to the surface and soil water content was high.

The overall average soil CO_2 efflux for the 40-yr stand was 4.0 ± 0.3 g m^{-2} d^{-1} and for the CF was 2.8 ± 0.7 g m^{-2} d^{-1}. For the first 10 months after clearfelling, the 40-yr stand contributed with 21.14 ± 1.8 t CO_2 ha^{-1} (5.77 ± 0.5 t C ha^{-1}) to the atmosphere while the CF released 15.3 ± 3.7 t CO_2 ha^{-1} (4.13 ± 1 t C ha^{-1}). Over a one year period, these are equivalent to 24.7 ± 2.2 t CO_2 ha^{-1} (6.75 ± 0.6 t C ha^{-1}) and 18.7 ± 4.3 t CO_2 ha^{-1} (4.8 ± 1.2 t C ha^{-1}) for the 40-yr stand and CF, respectively (Table 6).

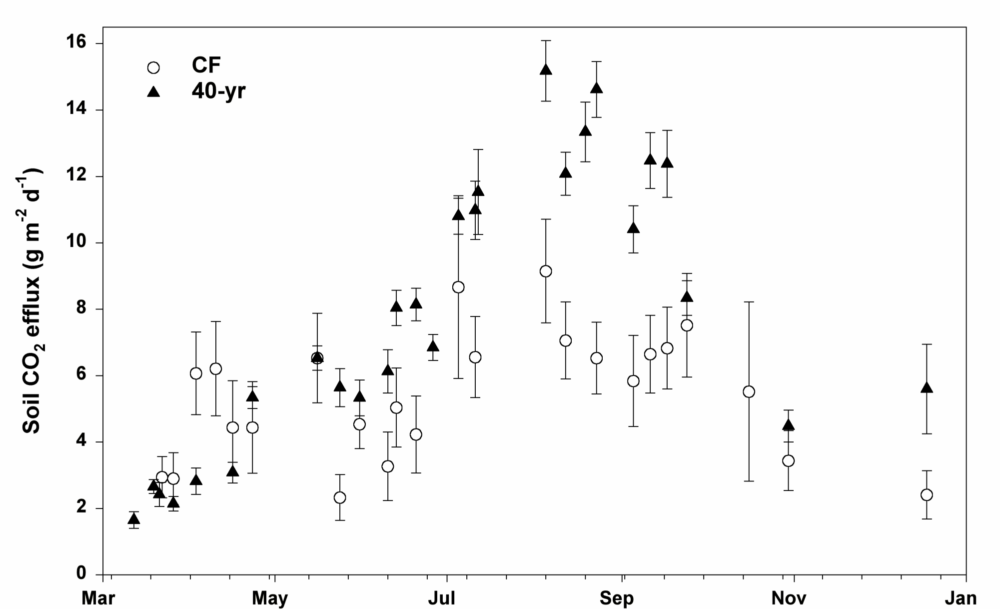

Figure 7: Weekly averages of soil CO_2 efflux in the CF and 40-yr stand (soil CO_2 efflux measured with the DC method). The vertical bars indicate the standard error of the mean.

Table 6: Comparison of daily and cumulative emissions of soil CO_2 efflux in the 40-yr stand and CF site. The number in the brackets indicate the standard error of the mean.

	40 yr	CF
Mean daily CO_2 efflux (g m^{-2} d^{-1})	4 .0 (0.3)	2.8 (0.7)
Mean daily C efflux (g m^{-2} d^{-1})	1.1 (0.1)	0.8 (0.2)
Cumulative CO_2 efflux (t ha^{-1}) over 10 months	21.3 (1.8)	15.1 (3.7)
Cumulative C efflux over 10 months (t ha^{-1})	5.77 (0.5)	4.13 (1)
Estimated yearly CO_2 efflux (t ha^{-1} y^{-1})	24.7 (2.2)	18.7 (4.3)
Estimated yearly C efflux (t ha^{-1} y^{-1})	6.75 (0.6)	4.8 (1.2)

Repeated-measures ANOVA on soil CO_2 efflux showed overall significant differences between the 40-yr and CF stands for the period March to December 2002

($P<0.001$, Table 5); however, March, May and October 2002 were not significantly different from each other ($P>0.05$).

3.4.4 Dependence of soil CO_2 efflux on soil temperature and soil water content.

Soil temperature alone explained between 79 and 90% (for all soil depths where temperature was measured) of the variability observed in CO_2 efflux in the mature stands (CF_{before} and 40-yr, Table 7, Figure 8). After clearfelling, soil temperature was not a major factor in soil CO_2 efflux, accounting for only 38 to 45% of the variability observed, with the best fit of the relationship with the soil temperature at the soil surface (T_1). When data from all sites were combined the R^2 varied between 50 and 53% (Table 7).

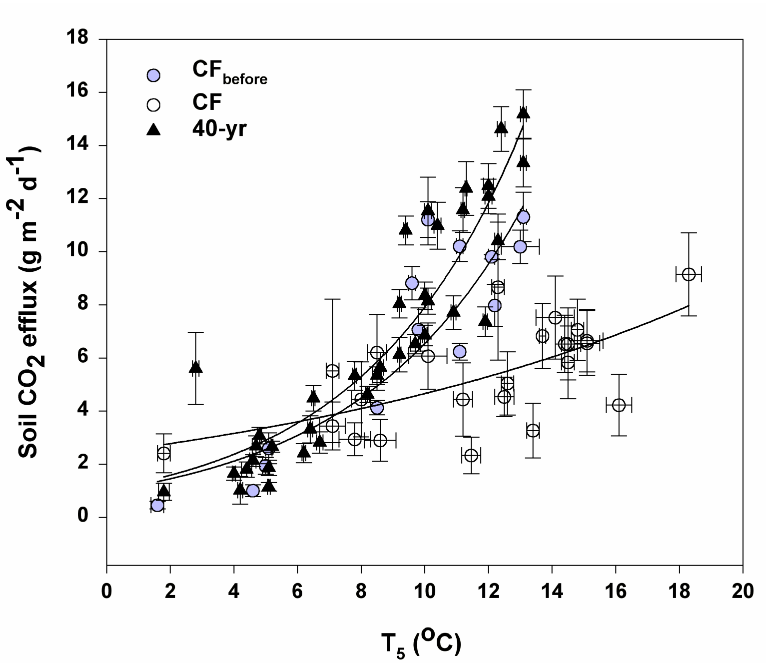

Figure 8: Exponential relationships of soil CO_2 efflux with soil temperature at 5 cm depth for the CF_{before} stand (R^2=0.89, $P<0.0001$), CF (R^2=0.39, $P<0.0001$) and the 40-yr stand (R^2=0.82, $P<0.0001$).

Table 7: Parameters of the exponential relationship of soil CO_2 flux (y) with soil temperature (T), goodness of fit (R^2), Q_{10}, number of samples and P value of exponential relationship. The Q_{10} for the CF_{before} stand is calculated for the period June 2001 to January 2002, for CF March to December 2002 and for the 40-yr stand for the period January to December 2002 and in the brackets are Q_{10} values calculated for the period March to December 2002.The numbers under (n) are the number of weekly average values employed to calculate the relationship. Weekly averages is the result of the sampling of 10 different collars (measured with the DC method). Soil temperatures measured at 1, 5 and 10 cm depth for the three sites, respectively.

Site	$y=R_0\, e^{bT}$	R^2	Q_{10}	n	P
CF_{before}	$y= 0.61e^{0.22T_1}$	$R^2=0.90$	8.2	14	<0.0001
	$y= 0.46e^{0.26T_5}$	$R^2=0.89$	15		<0.0001
	n. a.		n.a.		
CF	$y=2.18e^{0.06T_1}$	$R^2=0.45$	1.9	24	<0.0001
	$y=2.30e^{0.07T_5}$	$R^2 =0.39$	1.9		<0.0001
	$y= 2.36e^{0.07T_{10}}$	$R^2=0.38$	2.0		<0.0001
40-yr.	$y=1.02e^{0.19T_1}$	$R^2=0.79$	6.7 (5)	38	<0.0001
	$y=0.79e^{0.23T_5}$	$R^2=0.82$	9.0 (6.7)		<0.0001
	$y=0.60e^{0.27T_{10}}$	$R^2= 0.82$	12.2 (8.2)		<0.0001
All sites	$y=1.59e^{0.11T_1}$	$R^2=0.50$	1.8	76	<0.0001
	$y=1.13e^{0.14T_5}$	$R^2=0.53$	2.2		<0.0001
	$y=1.34e^{0.16T_{10}}$	$R^2=0.53$	2.7		<0.0001

The mature stands had calculated seasonal Q_{10} values higher than those for the CF (seasonal Q_{10} varied from 6.7 to 12.2) and these values increased with increasing depth (Table 7). Q_{10} was much lower in the CF site, and essentially constant with depth, with a value of 1.9 at the 1 and 5 cm depths and a value of 2.0 at the 10 cm depth. When the data from all sites were combined, the Q_{10} increased from 1.8 to 2.2 and 2.7 at 1, 5 and 10 cm depth, respectively. When the air temperature was used, the calculated Q_{10} for the CF was 1.6 while for the 40-yr stand it was 2.92 (there were not enough data for the calculation of Q_{10} for the CF_{before} stand), values that are lower than the calculated Q_{10} from soil temperature.

Soil CO_2 efflux in the CF_{before} stand was weakly and not significantly related to soil water content with a positive exponential relationship (R^2=0.11, P=0.7, Figure 9) while in the 40-yr stand soil CO_2 efflux was weakly but significantly and negatively related with soil water content (R^2=0.19, P=0.02, Figure 10). However, water content became a significant factor after clearfelling, with soil CO_2 efflux exponentially decreasing with increasing soil water content (R^2=0.42, P=0.003, Figure 11).

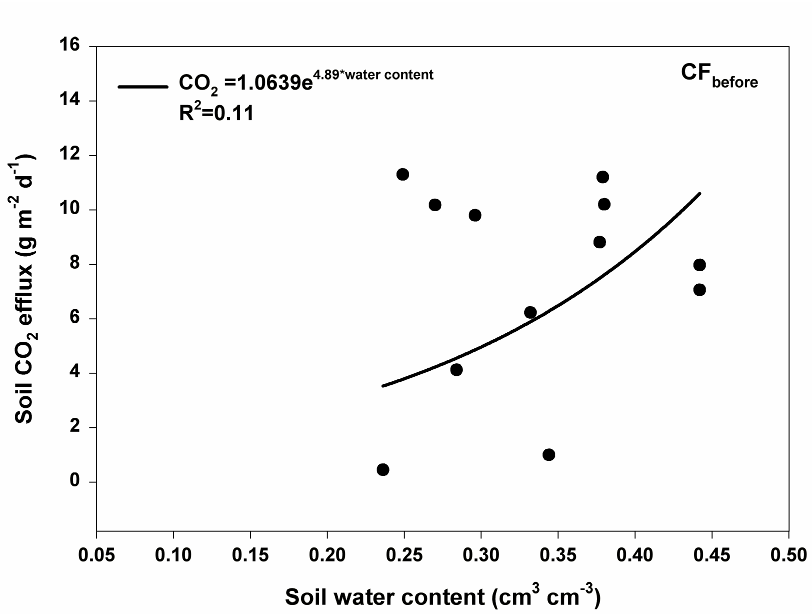

Figure 9: Exponential relationship (R^2=0.11, P=0.7) between soil CO_2 efflux (g m^{-2} d^{-1}) and soil water content (cm^3 cm^{-3}) in the CF_{before} stand.

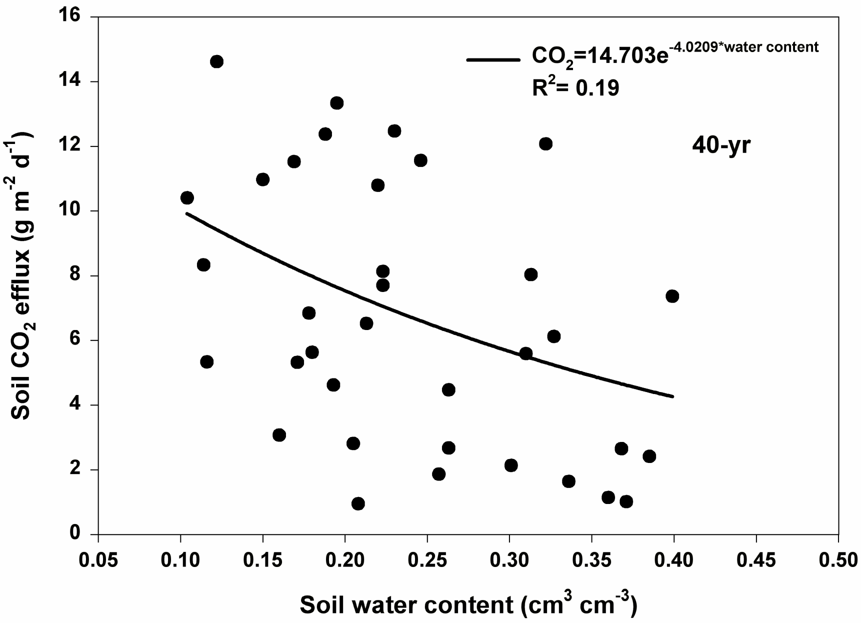

Figure 10: Exponential decay relationship (R^2=0.19, P=0.02) between the soil CO_2 efflux (g m^{-2} d^{-1}) and soil water content in the 40-yr stand.

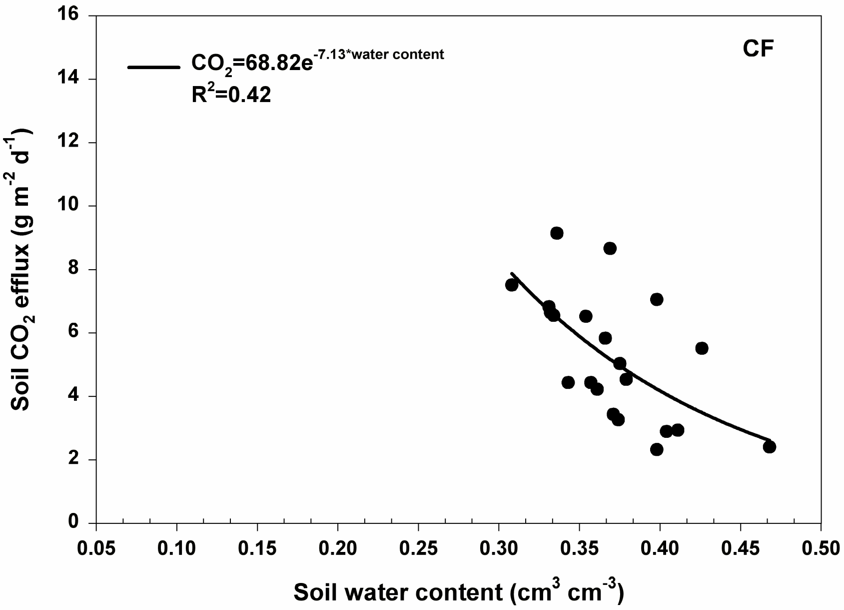

Figure 11: Exponential decay relationship (R^2=0.42, P=0.003) between the soil CO_2 efflux (g m^{-2} d^{-1}) and soil water content in the CF site.

In the mature stands CO_2 efflux was not significantly related to water table depth. In the CF_{before} stand there was a moderate and marginally not significant relationship (R^2=0.48, P=0.07, Figure 12) and in the 40-yr stand the relationship was very weak (R^2=0.09, P=0.3, Figure 13), but both sites showed a trend of soil CO_2 efflux decreasing with the rise of the water table. In the CF the dependence of soil CO_2 efflux on the water table became significant, although the relationship was weak (R^2=0.21, P=0.03, Figure 14), with CO_2 efflux decreasing with the rise of the water table.

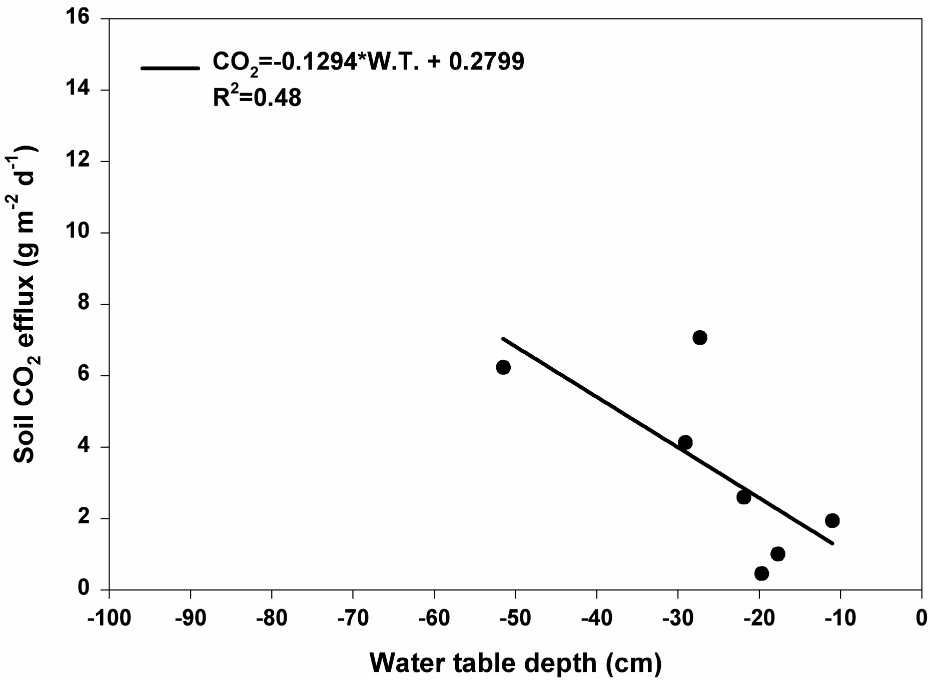

Figure 12: Linear relationship (R^2=0.48, P=0.07) between the soil CO_2 efflux (g m^{-2} d^{-1}) and the depth to the water table (cm) in the CF_{before} stand.

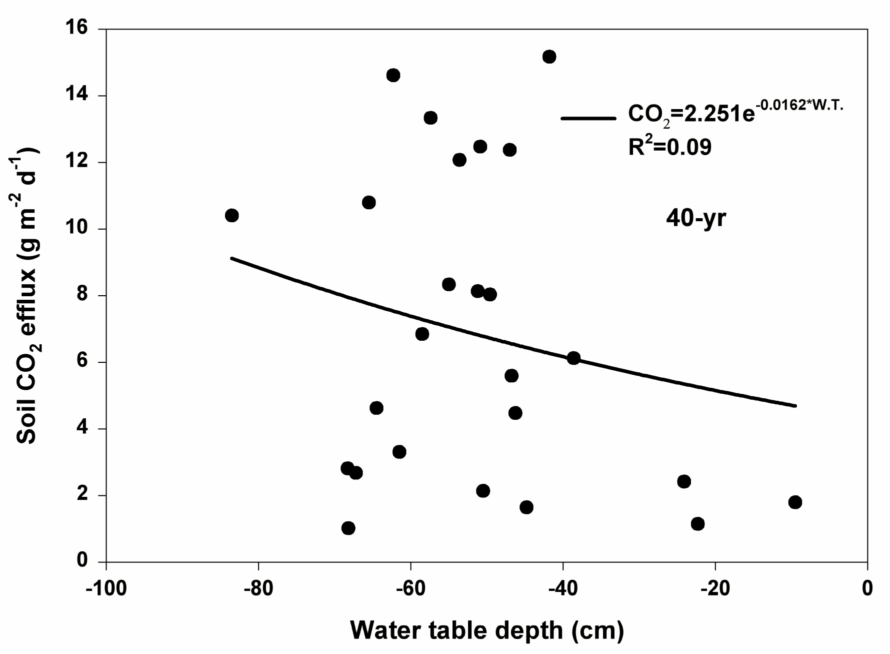

Figure 13: Exponential relationship (R^2=0.09, P=0.3) between soil CO_2 efflux (g m^{-2} d^{-1}) and depth to the water table (cm) in the 40-yr stand.

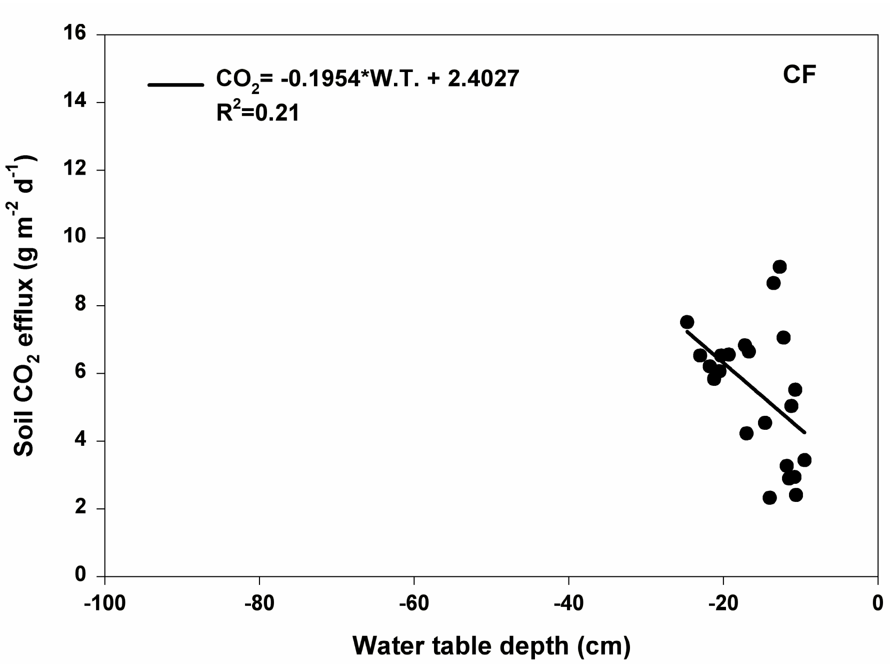

Figure 14: Linear relationship (R^2=0.21, P<0.05) between soil CO_2 efflux (g m^{-2} d^{-1}) and depth to the water table (cm) in the CF site.

Table 8 shows the parameters and goodness of fit (R^2) of the two models used (M.L.R. and a non-linear model) for the combined effect of soil temperature (at 1 cm depth) and water content on soil CO_2 flux. When soil water content was combined with temperature, it did not improve the goodness of fit for the CF_{before} stand, for either of the two models used. While the R^2 of the dependence of soil CO_2 efflux on soil temperature alone (T_1) was 0.90, the incorporation of the soil water content reduced the R^2 in both models (R^2= 0.83 and 0.80 for the M.L.R. and the non-linear model, respectively). The same pattern was found for T_5 as well (Table 9). For the 40-yr stand the R^2 of the dependence of soil CO_2 efflux on soil temperature alone (T_1) was 0.79 while the incorporation of soil water content in the M.L.R. slightly reduced the R^2 (0.77) and slightly increased it in the non-linear model (R^2=0.82). The model performance was slightly better for both models for T_5 (Table 9) and particularly for T_{10} (Table 10). The incorporation of soil water content with soil temperature improved the goodness of fit in the CF for depths 5 and 10 cm. While R^2 of the relationship of soil CO_2 efflux with temperature alone (T_5) was only 0.39, it became 0.45 in the M.L.R. and 0.46 in the non-linear. The same pattern was also found for T_{10} (Table 10), but not for T_1, where the inclusion of water content did not change the goodness of fit in the M.L.R., although it slightly improved it in the non-linear model (Table 8). These results confirm that water content was not a driving factor on soil CO_2 efflux in the mature stands but became a more significant factor after clearfelling.

Table 8: Parameters and goodness of fit of the two models used to describe the dependence of soil CO_2 efflux on soil temperature (at 1cm depth) and soil water content. The number in the brackets indicate the standard error for the multiple linear regression (M.L.R) and the asymptotic standard error for the non-linear model.

M.L.R. $Y=a*T+b*W+c$	CF_{before}	CF	40 -yr	All sites
a	0.81 (0.1)	0.24 (0.1)	0.99 (0.10)	0.18 (0.04)
b	1.2 (7.53)	-15 (15.0)	-4.61 (5.0)	-11.97 (0.04)
c	-1.41 (2.6)	7.98 (6.7)	-0.42 (1.69)	5.34 (1.2)
R^2	**0.83**	**0.45**	**0.77**	**0.49**
Non-linear Model	CF_{before}	**CF**	**40 -yr**	**All sites**
R_{ref} (g m^{-2} d^{-1})	6.59 (0.71)	4.13 (0.48)	7.99 (0.37)	6.37 (0.40)
E_0 (K)	654.0 (987.98)	331.47 (989.09)	920.2 (464.32)	283.07 (463.85)
T_{ref} (°C)	10	10	10	10
T_0 (°C)	-46	-46	-46	-46
$W_{½}$ (cm^3 cm^{-3})	0.150 (0.63)	0.150 (1.5)	0.150 (0.19)	0.150 (0.76)
R^2	**0.80**	**0.46**	**0.82**	**0.27**

Table 9: Parameters and goodness of fit of the two models used to describe the dependence of soil CO_2 efflux on soil temperature (at 5 cm depth) and soil water content. The number in the brackets indicate the standard error for the multiple linear regression (M.L.R) and the asymptotic standard error for the non-linear model.

M.L.R. $Y=a*T+b*W+c$	**CF_{before}**	**CF**	**40 -yr**	**All sites**
a	0.956 (0.2)	0.24 (0.1)	1.17 (0.1)	0.23 (0.05)
b	0.5 (8.5)	-16.6 (14.3)	-4.1 (4.2)	-10.80 (2.95)
c	-2.11 (3.0)	8.64 (6.3)	-1.98 (1.63)	4.58 (1.14)
R^2	**0.78**	**0.45**	**0.81**	**0.35**

Non-linear Model	**CF_{before}**	**CF**	**40-yr**	**All sites**
R_{ref} (g m^{-2} d^{-1})	9.1 (4.08)	7.61 (12.08)	8.43 (0.84)	6.56 (1.52)
E_0 (K)	524.75 (125.98)	250.21 (71.90)	863.23 (59.84)	253.94 (56.62)
T_{ref} (°C)	10	10	10	10
T_0 (°C)	-46	-46	-46	-46
$W_{½}$ (cm^3 cm^{-3})	0.091 (0.19)	0.27 (1.10)	0.100 (0.02)	0.150 (0.06)
R^2	**0.79**	**0.46**	**0.84**	**0.36**

Table 10: Parameters and goodness of fit of the two models used to describe the dependence of soil CO_2 efflux on soil temperature (at 10 cm depth) and soil water content. The number in the brackets indicate the standard error for the multiple linear regression (M.L.R.) and the asymptotic standard error for the non-linear model.

M.L.R. $Y=a*T+b*W+c$	**CF_{before}**	**CF**	**40 -yr**	**All sites**
a	n.a.*	0.27 (0.1)	1.46 (0.1)	0.27 (0.06)
b	n.a.	-16.6 (13.6)	0.77 (4.2)	-11.51 (3.11)
c	n.a.	8.43 (5.92)	-5.3 (1.7)	4.53 (1.21)
R^2	n.a.	**0.48**	**0.86**	**0.59**
Non-linear Model	**CF_{before}**	**CF**	**40 -yr**	**All sites**
R_{ref} (g m^{-2} d^{-1})	n.a.	4.76 (0.43)	9.2 (0.32)	6.43 (0.44)
E_0 (K)	n.a.	297.79 (873.70)	983.85 (366.28)	419.86 (610.16)
T_{ref} (°C)	n.a.	10	10	10
T_0 (°C)	n.a.	-46	-46	-46
$W_{½}$ (cm^3 cm^{-3})	n.a.	0.150 (1.22)	0.150 (0.12)	0.150 (0.67)
R^2	n.a.	**0.47**	**0.89**	**0.33**

*n.a.: not applicable

Comparing the two multiple regression models, they gave similar performances, with the non-linear model giving slightly better correlation coefficients that the M.L.R. model for each site separately. But when combining the data from all sites the MLR model gave better performance than the non-linear model.

The performance of the models was also checked against the residuals of soil CO_2 efflux against soil temperature and water content. Figure 15 and Figure 16 depict the residuals of soil CO_2 efflux for T_5 and water content: the residuals were unevenly distributed with no clear pattern for both models indicating an adequate fit. The residuals followed also a similar pattern for T_1 and T_{10}.

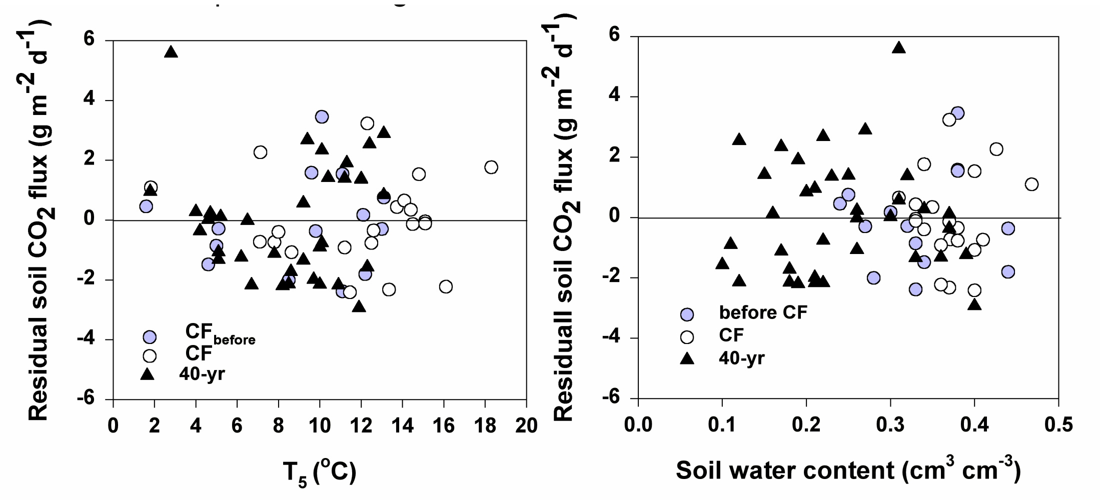

Figure 15: Residuals plots for the multiple linear regression model, of soil CO_2 efflux dependent on soil temperature and water content.

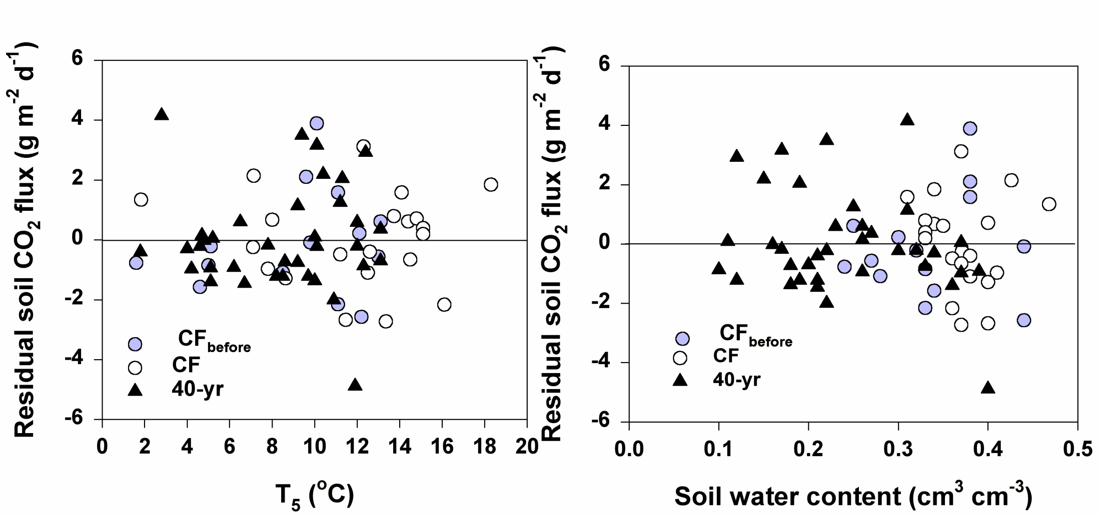

Figure 16: Residuals plots for the non-linear regression model, of soil CO_2 efflux dependent on soil temperature and water content.

3.5 Discussion

3.5.1 Effect of clearfelling on environmental parameters

Clearfelling in general alters the surface thermal properties (eg. albedo) and energy and material balances (e. g. solar radiation and precipitation) near the ground, because of the removal of the forest canopy (Chen *et al*., 1993). Clearfelling of a forest stand in Harwood caused a rise in soil temperature and it also caused higher soil temperature fluctuations during the growing season. The CF site had soil temperature values 2.0 to 7.6 °C higher compared with the closed canopy 40-yr stand, while the CF site also exhibited greater fluctuations in soil temperature at 5 cm depth compared with a closed canopy 30-yr stand. The air temperature in the CF site was also much greater than the air temperature in the 40-yr stand. These patterns of air and soil temperature in the CF and 40-yr stand agree with the ones by Chen *et al*. (1993), who measured higher mean daily soil temperatures and higher mean daily ranges in a clearfelled site than in the control stand in a Douglas fir–western hemlock (*Pseudotsuga menziesii* (Mirb.) Franco)-*Tsuga heterophylla* (Raf.) Sarg.)) forest in Washington, U.S.A.

Before clearfelling, the two mature stands exhibited different patterns in soil water content and water table depth, with the CF_{before} stand having significantly higher soil water content ($P<0.0001$) and water table depth ($P<0.0001$) compared to the 40-yr stand. This was an unexpected consequence of the lack of randomisation of the treatments, due to the spatial separation of the clearfelled from the “control” stand. However, we had no control over the decision on which stand should be felled. Nonetheless, clearfelling of trees led to a further increase in soil water content and rise of the water table. While before clearfelling the CF_{before} stand had a soil water content 11 to 22 % higher than the 40-yr stand, after clearfelling this range increased from 15 to 253%. The same pattern was also observed in the water table depth.

Before clearfelling the CF_{before} stand had a shallower water table (between 17 and 44 cm depth) than the 40-yr stand (between 35.5 and 64.5 cm depth). After clearfelling the water table depth in the CF site ranged between 10.7 and 24.7 cm, while in the 40-yr stand it varied between 24.1 and more than 90 cm depth. This happened because of the absence of trees taking up water and the reduced rates of evapotranspiration. Adams *et al*. (1991), in a long term study in a Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forest in Oregon, also observed significantly higher soil water contents in the clearfelled site than in the control stand, during the first 2 years after clearfelling. Smethurst and Nambiar (1990) measured up to 50% higher soil water content in clearfelled stands compared with uncut stands of *Pinus radiata* in Australia, for the first 18 months after clearfelling.

3.5.2 Effects of clearfelling on soil CO_2 efflux

Before clearfelling the two mature stands did not significantly differ in soil CO_2 effluxes ($P=0.7$). Clearfelling had a significant effect on soil CO_2 efflux ($P<0.001$) although effluxes in March, May and October 2002 were not significantly different between the CF and the 40-yr stand ($P>0.05$). The effluxes from the CF were mostly lower than the ones in the 40-yr stand, except for March and April. The higher effluxes during March and April were probably caused by the flush of decomposition of fine roots that died after tree harvesting. Fahey and Arthur (1994) estimated that most fine roots in the forest floor of a northern hardwood forest in New Hampshire died within the first two months after harvesting. The high variability in soil CO_2 efflux in the CF is the reason why the means for the treatments for the months of May and October were not significantly different from each other, though the mean effluxes were still much lower compared to the 40-yr. Generally, soil CO_2 efflux was more variable in the CF than the 40-yr stands, reflecting the effects of the disturbance to the soil due to harvesting operations.

Clearfelling during the first ten months overall decreased the soil CO_2 efflux in the CF compared to the 40-yr stand. CF had a mean daily CO_2 efflux of 2.8 ± 0.7 g m^{-2} d^{-1} compared to the 4.0 ± 0.3 g m^{-2} d^{-1} of the 40-yr stand. From March to December 2002 CF emitted to the atmosphere 4.13 1.0 t C ha^{-1} and the 40-yr stand 5.77 ± 0.5 t C ha^{-1}. The estimated soil CO_2 efflux for the first year after clearfelling was 4.8 ± 1.2 t C ha^{-1} for the CF site and 6.75 ± 0.6 t C ha^{-1} for the 40-yr stand, which is close to the 6.81 ± 0.95 t C ha^{-1} y^{-1} estimated by Raich and Schlesinger (1992) for temperate conifer forests.

The decrease in soil CO_2 efflux after clearfelling is probably mostly due to the lack of living fine roots and the cease of root respiration. Ewel *et al*. (1987a) estimated that root respiration contributed 51% to the total soil CO_2 efflux in a slash pine plantation (*Pinus elliottii*). Irvine and Law (2002) estimated that root respiration contributed about half of the total soil surface CO_2 efflux through the growing season in young and old ponderosa pine forest in Oregon. Extensive measurements to separate autotrophic from heterotrophic respiration are not available for Harwood Forest. However, six trenched plots were established in Harwood as part of the CARBO-AGE project, and their emissions were occasionally monitored. The available estimates suggest that autotrophic respiration represents a fraction of the order of 40% of total soil CO_2 efflux at this forest (M. Mencuccini, personal communication).

The reduced soil CO_2 efflux could also be caused by the reduction of microbial populations because of the limited availability of organic substrates (Zak *et al*., 1990; Zak *et al*., 1994; Gallardo and Schlesinger, 1994), which are directly influenced by above-ground and below-ground litter input into the soil. Litter inputs, through the process of mineralization, contribute approximately half of total soil respiration (Coûteaux *et al*., 1995). Microbial populations are also sensitive to soil temperature and water, while community size and composition in a given soil vary with fluctuations in water content (Fisher and Binkley, 2000). Skopp *et al*. (1990) used a model to simulate the effect of soil water content on microbial activity. They concluded that microbial activity increases with water content and reaches a maximum at a water content where the limiting effects of substrate diffusion and oxygen supply are equal and then it declines with increasing water content. Schilling *et al*. (1999) found that clearfelling of a bottomland hardwood forest in Mississippi caused a decline in soil microbial biomass. The same trend after clearfelling was observed by Bååth *et al*. (1995) in a mixed conifer forest (Norway spruce-Scots pine) in Finland and by Pietikainen and Fritze (1995) after clearfelling of a Norway spruce stand in Finland, but in both studies measurements had taken place three and four years after clearfelling. Lundgren (1982) measured higher bacterial biomass during the first two years after clearfelling in a Scots pine forest in Sweden. The bacterial biomass decreased compared to that in the mature pine stand after the third year since clearfelling.

Finally, a decrease in the soil CO_2 efflux after clearfelling could also be attributed to the increase of the water table after tree harvesting. The water table in the clearfelled site was very close to the surface (water pools at places), thus creating anaerobic conditions and decreasing the O_2 available to the micro-organisms, and thereby slowing the CO_2 evolution (Bunnell *et al*., 1977; Skopp *et al*., 1990). It is also possible that some CO_2 may have dissolved in the soil water and gone undetected.

Reduced soil CO_2 efflux after clearfelling has been commonly reported. Nakane *et al*. (1986), found that soil CO_2 efflux in a *Pinus densiflora* stand in Japan decreased after clearfelling. They attributed this decline to the cessation of root respiration. Fernandez *et al*. (1993) found lower soil CO_2 efflux (4.56 g CO_2 m^{-2} d^{-1}) at a clearfelled site, 4 to 6 years after clearfelling, compared to an uncut mixed coniferous forest (7.68 g CO_2 m^{-2} d^{-1}) of red spruce-balsam fir (*Picea rubens* Sarg. and *Abies balsamea* (L.) Miller, respectively) in Canada, although the difference was not significant ($P > 0.05$). Griffiths and Swanson (2001) measured lower forest floor CO_2 efflux in recently harvested stands compared to 40 yr stands and old growth stands in a harvested chronosequence of Douglas fir (*Pseusotsuga menziesii* (Mirb.) Franco) in Oregon. Hendrickson *et al*. (1984) found that laboratory incubated soil from a clearfelled mixed-deciduous forest had lower rates of soil CO_2 efflux than incubations from an intact forest soil. Striegl and Wickland (1998) found that clearfelling of a boreal jack pine (*Pinus banksiana* Lamb.) forest in Canada, reduced soil CO_2 efflux to about 40% of that at an uncut mature jack pine stand (60 to 90-yr old), in the first season following harvest. They attributed the majority of this reduction to destruction of near-surface soil autotrophic and heterotrophic respiration and to tree-root die off. Smethurst and Nambiar (1995) calculated a decrease in the soil CO_2 efflux after clearfelling for the first 3 years after planting in a *Pinus radiata* plantation (from 7.08 t C ha^{-1} yr^{-1} to 3.12 t C ha^{-1} y^{-1}). Steudler *et al*. (1991) reported that clearfelling a wet tropical forest in Puerto Rico, decreased soil CO_2 efflux by 14% to 9.5 t C ha^{-1} y^{-1} compared to 11.1 t C ha^{-1} y^{-1} for the uncut reference plot.

Contrary to these results, Ewel *et al*. (1987a) reported higher soil CO_2 evolution at a clearfelled site (22.96 g CO_2 m^{-2} d^{-1}) than at a 9-yr- old stand (8.88 g CO_2 m^{-2} d^{-1}) and at a mature (29- yr-old) slash pine (*Pinus elliotti* Engelm.) plantation (7.24 g CO_2 m^{-2} d^{-1}). Gordon *et al*. (1987) studied soil CO_2 efflux 4 to 5 years after harvesting in white spruce forests in interior Alaska and found that soil CO_2 effluxes in midsummer (16.8 g CO_2 $m^{-2}d^{-1}$) were significantly higher than those of the control stand (9.6 g CO_2 m^{-2} d^{-1}). Lytle and Cronan (1998) found that soil CO_2 efflux increased about 16% during the first six months (growing season) after clearfelling of a spruce- fir forest (*Picea rubens* Sarg. and *Abies balsamea* Mill.). The mean daily soil CO_2 efflux for the clearfelled stand was 8.9 g CO_2 m^{-2} d^{-1} versus 7.7 g CO_2 m^{-2} d^{-1} in the uncut stand. Johnson *et al*. (1995) measured carbon dynamics in a northern hardwood forest in New Hampshire prior and after clearfelling and found that 8 and 10 years after clearfelling, the estimated efflux of soil CO_2 was 20% greater in the clearfelled watershed than in the adjacent forest (average efflux 5.7 t C ha^{-1} and 4.7 t C ha^{-1}, respectively). Londo *et al*. (1999) reported higher soil CO_2 in a clearfelled bottomland hardwood forest in Texas between 6 to 22 months after clearfelling (with mean soil CO_2 effluxes of 4.95 ± 0.25 g m^{-2} d^{-1} and 7.15 ± 0.38 g m^{-2} d^{-1} in the control and clearfelled stand, respectively). They also reported vigorous vegetation recovery in the first growing season following harvesting, with a rapid invasion of herbaceous species. By comparison, the CF site at Harwood was bare till September, when grass started appearing. The data from the studied CF may be compared with those from an older (5-yr-old) clearfelled site (CF_{old}) in the same forest, which was being monitored in parallel for a separate study (Tom Ball, personal communication). The CF_{old} generally had higher effluxes (average efflux the period from March to October 2002: 7.94 ± 1.89 t C ha^{-1}), 44% higher than the equivalent average efflux from the CF (5.51 ± 0.38 t C ha^{-1}) (T. Ball, personal communication).

The absence of significant effects of clearfelling on soil CO_2 effluxes has also been reported. Toland and Zak (1994) found no significant difference in the soil CO_2 efflux between clearfelled and intact plots of northern hardwood forests in Michigan (*Acer saccharum-Quercus rubra*, and *Acer saccharum-Tilia americana*). They attributed that to the input of logging slash that increased the soil C availability and amount of substrate available for heterotrophic metabolism in the soil, although root respiration decreased because of root mortality. So the decrease in root respiration was offset by a proportional increase in microbial respiration. Edwards and Ross-Todd (1983) also observed no significant difference in annual soil respiration between clearfelled and intact mixed deciduous forests in Tennessee (annual carbon losses were 4.83 t ha^{-1} from the clearfelled site, where harvest residues were left, and 5.29 t ha^{-1} from the control stand). Weber (1990) found similar results in young *Populus tremuloides* and *Populus grandidentata* ecosystems. Mallik and Hu (1997) observed no significant differences during one growing season in a boreal mixed-wood forest. They found that soil CO_2 efflux ranged from 16.32 to 20.16 g m^{-2} d^{-1} in the cut plots and from 13.44 to 19.68 g m^{-2} d^{-1} in the uncut plots.

Laporte *et al*. (2003) evaluated the effects of clearfelling, selection cutting and shelterwood cutting in a hardwood forest ecosystem (*Acer saccharum* Marsch. and

Betula alleghaniensis Britton) in Ontario, for one growing season. They found that selection and shelterwood cutting had the greatest effect compared to control, while soil CO_2 from the clearfelled plots were intermediate between the control and the other treatments. Finally, Irvine and Law (2002) after three years of measurements in ponderosa pine stands, reported that whether a young stand (14 years after clear felling) or an old growth stand (250-yearsr-old) will exhibit greater soil CO_2 efflux depends on the year-to-year climatic variability.

It seems likely that each ecosystem has a specific response of soil respiration to disturbances such as clearfelling and this makes it difficult to draw general conclusions on the effects of clearfelling on this process. Possible explanations for the discrepancies among studies are: i) clearfelling affects the patterns of soil temperature and soil water content differently in each ecosystem; ii) the time elapsed since clearfelling is not the same for all studies, so some of them have more time for recovery than others; iii) the disturbance caused to the soil by harvesting operations may vary between ecosystems and methods of harvesting; and iv) the percentage of disturbed and undisturbed areas sampled within the clearfelled site may be unrepresentative of the ecosystem. For example, in this study the collars and chambers only covered a small surface area, which could include only small pieces of woody debris due to chamber size and depth and the potential contribution of tree stumps and larger piles of brash could not be systematically investigated. Laporte *et al*. (2003) found that soil CO_2 effluxes in scarified microsites were significantly lower that on undisturbed soil. Dulohery *et al*. (1996) found that soil CO_2 efflux tended to be depressed in bedded areas, especially where the soil had been previously disturbed during timber harvest. It is thus important to extend short-term studies like the one reported here for longer periods of time, in order to determine the extent to which changes occur in the soil processes responsible for CO_2 efflux.

3.5.3 Dependence of soil CO_2 efflux on soil temperature and soil water content

The mature stands exhibited a strong seasonal pattern, which was associated with the seasonal changes in temperature. Soil CO_2 efflux was strongly controlled by temperature in the mature stands (R^2 = 0.79 to 0.90). Temperature has been found to explain much of the variation in soil CO_2 in temperate forests. For instance, Ewel *et al*. (1987a) found that temperature explained 75 to 89% of the soil CO_2 efflux in slash pine plantations in Florida. For *Picea abies* stands in Germany, it accounted for between 62 to 93% of the temporal variability (Buchmann, 2000). The response of soil CO_2 efflux to temperature became weaker after clearfelling (R^2 = 0.38 to 0.45), probably because of the increased water content, the destruction of fine roots and the disturbance of the soil caused by tree harvesting. Higher regression coefficients for the mature stand than the CF site suggest that root respiration may have been more responsive to temperature than microbial respiration. Dulohery *et al*. (1996) found that in undisturbed soils in a clearfelled area an exponential temperature function accounted for 85% of the variation, while with increasing severity of disturbance temperature accounted for less and less variation (R^2 between 0.54 and 0.64). Arneth *et al*. (1998) found that soil CO_2 efflux in a clearfelled *Pinus radiata* plantation did not follow the exponential relationship with soil temperature and a linear relationship, accounted for only 7% of the total variance.

However, the values of seasonal Q_{10} for the mature stands (6.7 to 12.2) found in this study are much higher than the median of 2.4 for various soils (Raich and Schlesinger, 1992). Also, Borken *et al*. (2002) reported values from 1.83 to 3.48 for mature stands of Norway spruce in Germany, while Buchman (2000) reported Q_{10} values of 2.3 to 3.22 for Norway spruce stands of different age (47 to 146- years-old), also in Germany. It is difficult to make comparisons between reported Q_{10} values because of the different ways they have been calculated. Widely reported values of Q_{10} are often given without explicit reference to the depth at which the soil temperature was measured at (Kicklighter *et al*., 1994) and whether that depth was determined to be the one yielding the best correlation between temperatures and soil CO_2 efflux throughout a year. The calculated Q_{10} is also normally lower when estimated by using air temperature instead of soil temperatures (Kicklighter *et al*., 1994). Indeed, Q_{10} values calculated from air temperatures (1.6 and 2.92 for the CF and 40-yr stand, respectively) were lower that those based on soil temperature, as microbes are more metabolically responsive to soil temperature than air temperature (Raich and Potter, 1995). For instance, Raich and Potter (1995) calculated a Q_{10} of 2 based on soil temperature and 1.7 for air temperature, for a young irrigated pine stand in Massachusetts.

An important source of variability among studies is the length of the period employed to calculate Q_{10}. Q_{10} estimated on the basis of measurements over a short-term period, can be subject to environmental influences, such as recent rain events, and that can lead to biased estimates. For instance, Widen (2002) estimated Q_{10} values for two month periods in a mixed Scots pine and Norway spruce forest in Sweden by using nocturnal data and found Q_{10} values of about 9 for the period of April to May, 2.2 for June to July with Q_{10} increasing to 9 for August to September and going up to 44 for December to January period, to reach more than 22,000 for February to March period. Keith *et al*. (1997) estimated a Q_{10} of 1.4 for a *Eucalyptus pauciflora* forest in Australia for temperatures greater that 10 °C and a Q_{10} of 3.1 for temperatures less than 10 °C. This pattern of higher Q_{10} at lower temperatures and lower Q_{10} at higher temperatures has commonly been observed (Raich and Schlesinger, 1992; Lloyd and Taylor, 1994; Kirschbaum, 1995). This means that the relationship between soil CO_2 efflux and temperature is not a simple exponential over the normal range of physiological temperatures (Lloyd and Taylor, 1994). Additionally, many of the Q_{10} values reported in the literature are based on soda lime estimates of soil CO_2 efflux, which probably underestimated high effluxes and overestimated low effluxes, thereby leading to underestimates of Q_{10} (Kirschbaum, 1995). On the other hand, Q_{10} estimated over very long time periods can potentially confuse the short-term temperature responses of existing microbial populations, mycorrhyzas and fine roots with long-term changes in microbial population sizes, fine phenology and availability of detritus.

Soil CO_2 effluxes measured under laboratory conditions can also affect the estimation of Q_{10}. Kirschbaum (1995) estimated a mean Q_{10} of 5.15 for a range of soils with values ranging from 2.9 to 9.3 and higher Q_{10} values were observed at lower temperatures. Howard and Howard (1993) found Q_{10} values in the range 2.01-2.83 for a range of soil types and for a range of temperatures from 0 to 20 °C. The above researchers obtained these values from soil respiration measurements under laboratory conditions. This estimation of Q_{10} under laboratory incubations can be biased because manipulation of soil cores can totally exclude and modify root respiration and microbial activity, respectively. Laboratory measurements on soil cores usually ignore the effects of disturbance, water content, temperature and wind, which may be considerable (Schlenter and Van Cleve, 1985). Edwards and Ross-Todd (1983) found exceptionally high values of soil CO_2 efflux during the first two weeks of measurements. In fact they concluded that all their measurements (the measurements lasted for 32 days) probably represented overestimates due to effects of disturbance prior to soil incubations.

The low Q_{10} at the clearfelled site is probably connected with the absence of roots and root respiration. Boone *et al*. (1998) calculated a Q_{10} of 4.6 for root respiration including microbial decay of root exudates in the rhizosphere and a Q_{10} of 2.5 for soil respiration excluding roots. This relatively low Q_{10} for heterotrophic respiration is in the range of Q_{10} values from laboratory incubations of soils. Winkler *et al*. (1996) obtained Q_{10} values of 1.9 to 1.7 over a temperature range of 4 to 28 °C for the A horizon of forest soils. It could then be inferred that Q_{10} values derived from field measurements could overestimate the response of heterotrophic soil respiration at higher temperatures. In a mixed hardwood forest, the observed Q_{10} in trenched plots that are presumable nearly void of roots was only 2.5 and the control area had a

Q_{10} of 3.5 (Boone, unpublished data, cited in Davidson *et al*., 1998). This is indicated in this study by comparing the high Q_{10} values in the mature stand with the low Q_{10} value in the clearfelled site where there is no root respiration. The increased soil temperature in the clearfelled site, not followed by a significant increase in soil CO_2 efflux, indicates that the release of soil CO_2 to the atmosphere controlled by the microbial decay of the organic matter does not have a strong seasonal temperature dependency. This low Q_{10} in the clearfelled site could be also explained by the high soil water content which can impede oxygen diffusion, creating anaerobic conditions, depress microbial activity and thereby reduce emissions of soil respiration, thus making it less responsive to temperature (particularly at high temperatures). However, Rey *et al*. (2002) stated that soil respiration is a relatively conservative process with a well-established Q_{10} in the region of 1.8 to 2.4, so that variation from this range is most likely to result either from substrate limitation or from changes in microbial population size or plant phenology as the temperature increases over the growing season.

An increase in Q_{10} with increasing depth was also found (Table 7). Taking the regression coefficients into account (although they were not significantly different for the depths that were studied here), it can be proposed that the most appropriate depth (i.e., the depth where most of CO_2 production likely took place) was the 5 to 10 cm range. An increasing Q_{10} value with increasing depth has been confirmed by other researchers, although the differences at different depths were not as large. Bunnell *et al*. (1977) noted that Q_{10} increased from 1.87 in the litter layer of an aspen forest to 1.91 in the fermentation layer and at 2.23 at the humus layer. Russell and Voroney (1998) found a Q_{10} value of 3.9 for the 0 to 10 cm depth and a value of 5.1 for the 10 cm depth.

Considering the relationship of soil CO_2 efflux with the water content alone, CO_2 efflux decreased exponentially with increasing soil water content (R^2=0.42, P=0.003 in CF) while the relationship in the 40-yr was much weaker although still significant

(R^2=0.19, P=0.02). Soil water content did not exhibit a strong seasonal variation at this site, therefore it was not a limiting factor for soil respiration. The rise of the water table after clearfelling was also found to weakly affect soil CO_2 efflux (R^2 =0.21, P=0.03), with CO_2 decreasing with increasing water table, while there was no relationship found for the 40-yr stand (P=0.3).

It has generally been found that soil CO_2 production is driven mainly by temperature rather than soil water content (Howard and Howard, 1993). Klopatek (2002) found that the inclusion of soil water content in the regression equations reduced R^2 values. The inclusion of soil water content in a M.L.R. and a non-linear model in this study did not improve the performance of the model for the 40-yr stand, but it improved it slightly for the CF, indicating that soil water content was a factor regulating the soil CO_2 efflux at this site. Several studies have tried to describe the relationship of soil respiration with soil temperature and water content. Howard and Howard (1993) investigated the relationship of CO_2 effluxes with temperature and water content in different soil types and under controlled laboratory conditions. The relationship of soil CO_2 efflux with water content was described with curves of different shapes between soil types, while the response of the CO_2 efflux to temperature was approximately linear and the lines between soil types were remarkably close to a set of parallel straight lines for a temperature range between 5 and 20 °C.

Carlyle and Than (1988) found that soil CO_2 efflux in a *Pinus radiata* stand in Australia was significantly correlated with soil temperature (R^2=0.85) when soil water content was non-limiting (>12.5%), while when soil water content was below 12.5% there was no significant relationship (R^2=0). Londo *et al*. (1999) reported that soil CO_2 efflux was exponentially related to temperature and explained 31 to 58% (P<0.05) of the variation in clearfelled and control stands in a hardwood forest in Texas and exerted greater control than soil water content (P>0.05), although the coefficients of regression were higher (R^2= 0.40 to 0.43). They also used an equation where CO_2 efflux was linearly related to soil temperature and parabolically related to soil water content for averaged CO_2 effluxes among treatments. Edwards and Ross - Todd (1983) found that soil CO_2 efflux was significantly affected by soil temperature (R^2=0.90) but not significantly affected by soil water content (P=0.05) in a mixed hardwood forest in Tennessee. Schlenter and Van Cleve (1985) observed that soil CO_2 efflux was responsive to temperature changes for water contents between 100 to 250% in black spruce (*Picea mariana* (Mill.) B.S.P.) and white spruce (*Picea glauca* (Moench). Voss) forests in Alaska. They used three different models to describe the dependence of soil CO_2 efflux on soil temperature and water content. They found that the best models were obtained when the soil temperature at 15 cm depth was used, while the best fit was provided by a fourth order polynomial equation (R^2= 0.78) for the white spruce. Rey *et al*. (2002) used an empirical linear model to describe the dependence of soil CO_2 efflux on soil temperature and water content (both measured at 10 cm depth) in an oak forest in Italy. They found that the model explained 91% of the observed annual variation of soil CO_2 efflux, by using a threshold value of 20% water content. Above this value soil CO_2 efflux was exponentially related to soil temperature and below this value, soil CO_2 efflux was linearly related to soil water content.

It seems the type of equation to describe the relationship between soil CO_2 efflux and soil water content differs among ecosystems and it depends mostly on the relative limitation of each variable, temperature or water content. Different responses also indicate differences in soil microbial activities, which in turn depend on soil organic matter and soil physical and chemical conditions (Howard and Howard, 1993).

3.6 Conclusions

Clearfelling of a Sitka spruce stand on peaty gley soil caused significant changes in environmental variables. Air and soil temperatures increased in the CF than in an uncut 40-yr stand and soil temperature exhibited higher fluctuations. Clearfelling also caused an increase in soil water content and a rise of the water table.

Clearfelling also had a significant effect on soil CO_2 effluxes, and led to reduced effluxes compared to the uncut stand. For the first season following tree harvesting, the emissions of soil CO_2 in the CF were 30% lower compared to the uncut 40-yr stand. However, CF was a net source of CO_2 to the atmosphere because there was no photosynthetic uptake from the trees in the clearfelled site, therefore the soil respiration equaled the net CO_2 exchange with the atmosphere. It is be expected (given due account for respiration by the harvest residues) that soil CO_2 efflux increases together with photosynthetic uptake in the years following clearfelling, with the re-establishment of vegetation and trees and the soil microbial communities.

Soil temperature was a stronger predictor of soil CO_2 efflux in the mature stands compared to the water content. Clearfelling caused changes in the dependence of soil CO_2 efflux on these environmental variables and soil CO_2 efflux became less dependent on soil temperature, while soil water content became more important.