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Harvesting of trees or the loss of trees due to strong winds may lead to large variations at the ground surface that, in turn, causes spatial and temporal variability of soil respiration. We performed thinning (partial harvest) on a mature larch plantation (ca. 50 yr-old) in Tomakomai National Forest (Japan) with the purpose of studying the effects of thinning on soil respiration ($R_s$). We conducted field measurements to determine how soil temperature ($T_s$), mineral soil water content (MSWC), litter water content (LWC), fine root density, litter density, and carbon to nitrogen ratio (C/N) individually influence soil respiration. Soil respiration values did not differ significantly at the disturbed site. Soil temperature was significantly greater at the disturbed site than at the control site (t-test= -12.7, $P<0.05$), and the MSWC and LWC did not differ between sites. Despite these observations we found no proof that $T_s$ or MSWC influences $R_s$. At the disturbed site, LWC appeared to be a primary microclimatic factor driving spatial variations in $R_s$ (r= -0.41, $P<0.05$). Thinning led to large variations in $R_s$, $T_s$, fine root density, and litter density. Root and litter densities were 18% (insignificant value) and 15% (t-test=2.86, $P<0.05$) lower in the disturbed site, respectively. In fact, variations in soil respiration can be explained on the basis of litter density and C/N.

*Key words*: *soil respiration; mineral soil moisture content; litter water content; soil N content; soil C content; density of fine roots, disturbance, larch, partial harvest*

## INTRODUCTION

Soil respiration is a general name for many important processes, including respiration by live roots and associated mycorrhizae, as well as the oxidation of plant detritus such as roots, leaves, woody inputs, root exudates, and humified organic matter by soil heterotrophs. These processes all lead to the release of $CO_2$ through the surface of the soil, which is referred to as the total soil respiration. Several factors affect the respiration of soil into the atmosphere. These include soil moisture, soil temperature, vegetation type, substrate quality (e.g. type of organic matter), net ecosystem productivity, allocation of assimilate to above- and belowground biomass, population and community interactions, and land use disturbances (Rustad *et al.,* 2000). Temporal (i.e. daily and seasonal) and micro-topographic variation in soil respiration and its components are largely driven by differences in $T_s$ and moisture (Howard and Howard, 1993). The

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various components of $R_s$ may show different responses to $T_s$ and soil water content (Boone *et al.,* 1998). Measurements of environmental factors, soil C, and root parameters, paired with soil respiration measurements, may assist in explaining the variability in soil respiration (Pangle and Seiler, 2002). However, no studies have yet simultaneously examined the influence of $T_s$ and moisture on soil respiration alongside other factors such as root and soil C characteristics on spatial and temporal scales.

On the global scale, soil respiration at 75 Pg C $year^{-1}$ is the second largest carbon flux into the atmosphere after the contribution of the oceans (Schlesinger and Andrews, 2000), and small changes in $R_s$ could therefore significantly affect the atmospheric $CO_2$ concentration. Raich and Schlesinger (1992) estimated that global soil respiration is comprised of 50 Pg C $year^{-1}$ from detritus and 18 Pg C $year^{-1}$ from live roots and mycorrhizae. The contribution of each component needs to be determined in order to evaluate the implications of environmental change on soil carbon cycling. Concern over rising atmospheric $CO_2$ levels has raised questions about the effects of forest management on soil C and the ability of a forest to act as a C sink or source (Johnson, 1992). Forest harvesting has at least three main effects on forest carbon sources. First, timber harvesting effectively removes the aboveground carbon biomass and transfers it into products with short or intermediate residency time (paper products, lumber, building products) relative to natural forest carbon stocks (Harmon *et al.,* 1990). Second, elimination of the photosynthetic tree biomass causes a reduction in the uptake of C through photosynthesis in the years immediately following harvest, which may affect site productivity. Finally, changes in belowground carbon and soil physical and chemical properties following harvesting can alter $CO_2$ fluxes. The combination of the above-mentioned effects has led to speculation that intensified forest management (deforestation) will cause a reduction in soil C between 10% and 50%, depending on the treatment (Johnson, 1992; Davidson and Ackerman, 1993); these effects are also primarily responsible for increases in the exchange of $N_2O$, $CO_2$, and $CH_4$ between soils of terrestrial ecosystems and the atmosphere (Bouwman, 1990).

The literature describes different effects of forest management on soil respiration. First, forest management increases the $R_s$ rate, because, for example, clear-cutting may accelerate the turnover of detrital and soil C pools, including roots, litter, forest floor organic matter, litter fall, and mineral soil organic matter. This management practice may cause significant net export of carbon from the belowground system to the atmosphere (Lytle and Cronan, 1998). Clear-cutting in coniferous ecosystems has been shown to cause increased soil respiration (Ewell *et al.,* 1987; Toland and Zak, 1994). Edwards and Ross-Todd (1983) observed greater forest floor respiration rates in uncut control mixed deciduous eastern (USA) forests than in harvested stands approximately 5 months after harvest. Frazer *et al.* (1990) reported a similar pattern in mixed conifer forests on the Sierra Nevada (USA). Other studies have found similar responses of $R_s$ to clear-cutting. These reduced field respiration rates could be caused by a reduction in root respiration (Ewell *et al.,* 1987; Ohashi *et al.,* 2000) due to the reduction in the number of living roots.

Forest management also can affect intrasite microclimatic conditions. Removal of aboveground vegetation is known to increase $T_s$ (Lewis, 1998), and a strong positive correlation has been found between soil respiration and $T_s$ (Fernandez et *al.,* 1993), which can lead to the mobilization of belowground carbon stocks.

The objectives of this study are: (1) to investigate the variation of $R_s$, water content, and temperature across sites in a mature larch stand at Tomakomai National Forest; (2) to analyze the effect of timber harvesting (thinning) on $R_s$; and (3) to determine the relationships between $R_s$ and chemical soil properties. We chose a thinning site and a matched control site to assess the effect of disturbance on $R_s$. Temperature, water content, density of fine roots, and the C/N ratio were measured to explain the variation in $R_s$ at these sites.

## MATERIALS AND METHODS

### Area descriptions

The present work was undertaken in a 50-year-old (in 2003) larch plantation located in Tomakomai National Forest (42°44'N, 141°31'E, altitude is 115-140 m a.s.1.) in Hokkaido, Japan. The site has a flat topography, with gentle slopes not exceeding a gradient of 1 to 2 degrees. The soil is homogeneous, well-drained arenaceous soil derived from volcanic ash from Mt. Tarumae, an active volcano, and is classified as Volcanogenous Regosols (pumice). The soil pH ranges from 5.0 to 6.0, and

**Table 1.** Stand characteristics before and after thinning in January 2003 (personal communication with Prof. T. Hirano).

| Species | Condition | Density (trees $ha^{-1}$) | Basal area ($m^2$ $ha^{-1}$) | Aboveground biomass (ton $ha^{-1}$) |
|---|---|---|---|---|
| Larch trees | Before thinning | 716.0 | 24.1 | 82.8 |
| | After thinning | 480.0 | 17.7 | 61.2 |
| | Difference, % | 33 | 27 | 26 |
| Broadleaved trees | Before thinning | 505.0 | 5.9 | 23.8 |
| | After thinning | 421.0 | 5.4 | 22.2 |
| | Difference, % | 17 | 9 | 7 |

the nutrient level is poor with a high porosity. The humus content is about 0.1%, and the litter layer has a thickness of 1 to 2 cm. The estimated root biomass of 13.1 Mg $ha^{-1}$ was mainly confined to a narrow soil zone (10-15 cm) between the overlying layer of litter and the underlying, water-deficient, porous pumice (Qu, 2004). This forest lies in a cool temperate forest zone.

The tree cover at the site was predominantly Japanese larch *(Larix kaempferi* (Lam.) Carr.), and was interspersed with Japanese spruce *(Picea jezoensis* Sieb. et Zucc.) and mixed broadleaved species (birch, oak, magnolia, etc.). Stand characteristics before and after thinning in January 2004 are shown in Table 1. General stand traits of *L kaempferi are* as follows: the mean tree height measured in 2000 was 18-20 m, the depth of the forest canopy was 8.9 m, the tree age (as of 2003) was 50 years, the stand volume measured in 1999 was 145 $m^3$ $ha^{-1}$ (Qu, 2004). The forest understory was mainly composed of *Dryopteris crassirhizoma* Nakai, *Dryopteris expansa* (C.Presl) Fraser-Jenk. & Jermy, and *Pachysandra tenttinalls* Sieb. et Zucc.

The site is characterized by a humid climate, with cold winters and cool summers. The mean annual precipitation at the site is approximately 1250 mm, and the mean annual temperature is 7.3℃, with a variation in the monthly mean value ranging from 19.1℃ in August to -3.2℃ in January. Maximal, minimal, and mean air temperatures at 1.3 m measured from June to October 2003 were 26.4℃, 0.8℃, and 16.1±0.1℃, respectively. Maximal, minimal, and mean $T_s$ values at 10 cm depth, measured at the same time, were 20.9℃, 9.7℃, and 16.3 ± 0.1 ℃, respectively (Qu, 2004).

To examine the effects of thinning on soil respiration ($R_s$), we selected two sites. One of them was selected as a control site (which had been thinned approximately 15 years ago), and another one adjacent to it was used as the disturbed site (thinned in January 2004). The size of both control and disturbed sites was about 40 m x 40 m each, and they were immediately adjacent to each other. The thinning treatment (i.e., partial harvest) was conducted on the mature plantation in January 2004, i.e. half a year before $R_s$ measurements. To evaluate the soil $CO_2$ flux of the larch plantation, we measured the spatial variation of the $R_s$. We established 30 sample plots in the control site and 36 sample plots in the disturbed site. The size of each sample plot was 1 m x 1 m, and sample plots were adjacent to each other within the control or disturbed site. We combined $R_s$ measurements with measurements of temperature, mineral soil water content, and other environmental variables to track the component fluxes of the $R_s$.

**Soil respiration measurements**

Soil respiration ($R_s$) was measured at the end of July (27-30 July, 2004) at all plots in the control and disturbed sites. We measured $R_s$ with a Li-Cor LI-6400 infrared gas analyzer equipped with a chamber (Li-Cor 6000-09). Measurements were made on fixed collars in the control and harvested sites in order to minimize measurement errors associated with disturbance of the soil and roots. Three respiration collars were put in place in each sample plot (sample plot size: 1 m x 1 m). Two collars were placed on the sides of a sample plot and one collar was positioned in the center of the plot. The total number of collars at the control and disturbed sites was, therefore, 90 (30 sample plots x 3 collars) and 108 (36 sample plots x 3 collars). The collars (diameter 10.2 cm, PVC) were inserted to a depth of 1.5 cm to ensure a good seal between the soil and collar, but also to minimize root severing at least 10 days prior (16 July, 2004) to the initial measurements; they were left in place for the duration of the experiment. No vegetation was present inside the collars. A portable

thermometer was used to measure $T_s$ at a 5 cm depth concurrently with $R_s$ measurements at each collar. The soil respiration was calculated from the increase in $CO_2$ concentration over time, the volume of the entire system (991 $cm^3$), and the enclosed soil surface area (71.6 $cm^2$). The closed chamber employed a pressure equilibration tube, which eliminated the effect of chamber pressurization on the measured soil respiration. The measurements customarily started at 10:30 and ended at 18:00. For analysis, we used the average value of the three collar measurements per sample plot (30 sample plots at the control site and 36 sample plots at the disturbed site). Variability of the $R_s$ values within an ecosystem was described by the coefficient of variation (CV). The significance of differences in values between the control and disturbed sites was determined using the appropriate t-test. Statistical analysis of the data was performed with STATISTICA 6.0, StatSoft routines.

**Chemical and soil properties**

Two soil cores (5.3-cm diameter, 10 cm deep) were taken just after the respiration measurement from each respiration collar (the same spot the $R_s$ measurements were taken) to obtain soil textures and determine the density of roots, mineral soil water content, litter water content, and C/N in the soil core. In total, 180 and 216 soil cores were taken from the control site and the disturbed site, respectively. These parameters should suffice to explain the variations in $R_s$.

One soil core was used for mineral soil and litter gravimetric water determination. The soil sample was divided into mineral soil and litter subsamples, which were weighed before and after drying at 70°C for 72 hours to a constant weight. The water content (%) was calculated using the following equation:

$$W = \frac{M_f - M_d}{M_f} * 100$$

where W is the gravimetric water content (%), $M_f$ is the weight of fresh mineral soil or litter (g), and $M_d$ is the weight of mineral soil or litter dried at 70°C for 72 hours (g).

The second soil core was sieved (<2 mm) and the roots were removed by hand-picking and washing. The amount of root tissue was determined by weighing after drying, and was calculated per core volume (g $m^{-3}$) as the density of fine roots. Mineral soil subsamples were oven-dried at 70°C for 72 hours and homogenized. The C and N content were analyzed with an N-C analyzer (NC900, Shimadzu, Kyoto, Japan).

## RESULTS

**Soil respiration**

During the study period (27-30 July, 2004), the $R_s$ rate varied from 5.6 to 12.1 μmol $m^{-2}$ $s^{-1}$ at the control site, and from 4.5 to 19.8 μmol $m^{-2}$ $s^{-1}$ at the disturbed site (Figure 1). $R_s$ values in the disturbed site had higher variation than in the control site (CV=18.6% for control site, and CV=33.2% for the disturbed site) (Figure 1). The t-test found no significant differences in mean $R_s$ values (Table 2) between the control and disturbed sites.

**Effect of soil temperature and water content on soil respiration**

The soil temperature varied more at the disturbed site than at the control site (CV=1.6% for control site vs. CV=3.4% for disturbed site)

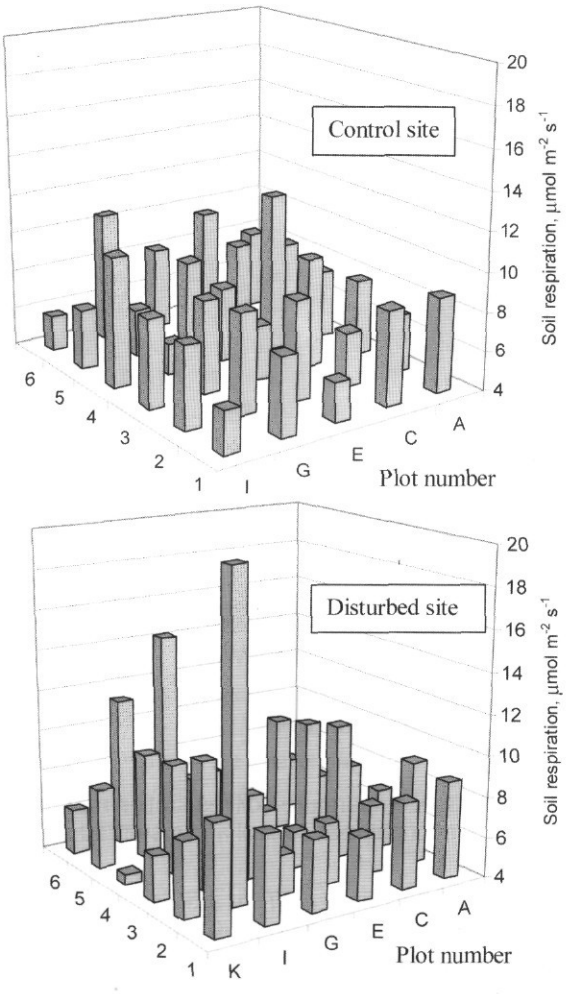


**Figure 1.** Variation of soil respiration (mmol $m^{-2}$ $s^{-1}$) at control and disturbed sites.

**Table 2.** Mean values with SE of soil respiration and related factors at control and disturbed sites.

| Parameters | Control site | Disturbed site | t-test | P |
|---|---|---|---|---|
| $R_s$ rate (μmol $m^{-2}$ $s^{-1}$) | 8.1±0.3 | 8.3±0.5 | -0.33 | 0.73 |
| $T_s$ (°C) | **19.6±0.06** | **21.5±0.1** | **-12.74*** | **0.00000** |
| MSWC (%) | 45.6±1.38 | 47.6±1.2 | -1.13 | 0.26 |
| LWC (%) | 67.2±0.7 | 65.3±0.7 | 1.83 | 0.07 |
| MSWC+LWC (%) | 60.3±1.0 | 58.0±1.4 | 1.29 | 0.20 |
| Density of fine roots (g $m^{-3}$) | 74.0±3.9 | 60.6±9.0 | 1.29 | 0.20 |
| **Density of litter (g $m^{-3}$)** | **1344.2±44.7** | **1150.5±49.7** | **2.86*** | **0.006** |
| C (%) | 11.5±0.9 | 12.4±0.7 | -0.82 | 0.42 |
| **N (%)** | **0.75±0.03** | **0.91±0.04** | **-3.29*** | **0.002** |
| C/N | 15.3±1.0 | 13.5±0.4 | 1.84 | 0.07 |

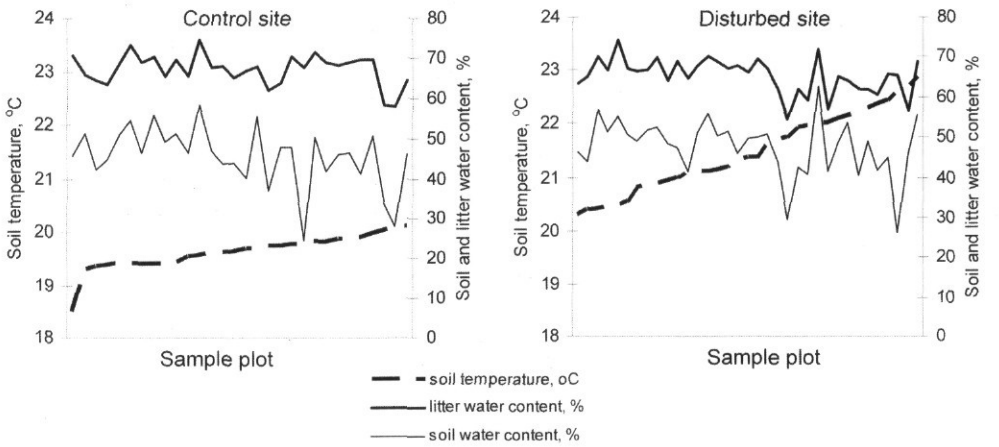


**Figure 2.** Spatial variation of soil temperature, mineral soil water content, and litter water content at control and disturbed sites.

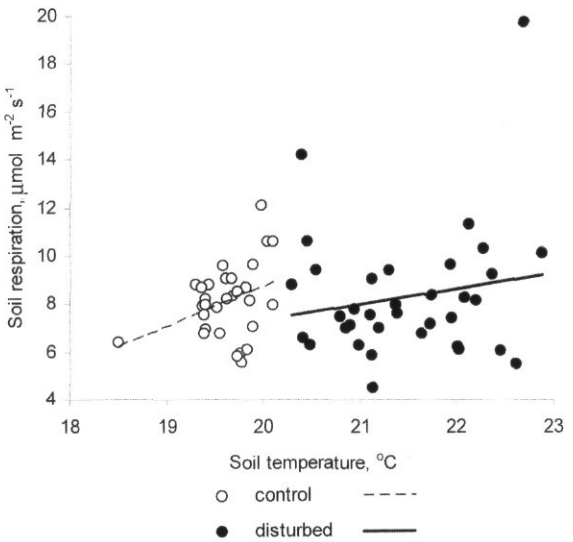


**Figure 3.** Soil temperature-soil respiration rate (μmol $m^{-2}$ $s^{-1}$) relationships at control and disturbed sites.

(Figures 2-3). The mean $T_s$ at the control site was significantly lower than that at the disturbed site (Table 2), and this difference could be due to location. No significant correlation was observed between spatial variations in $T_s$ and $R_s$ at either the control site or the disturbed site (Table 3). However, we found significant negative correlations between $T_s$ and LWC and between $T_s$ and MSWC+LWC at the disturbed site (Table 5).

MSWC showed an insignificant correlation to $R_s$ at both sites (Table 3). However, we found significant positive correlations between MSWC and LWC at the control site (Table 4) as well as at the disturbed site (Table 5). In addition, there were reliable correlations between MSWC and soil C, soil N, and the C/N ratio at the control site (Table 4) and significant correlations between MSWC and soil C, soil N, and the C/N ratio at the disturbed site (Table 5). MSWC varied slightly more at the control site than at the disturbed site (CV=16.5% for the control site, CV=14.8% for the disturbed site), and was in the range of 24.5% to 58.1% at the control site and 26.3% to 62.5% at the disturbed site (Figure 2). We did not find any significant difference between the MSWCs at the control and disturbed sites (Table 2).

LWC showed insignificant correlation with $R_s$ at the control site, while at the disturbed site, it was negatively correlated with $R_s$ (r=-0.41, P<0.05, Table

**Table 3.** Analysis of the correlation of factors influencing soil respiration (μmol $m^{-2}$ $s^{-1}$) at control and disturbed sites.

| Factors | Control site | Disturbed site |
|---|---|---|
| $T_s$ (°C) | 0.35 | 0.17 |
| MSWC (%) | 0.11 | **-0.04** |
| LWC (%) | -0.23 | -0.41* |
| MSWC+LWC (%) | 0.20 | -0.05 |
| Density of fine roots (g $m^{-3}$) | 0.25 | -0.06 |
| Density of litter (g $m^{-3}$) | 0.18 | **0.40*** |
| C (%) | 0.08 | 0.09 |
| N (%) | 0.06 | -0.14 |
| C/N | 0.10 | **0.39*** |

*Marked correlations are significant at P<0.05.

3). Significant correlations were found between LWC and soil C and N at both sites (Table 4 and 5). LWC varied slightly more at the disturbed site than at the control site (CV=5.6% for control site, CV=6.7% for disturbed site), ranging from 57.8% to 74.5% at the control site and 54.4% to 74.1 % at the disturbed site. LWC at the control site did not differ significantly from that at the disturbed site (Table 2).

Within the study period, $R_s$ was better correlated with LWC (r=-0.41, P<0.05) than with $T_s$ or MSWC at the disturbed site; for the control site, we did not find any statistically significant correlations between $R_s$ and $T_s$, MSWC, or LWC. Correlations between $R_s$ and MSWC or LWC tend to be negative at both the control and disturbed sites.

**Effect of density of fine roots on soil respiration**

There were no statistically significant relationship between $R_s$ and the density of fine roots was observed at either site (Table 3, Figure 4). Therefore, root density was not an important factor influencing the $R_s$ rate in this study. The mean value of the density of fine roots at the control site was 18% higher than at the disturbed site, but this difference was not statistically significant (Table 2). This reduction in root density seems to be due to the thinning of the stand at the disturbed site in January 2004. The variation in root density was

**Table 4.** Within-site correlations of variables at the control site (N=30).

| Factors | $R_s$ | $T_s$ | MSWC | LWC | D | LD | MSWC +LWC | C | N | C/N |
|---|---|---|---|---|---|---|---|---|---|---|
| $R_s$ | 1 | | | | | | | | | |
| $T_s$ | 0.35 | 1 | | | | | | | | |
| MSWC | 0.11 | -0.35 | 1 | | | | | | | |
| LWC | -0.24 | -0.34 | 0.63* | 1 | | | | | | |
| Density of fine roots (D) | 0.25 | -0.16 | -0.13 | -0.40* | 1 | | | | | |
| Density of litter (LD) | 0.18 | 0.27 | -0.36* | -0.79* | 0.27 | 1 | | | | |
| MSWC+LWC | 0.20 | -0.24 | 0.88* | 0.76* | -0.24 | -0.47* | 1 | | | |
| C | 0.08 | -0.18 | 0.67* | 0.37* | -0.13 | -0.04 | 0.63* | 1 | | |
| N | 0.06 | 0.02 | 0.42* | 0.40* | 0.02 | -0.07 | 0.46* | 0.51* | 1 | |
| C/N | 0.10 | -0.17 | 0.54* | 0.15 | -0.12 | -0.01 | 0.46* | 0.83* | -0.02 | 1 |

*Marked correlations are significant at P<0.05.

**Table 5.** Within-site correlations of variables at the disturbed site (N=35).

| Factors | $R_s$ | $T_s$ | MSWC | LWC | D | LD | MSWC+ LWC | C | N | C/N |
|---|---|---|---|---|---|---|---|---|---|---|
| $R_s$ | 1 | | | | | | | | | |
| $T_s$ | 0.17 | 1 | | | | | | | | |
| MSWC | -0.04 | -0.32 | 1 | | | | | | | |
| LWC | -0.41* | -0.45* | 0.69* | 1 | | | | | | |
| Density of fine roots (D) | -0.06 | -0.06 | 0.16 | 0.16 | 1 | | | | | |
| Density of litter (LD) | 0.40* | -0.18 | 0.28 | 0.09 | 0.15 | 1 | | | | |
| MSWC+LWC | -0.05 | -0.42* | 0.89* | 0.73* | 0.26 | 0.43* | 1 | | | |
| C | 0.09 | -0.08 | 0.91* | 0.38* | 0.01 | 0.22 | 0.53* | 1 | | |
| N | -0.14 | -0.22 | 0.61* | 0.52* | 0.21 | 0.15 | 0.61* | 0.77* | 1 | |
| C/N | 0.39* | 0.08 | 0.56* | -0.10 | -0.21 | 0.25 | 0.13 | 0.56* | -0.07 | 1 |

*Marked correlations are significant at P<0.05.

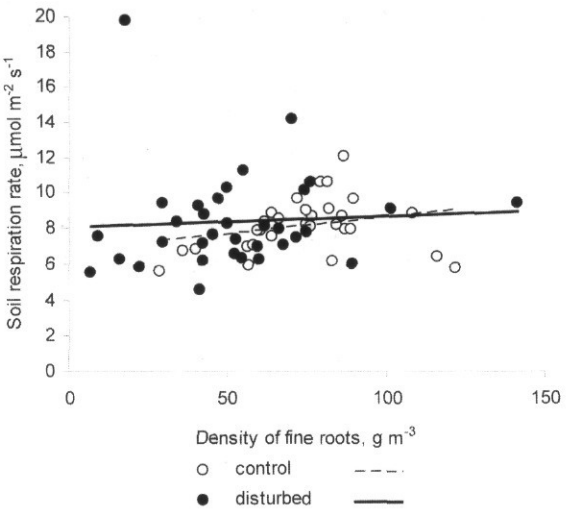


**Figure 4.** Soil respiration rate (μmol $m^{-2}$ $s^{-1}$) depending on fine root density (g $m^{-3}$) at control and disturbed sites.

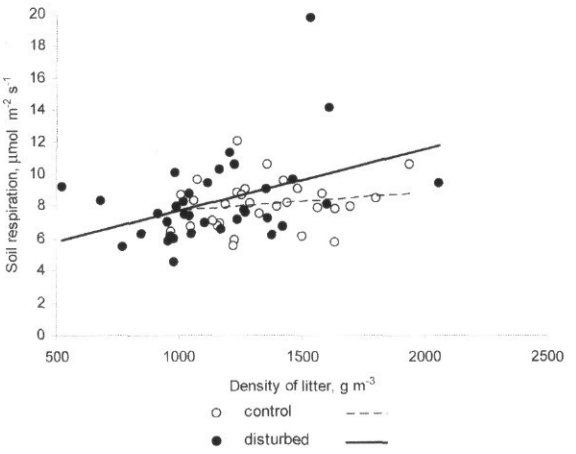


**Figure 5.** Soil respiration rate (μmol $m^{-2}$ $s^{-1}$) depending on litter density (g $m^{-3}$) at control and disturbed sites.

much greater at the disturbed site (CV=88.1%) than at the control site (CV=28.6%) (Figure 4).

**Effect of litter density on soil respiration**

Next, we looked at how the density of litter can affect the $R_s$ rate. The litter density at the disturbed site was significantly lower (by 15%) than that at the control site (Table 2). The litter density at the disturbed site (CV=25.6%) showed greater variation than at the control site (CV=18.2%), varying from 965.0 to 1941.3 g $m^{-3}$ at the control site and from 524.8 to 2057.5 g $m^{-3}$ at the disturbed site (Figure 5). We did not find any significant correlation between $R_s$ and litter density at the control site, but there was positive correlation between these variables at the disturbed site (Table 3).

**Soil respiration and soil C, soil N, and C/N ratio**

The soil carbon-nitrogen ratio showed significant correlation with $R_s$ only at the disturbed site (Table 3). The C and N content did not significantly influence the $R_s$ rate at either site (Table 4-5). Moreover, the soil C content was correlated with the soil N content and the C/N value at both the control site and the disturbed site (Table 4-5). These C and C/N values varied slightly more at the control site than at the disturbed site, whereas the N values showed higher variation at the disturbed site. The soil C content ranged from 4.0% to 22.5% at the control site and from 5.5% to 23.0% at the disturbed site. The soil N content varied from 0.5% to 1.1% at the control site and from 0.4% to 1.4% at the disturbed site. The soil C/N value ranged from 7.2 to 28.4 at the control site and from 8.9 to 22.8 at the disturbed site. The soil C content at the control site did not differ significantly from that at the disturbed site, whereas the soil N content was significantly higher at the disturbed site than at the control site (Table 2). The soil C/N value at the control site was not significantly different from that at the disturbed site (Table 2).

**Combined effect of factors on $R_s$**

Multiple regression analysis for the variables measured at the control and disturbed sites showed that $R_s$ was influenced by the following factors: at the control site ($R^2$=0.54, F=5.55, P=0.002, N=30) - $T_s$ (partial coefficient of correlation (PCC) = 0.42, P=0.03), LWC (PCC=-0.49, P=0.01), MS+LWC (PCC=0.64, P=0.0004), root density (PCC=0.27, P=0.18), and litter density (PCC = -0.24, P=0.24); and at the disturbed site ($R^2$= 0.42, F=7.55, P=0.0006, N=35) - LWC (PCC= -0.48, P=0.005), litter density (PCC=0.43, P=0.01), and the C/N value (PCC=0.31, P=0.08). The combined effect of $T_s$, LWC, MS+LWC, root density, and litter density explains 54% of the variation in $R_s$ at the control site. At the disturbed site, the joint influence of LWC, litter density, and C/N value explains 42% of the variation.

## DISCUSSION

Soil **respiration**

The soil respiration rates observed in a larch plantation at control and thinned sites displays a strong pattern of spatial variation (Figure 1). At the control site, variation of $R_s$ (from 5.6 to 12.1 μmol $m^{-2}$ $s^{-1}$) was less than that recorded at the dis-

turbed site (from 4.5 to 19.8 μmol $m^{-2}$ $s^{-1}$). As mentioned, there are several possible causes of this large spatial heterogeneity, including horizontal heterogeneity in the amount of roots, in litter availability and thickness, in the C/N ratio, etc. The observed $R_s$ rates are consistent with rates found in other ecosystems at similar temperatures. Thus, Klopatek (2002) estimated a soil respiration of 5 μmol $m^{-2}$ $s^{-1}$ for old-growth Douglas-fir stands in south central Washington State (USA). According to Yim *et al.* (2003), the mean $R_s$ rate at the end of August in a larch plantation in Hokkaido was 797.0 mg $CO_2$ $m^{-2}$ $h^{-1}$ (8.0 μmol $m^{-2}$ $s^{-1}$).

Forest management can influence the $R_s$ rate in various ways. We find that thinning management tends to increase $R_s$ and leads to large variation in the $R_s$ rate seven months after treatment. For example, we found that after thinning, the $R_s$ rate was slightly but not significantly higher than that at the control site (Table 2), averaging about 8.3 μmol $m^{-2}$ $s^{-1}$ at the disturbed site; this tendency is consistent with the others reported for other coniferous ecosystems. Thus, according to Carter et *al.* (2002), harvesting in *Pinus taeda* L. stands did not affect $R_s$, which varied from 10.7 to 10.9 g $m^{-2}$ $day^{-1}$ (2.8 to 2.9 μmol $m^{-2}$ $s^{-1}$) at their control site and from 10.6 to 11.7 g $m^{-2}$ $day^{-1}$ (2.8 to 3.1 μmol $m^{-2}$ $s^{-1}$) at their harvested site at 17.5°C. Ohashi et *al.* (2000) found that $R_s$ rates in a Japanese cedar *(Cryptomeria japonica* D. Don) forest in the first year of felling in July ranged from 442.0 to 520.0 mg $CO_2$ $m^{-2}$ $h^{-1}$ (2.8 to 3.3 μmol $m^{-2}$ $s^{-1}$), with a comparable mean of 482.0 mg $CO_2$ $m^{-2}$ $h^{-1}$ (3.0 μmol $m^{-2}$ $s^{-1}$) for control plots. Soil $CO_2$ losses from harvest sites were equal to losses at control sites in these studies, which suggests that greater microbial respiration in the clear-cut plots should compensate for reduced respiration of living roots.

Some studies have reported increased release of soil $CO_2$ in the aftermath of forest clear-cutting. Thus, Ewell *et al.* (1987) estimated that the release of forest floor $CO_2$ doubled after clear-cutting in a Florida slash pine system. According to Londo *et al.* (1999), harvesting significantly increased ***in situ*** $R_s$ to 6.0 g $CO_2$ $m^{-2}$ $day^{-1}$ (1.6 μmol $m^{-2}$ $s^{-1}$) after partial cutting; the control value is 5.0 g $CO_2$ $m^{-2}$ $day^{-1}$ (1.3 μmol $m^{-2}$ $s^{-1}$). This increase can be attributed to an increase in live roots and microflora activity, and increased decomposition associated with postharvesting, revegetation, and recolonization. In our study, the effect from thinning was not so sizeable because the larch stand density and broad-leaved tree density were reduced by only 33% and 17%, respectively, after thinning management (Table 1). Therefore, the thinning was not so severe as to cause critical changes in soil respiration.

However, some reports assert that partial or clear-cutting reduces the $R_s$ value. According to Striegl and Wickland (2001), the clear-cutting of a Saskatchewan jack pine forest resulted in a >50% reduction in $R_s$ compared with mature forest (12.1 mol C $m^{-2}$ in clear cut versus 24.9 mol C $m^{-2}$ in mature stand). Our observations disagree with those of Striegl and Wickland. In their study, the initial decline probably resulted from the death of the roots of trees and ground-cover plants, and the subsequent increase is probably due to the establishment and growth of new plants that benefit from the removal of the canopy. Microbial respiration also probably increases as the decomposition of dead tree roots and slashed material proceeds, and the peak daily $T_s$ increases because of the absence of the canopy.

**Effect of soil temperature and water content on soil respiration**

The dynamics of soil and litter are governed by a complex interaction of factors that include respiration rate, litter input, climatic parameters, and soil C and N (Covington et *al.,* 1981). Concerning climatic factors, some authors propose that $R_s$ depends mostly on $T_s$ (Ohashi et *al.,* 2000; Klopatek, 2002; Gough and Seiler, 2004); few studies assert that it depends strongly on soil water content (Parker et *al.,* 1983; Jiang et *al.,* 2005). Kang et *al.* (2003) did not observe significant correlations between $R_s$ rates and $T_s$ for temperate mixed-hardwood forests at latitudes similar to those of the present study. Merino et *al.* (2004) found that in oak *(Quercus robur)* forest soil, the $CO_2$ flux was weakly correlated with soil moisture and $T_s$.

There are different opinions regarding the effect of harvesting and thinning management on the environmental parameters of the soil. Some studies did not find any significant changes in $T_s$ or water content (Carter *et al*., 2002), and some found differences in microclimatic parameters after thinning or clear-cutting, particularly higher $T_s$ (Lytle and Cronan, 1998).

Although the effect of $T_s$ on $R_s$ has been widely confirmed by many researchers, we found that $R_s$ was not strongly dependent on either $T_s$ or soil water content (e.g., Jiang et *al.,* 2005). A likely explanation for the absence of any relationship

between $T_s$ and $R_s$ is the 7.5-hour study period (from 10:30 to 18:00) and the use of only a few days in July, which restricted the overall variation in the $T_s$ during the study period. Specifically, the $T_s$ varied from 18.5℃ to 20.1℃ at the control site and from 20.3℃ to 22.9℃ at the disturbed site. It is not easy to find a correlation between respiration and $T_s$ within a range of 2 to 3℃. However, we observed significant negative correlation between $R_s$ and LWC at the disturbed site (Tables 3, 5). This finding points to the high sensitivity of litter microbiota to moisture and their important role in the process of litter decomposition, especially after thinning. Consequently, the main decomposition process takes place in litter rather than in soil. This is confirmed by the fact that most fine roots of larch trees are located in the litter layer; after thinning, they become damaged and start to decay. Therefore, although $R_s$ depends strongly on the $T_s$ and MSWC, these two factors do not contribute greatly to the spatial variability of $R_s$ observed in this study. These relationships suggest that the $T_s$ and moisture content influence the temporal variability of $R_s$ even more strongly than they affect the spatial variability.

In our study, the temperature during measurement was within the normal range, and rainfall was adequate to abundant for the study region (Qu, 2004). The mean $T_s$ at the control site (19.6℃) differed significantly from that at the disturbed site (21.5℃) because the stand density of the disturbed site was decreased after thinning (Table 1). The mean MSWC values did not differ significantly between the control site (45.6%) and the disturbed site (47.6%) (Table 2). In addition, there were no consistent significant differences in litter water content between the sites (at control site, LWC=67.2%; at disturbed site, LWC=65.3%; Table 2). In spite of the significant differences in $T_s$ between the sites, MSWC and LWC displayed similar patterns at both sites (Figure 2). Many authors (e.g., Witkamp, 1971; Marks and Bormann, 1972) have speculated that devegetation of forest lands leads to higher rates of decomposition and higher $R_s$ rates as a result of increased $T_s$ and moisture content. In spite of these hypothesized relationships with $T_s$ and water content, we did not observe any significant difference in the $R_s$ rate after thinning.

**Soil respiration affected by fine root density**

The relationship between roots and $R_s$ is obvious. In particular, $R_s$ can be affected by variation in tree roots at differing positions. Pangle and Seiler (2002) reported a relationship between measurement position and soil respiration, finding higher rates near the base of trees than between rows in a *Pinus taeda* L plantation in the Virginia Piedmont. Consequently, spatial differences in $R_s$ may be due, in part, to variability in the distribution of roots within sites. In addition, Boone *et al.* (1998) showed that variations in $R_s$ throughout the growing season in a temperate hardwood forest are determined mainly by the responses of root respiration and rhyzospheric heterotrophs to variations in temperature. Nevertheless, some studies have reported no significant correlation between roots and $R_s$. On the South Carolina Coastal Plain, Gough and Seiler (2004) found that the root surface area or root volume in the top 20 cm of mineral soil directly below the chamber was not related to soil respiration. We also did not find any significant difference in the density of fine roots between control and disturbed sites; the average root density at the control site was 18% greater than that at the disturbed site (Table 2), and can result from the removal of 26% of larch tree biomass and 7% broad-leaved tree biomass (Table 1) after thinning management. According to Qu (2004), the proportion of root respiration in total $R_s$ at a larch plantation in Tomakomai National Forest in 2001-2003 ranged from 18% to 52%. Our study did not find any changes in the $R_s$ rate after thinning. We believe that the 18% reduction of fine root density following thinning in our study is compensated for by increased microbial respiration as a result of the decomposition of dead roots after felling. Toland and Zak (1994) similarly reported that acceleration of microbial respiration offsets a decline in root respiration in the first year of clear-cutting in northern hardwood forests. There have been similar findings in hardwood forest (Londo *et al.,* 1999) and spruce-fir stands (Lytle and Cronan, 1998). Clearly, the rapid decomposition of dead roots is able to compensate for the decrease in root respiration in the first year.

**Soil respiration affected by litter density and soil C and soil N content**

We found that the litter density is significantly lower at the disturbed site than at the control site. Even partial cutting (thinning) changed the litter density and increased its variation, which can influence the soil respiration. Thinning caused considerable variation in litter density, from 524.8 to 2057.5 g $m^3$ in the disturbed site compared to

965.0 to 1941.3 g $m^{-3}$ at the control site. Qu (2004) states that the contribution of litter respiration to $R_s$ varies from 8% to 32% at a larch plantation at Tomakomai National Forest. This indicates that litter decomposition is an important factor in the soil $CO_2$ flux. According to a number of studies, the total C and N in the surface soil (0-10 cm) responded to harvesting. Levels declined during the first year after harvesting, and increased during the second year (Carter *et al.,* 2002). After reviewing a number of studies, Johnson (1992) concluded that harvesting resulted in changes of <10% of the pre-harvest soil C content. Our findings are in agreement with this conclusion, although major fluctuations may last for months or years before the soil C returns to pre-harvest levels. In terms of the soil C and N contents, we found a fairly similar pattern to that reported by Johnson (1992); seven months after thinning, the C and N contents in the surface soil were higher (for C: about 7%, t-test=-0.82, P=0.42; for N: about 18%, t-test=-3.29, P=0.002) at the disturbed site (C= 12.4%, N=0.91%) than at the control site (C= 11.5%, N=0.75%), although the difference in the C content was not statistically significant. Our results are consistent with the data used by Qu (2004), in which the soil C at a larch plantation in Tomakomai National Forest varied from 5 to 25%, and the soil N ranged from 0.2 to 1.5%.

In our study, the C/N ratio in the upper 10 cm of mineral soil remained fairly constant, and the mean value of C/N was similar at the control and disturbed sites, with values of 15.3 and 13.5, respectively. The C/N ratio found in our study is lower than that observed by Carter *et al.* (2002) in soil in *Pinus taeda* L. stands in Los Angeles (USA), in which the C/N ratio was 22-27; Klopatek (2002) estimated the C/N value to be 24.9 and 28.0 for 40-year and old-growth sites, respectively. Like Gough and Seiler (2004), we observed a significant positive correlation between soil respiration and soil C/N in the top 10 cm of mineral soil at our larch plantation after thinning (Table 5).

**Combined effect of factors on soil respiration**

Analysis of the combined effect of all factors investigated in relation to $R_s$ revealed strong correlations between $R_s$ and the following factors (in upward order of coefficient of partial correlation): at the control site, MSWC+LWC, LWC, $T_s$, root density, and litter density; at the disturbed site, LWC, litter density, and C/N value. Of the climatic parameters studied, only LWC affected $R_s$ at both sites, and therefore can be considered the best predictor of $R_s$ in this study.

## CONCLUSIONS

We found that only a few parameters were influenced by harvesting (thinning) of a larch plantation in Tomakomai National Forest, Hokkaido, Japan, where the soil horizon is very shallow (around 20 cm) due to the deposition of volcanic ash. These parameters were $T_s$, litter density, and soil N content. This forest management practice resulted in only an insignificant increase in the $R_s$ rate, MSWC, and soil C content, and insignificant decreases of LWC, fine root density, and C/N ratio. Thinning management caused large variations in $R_s$, $T_s$, MSWC, fine root density, and litter density.

Of the microclimatic factors considered, LWC was the most significant factor influencing $R_s$ at the disturbed site, showing a greater effect than that of MSWC or $T_s$. However, the limited variation in the $T_s$ in this study (only 2-3℃) was insufficient to clarify the relationship between $T_s$ and respiration. At the control site, we did not observe any statistically significant correlation between microclimatic factors and soil respiration.

These changes in physical site conditions, along with changes in substrate availability, must cause changes in soil microbial respiration, but most likely also cause a decline in root respiration after thinning. This is because the loss of approximately 18% of fine root density can be compensated for by increased rates of heterotrophic respiration following the decomposition of dead roots after felling. The importance of soil C and N, and of $R_s$ for forest productivity and our global environment is such that further study is warranted to assess spatial variations in soil C and N levels.

Our results indicate that the application of standard temperature-based models to estimate soil respiration rates for larger geographic areas, covering different aspects or climatic conditions, can be insufficient if they do not include other factors such as LWC and C/N ratio.

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