Ecological Studies on Forest Soil Respiration

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Contents

Chapter 1 Introduction

1.1 Background

Atmospheric carbon fixed by photosynthesis of trees partly returns to the air through their respiration. However, most carbon stored above-and below-ground woody organs and are subsequently provided to soil as litterfall. These organic carbon compounds provided to the soil are stored and decomposed into CO_2 as a result of soil microbial respiration. Most CO_2 evolves from soil to air with the CO_2 produced by root respiration (Fig. 1-1-1). This CO_2 evolution from soil was described as soil respiration (Bodenatmung) by Lundegårdh (1924).

Pettenkofer (1873) measured soil respiration first as an indicator of soil microorganism activity. Waksman and Tenney (1928) demonstrated an increased bacterial response when soil was fertilized and early studies of soil respiration were carried out generally in order to ascertain fertility of soil in the laboratory and under agronomic conditions (Darbishire, et al., 1907; Gainey, 1919; Lundegårdh, 1924; Russell and Appleyard, 1915; Smith and Brown, 1931; Schlesinger, 1977). In the forest, soil respiration has been measured as an excellent indicator, representing the sum of soil metabolic activity, such as root system and soil microorganism, in order to estimate net primary production (Kirita and Hozumi, 1966; Kirita, 1971d; Hagihara et al., 1984; Kurser, 1989) and carbon cycling of the ecosystems (Witkamp, 1969; Kucera and Kirkham, 1971; Edwards and Sollins, 1973; Anderson, 1978; Simono et al., 1989).

Recently, the significance of the study of soil respiration has become more relevant because of environmental problems including

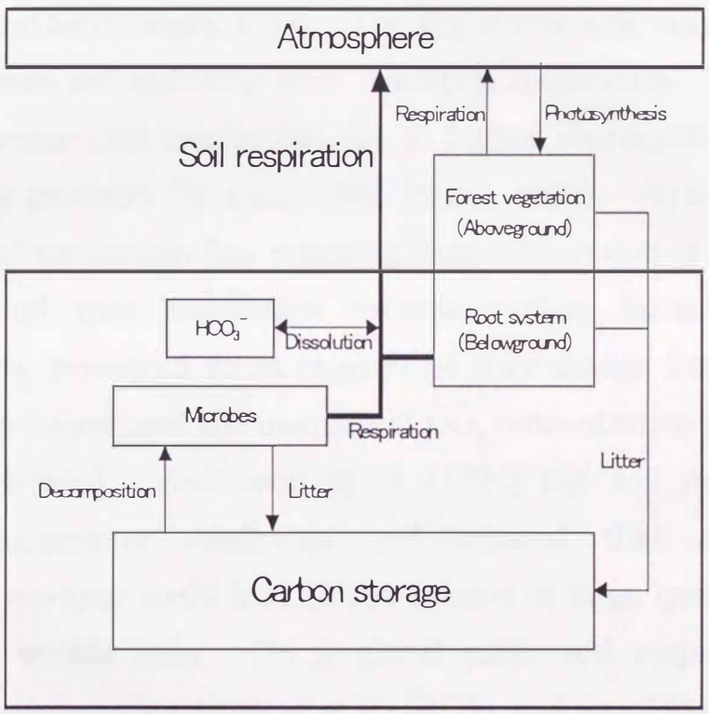


Fig. 1-1-1 Carbon cycle in the forest ecosystem.

global change in CO_2 concentration in the air. Global carbon is currently at about 750 GtC in atmosphere, 600 GtC in the world's standing biomass, and 1500 GtC in the world's soils (Fig. 1-1-2). Atmospheric CO_2 concentration is increasing rapidly by about 3.4 GtC per year due to fossil fuel burning and deforestation. Consequently, elevated CO_2 concentration would lead to global warming (Kirschbaum, 1995; Raich and Schlesinger, 1992). The global warming may increase carbon flux from soil resulting from microbial respiration. Warming may also increase root respiration due to higher photosynthesis and more primary products (Tsuruta, 1994; Pajari, 1995). As a result, if the increase of the carbon flux resulting from stimulation of microbial respiration and root respiration exceeds carbon fixing through photosynthesis, terrestrial forest ecosystems may change from carbon sink to carbon source and the increase in CO_2 concentration in the air may be accelerated. Jenkinson et al. (1991) ran soil models for different temperature conditions and showed that a future temperature increase could lead to the release of large quantities of carbon from worlds soils. On a global scale, soil respiration in terrestrial ecosystems is estimated at 50 GtC/yr and equal to or greater than the estimated global carbon terrestrial net primary production. By comparison fossil fuel burning and deforestation add about 5 GtC/yr and 1.6 GtC/yr, respectively. Even a small change in the soil respiration flux may profoundly influence the atmospheric CO_2 budget (Raich and Schlesinger, 1992; Kirschbaum, 1995).

Soil respiration is also important in evaluating the capacity of forest ecosystems to fix atmospheric carbon. Carbon fixing by photosynthesis and storage in above- and below-ground is expected to contribute to decreased carbon dioxide in the air. Houghton and Woodwell (1989) warned that global warming will continue into the

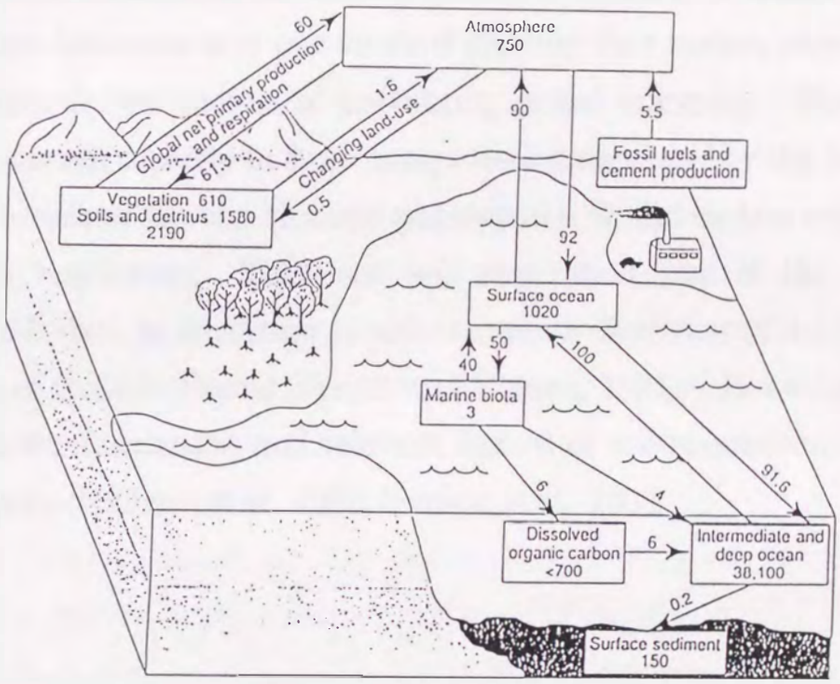


Fig. 1-1-2 The global carbon cycle, showing reservoirs (in GtC) and fluxes (GtC/yr) relevant to anthropogenic perturbation as an annual average over the period 1980 to 1989 (Houghton et al., 1995).

indefinite future unless we take deliberate steps, such as a massive program of reforestation, in order to slow or stop such warming. In addition, at the 3rd Conference of Parties to the United Nations Framework Convention on Climate Change in Kyoto in December 1977, the Kyoto Initiative was put forward starting that carbon storage by forestation is one means of preventing global warming. However, carbon storage capacity in forest ecosystems is regulated by the balance between carbon fixation through photosynthesis and carbon emission through respiration. Therefore, soil respiration, one of the major fluxes of carbon, is important in order to gain a clear view of the carbon storage of the ecosystems (Freijer and Bouten, 1991). However, data on amount, fluctuation and relevant factors of soil respiration is still inadequate (Haibara et al., 1993; Hanson et al., 1993).

1.2 History

Methodological approaches

Unfortunately, a wide variety of measurement techniques of soil respiration are utilized, making it difficult to compare results from different studies (Raich et al., 1992; Vose et al., 1995). Soil respiration has been measured using many techniques, such as the eddy correlation micrometeorological technique (Dugas, 1993; Baldocchi et al., 1997; Takeuchi, 1997), Fick's diffusion model (De Jong and Schappert, 1971; Osozawa and Hasegawa, 1995; Mariko et al., 1994; Eguchi et al., 1997), and chamber technique (Monteith et al., 1964; Kirita and Hozumi, 1966). However, since each technique has its own limitations (Inoue, 1986; Sparling and West, 1990; Behara et al., 1990; Dugas, 1993; Mariko et al., 1994; Komori and Seki, 1995; Shimada et al., 1998), accumulation of soil respiration data is still imperfect.

The chamber technique is the most common and direct method to measure soil respiration and is used widely (Schlesinger, 1977; Singh and Gupta, 1979; Gupta and Singh, 1981; Inoue, 1986). There are some variations in this technique and many researchers have discussed accuracy, the mobility and simplicity of each system (Witkamp, 1966; Kanemasu et al., 1974; Haibara et al., 1993; Mariko et al., 1994; Bekku et al., 1995; Uchida et al., 1997).

The static CO_2 absorption method determines CO_2 quantity released from the soil using a covered chamber, by irreversibly binding CO_2 to NaOH or soda lime in the chamber. This system is convenient under field conditions because of its simple construction and low-price (Monteith et al., 1964; Kirita and Hozumi, 1966; Kirita, 1971a～d; Parker et al., 1983; Buyanovsky et al., 1986; Meier et al., 1993; Robertson et al., 1995). However, some reports showed that the

difference in environmental factors inside and outside the chamber may influence readings (Kucera and Kirkham, 1971; Edwards and Sollins, 1973). Nakadai et al. (1993) reported that CO_2 concentration in the static chamber decreased greatly due to irreversible binding, thus, leading to overestimation of CO_2 evolution. Consequently, a closed chamber method, where CO_2 in the chamber is sampled periodically by syringes and which measured subsequently CO_2 concentration, was designed (Parkinson, 1981; Bekku et al., 1995).

The open-flow method calculates soil respiration from differences in CO_2 concentrations in the air flowing in and out of the chamber. This method is expected to have higher accuracy because environmental conditions in the chamber can be maintained parallel to ambient conditions (Nakadai et al., 1993; Vose et al., 1995). However, this method is considered to be less attractive for field measurements because it often requires bulkly equipment and an electric power supply (Kirita and Hozumi, 1966; Haibara et al., 1993; Bekku et al., 1995). In addition, Inoue (1986) noted that ventilation rate through the open-flow chamber might affect readings. Gyokusen and Saito (1995) addressed these problems by producing a portable soil respiration measuring system which could regulate CO_2 concentration, and wind speed in the chamber.

The closed-dynamic method or commercial soil respirometer (e.g. Li-Cor, Lincoln, NE) obtains measurements while CO_2 concentration in the chamber is increases due to air circulation through the system (Norman et al., 1992; Lassard et al., 1994; Garcia et al., 1997). Some have a fan in the chamber to make natural wind speed (Hanson et al., 1993). Therefore, this method is also expected to retain accurate readings because of the regulation of environment conditions in the chamber. However, unwieldy or expensive respirometers are difficult

to operate under field conditions.

Factors affecting soil respiration

Fluctuation in soil respiration from the forest floors can result from the interaction of many biological, physical and chemical factors. Accumulation of data on the fluctuation of soil respiration and factors that regulate that fluctuation are critical for the understanding soil respiration (Schlesinger, 1977; Reicosky and Lindstorm, 1993; Keith et al., 1997; Striegel and Wickland, 1998).

Temporal fluctuation in soil respiration corresponds mainly to changes in two environmental factors, soil moisture and temperature, because of the sensitive response of soil microbial activities and root respiration to these factors (Buyanovsky et al., 1986; Bowden et al., 1998; Singh and Gupta, 1977; Yata, 1989). Though seasonal change in soil respiration is influenced by the two factors, nevertheless the effect of the factors varies depending on geographical location (Singh and Gupta, 1977; Ohashi et al., 1999b). The strong effect of temperature (Kirita, 1971d; Anderson, 1973; Chiba and Tsutsumi, 1967; Mathes and Schriefer, 1985; Sakai and Tsutsumi, 1987), soil moisture (Carlyle and Than, 1988; Holt et al., 1990), and both factors (Buyanovsky et al., 1986; Schlentner and Van Cleve, 1985; Pajari, 1995) have been reported. Many studies reported that soil respiration increased exponentially (Kucera and Kirkham, 1971; Anderson, 1973; Hagihara et al., 1984; Sakai and Tsutsumi, 1987; Simono et al., 1989) or proportionally (Gupta and Singh, 1981; Mathes and Schrifer, 1985; Rochette et al., 1991; Lessard et al., 1994) with increasing temperature. Q_{10} value, calculated as the changing rate of soil respiration when the temperature increased by 10 ℃ (Johnson and Thronley, 1985), is a convenient index in comparing the sensitivity of soil respiration with

soil temperature (Sakai and Tsutsumi, 1987; Raich and Schlesinger, 1992). Recently, Q_{10} values are important to predict the response of ecosystems to global warming (Townsend et al., 1992; Kirschbaum, 1995). Q_{10} values tend to be higher in cooler regions compared with warm regions (Townsend et al., 1992; Kirschbaum, 1995), ranging 1.8～4.1 in temperate forests (Sakai and Tsutsumi, 1987), the mean of Q_{10} values for soil respiration being approximately 2.0 (Singh and Gupta, 1977; Raich and Schlesinger, 1992). Diurnal changes in soil respiration have not been investigated thoroughly because the static chamber method, which has been used widely in field measurement of soil respiration, often requires a long time (several hours) to gain a reading (Nakadai et al., 1996). Some studies reported that diurnal changes in soil respiration increased in the daytime and decreased at night, corresponding to temperature (Witkamp, 1969; Kanemasu et al., 1974; Parker et al., 1983; Grahammer et al., 1991; Osozawa and Hasegawa, 1995; Nakadai et al., 1996). However, no clear fluctuation was observed in some forests because of the absence of significant diurnal change in environmental factors inside the forests (Kirita, 1971d; Kurser, 1989; Gyokusen and Saito, 1995). Nocturnal increases in soil respiration have also been reported (Witkamp, 1969; Edwards and Sollins., 1973; Eguchi et al., 1997) because of changes in root respiration (Eguchi et al., 1997) and of thermal convection of subsurface air to the surface (Witkamp, 1969).

Spatial variability of soil respiration is caused by many factors directly and indirectly. In addition, the relative importance of these factors appears to vary greatly depending on geographical and environmental conditions at the site. Laboratory and field experiments have shown that spatial variability of soil respiration depends on soil aeration (Yabuki and Kitaya, 1984; Liebig et al., 1995),

soil organic matter (Seto et al., 1978; Seneviratne and Van Holm, 1998), soil nitrogen contents (Kowalenko et al., 1978; Seneviratne and Van Holm, 1998; Johnson et al., 1994), soil phosphorus nutrition (Keith et al., 1997) and soil pH (Sparling and West, 1990). However, in natural ecosystems, effects of these factors have not been fully understood and more data under natural conditions is required (Naganawa et al., 1989; Maggs and Hewett, 1990; Vose et al., 1997). In forest ecosystems, though some reports show variability of soil respiration on slopes, they were dependent on different factors. Shimada et al. (1998) reported higher soil respiration at lower sites than the flux at the other sites on a slope of a Japanese cedar and cypress forest. They considered the high soil respiration to be caused by high soil organic matter. Simono et al. (1989) reported higher soil respiration on the upper part of the slope in a young Japanese cypress forest because of differences in soil moisture conditions. Hanson et al. (1993) measured seasonal patterns of soil respiration at four topographically distinct locations in an upland oak forest in Tennessee and observed an isolated period when valley-bottom locations had reduced soil respiration relative to other topographic locations. They reported that lower soil respiration was consistent with reduced fine root density and elevated coarse fraction percentage.

Effect of vegetation

In forest ecosystems, not only microbial respiration but also root respiration may contribute a considerable amount to soil respiration (Singh and Gupta, 1977; Behara, 1990). Therefore, changes in root biomass and root activity, depending on aboveground vegetation conditions, change root respiration rate, thereby affecting soil respiration (Gupta and Singh, 1981; Eguchi et al., 1997). Changes in aboveground vegetation also influence the microclimate in forest

ecosystems (Mathes and Schriefer, 1985; Bauhus and Bartsch, 1995), and soil nutrient status (Maggs and Hewett, 1990) and affect soil respiration indirectly.

Measuring or estimating root respiration is one of the key points in understanding the drastic changes in soil respiration. Many attempts have made to estimate root respiration contribution to total soil respiration. However, each technique used to measure root respiration was shown to have limitations (Nakane et al., 1983; Katagiri, 1988; Ohashi and Saito, 1998) due to the difficulty in separating root systems from soil. Bowden et al. (1993) estimated root contribution to total soil respiration as 33% by terminating live root activity through construction of trenches and root barriers. They also reported that nearly two thirds of soil respiration can be attributed to root activity (root respiration and decomposition of root litter). Kawahara (1976) considered that natural root respiration may be equal to the difference between soil respiration and fallen litter in a mature red pine and oak forest, and estimated root contribution to total soil respiration to be 18～23%. Katagiri (1988) calculated natural root respiration from the linear relationship between soil respiration and root biomass. He estimated the proportion of root respiration to total soil respiration as 20～40% in a deciduous broad-leaved forest. Using similar methods, Behara et al. (1990) estimated the proportion of root respiration as 50.5 % in tropical forests. Nakane et al. (1983) estimated the proportion of root to total soil respiration as 50 % by clear-felling of a mature red pine forest. They concluded that the proportion of root respiration to soil respiration may converge at around 50 %, irrespective of the type of forest concerned, when soil organic carbon is in dynamic equilibrium in the forest ecosystem.

Many human activities, such as felling and planting, can clearly

have significant effects on the extent of soil respiration because they suddenly change volume and activity of root systems and microclimate of the ecosystems (Ewel et al., 1987; Wagai et al., 1998). Recently, studies on effects of human activity on soil respiration has become more important because forestation is expected to decrease carbon in the air, whereas it is feared that deforestation will increase carbon. Some reports suggest that clear-felling or artificial gap formation cause the diminution of root respiration, thereby decreasing soil respiration (Nakane et al., 1983; Brumme, 1995; Striegl and Wickland, 1998). Toland and Zak (1994) reported that the decomposition of dead roots after clear-felling offsets the decrease in soil respiration. It was also reported that soil respiration increased after clear-felling (Tulaphitak et al., 1985; Hendrickson et al., 1989; Londo et al,. 1999).

1.3 Objective

Soil respiration from the forest floor may profoundly influence the atmospheric CO_2 budget and the carbon fixing capacity of the ecosystems even to a small degree because of its large flux. However, data on the amount, fluctuation and affecting factors of soil respiration is still inadequate because a wide variety of measurement techniques have had limitations, causing problems in the comparison of results. In addition, in forest ecosystems, measurement of soil respiration has been restricted to a limited number of locations because of lack of portability of measuring systems. Therefore, in this study, a portable soil respiration measuring system which enhanced the precision of current models was established, and factors affecting soil respiration from the forest floor were investigated using the system.

The objective of chapter 1 is to study soil respiration methodologically. The chamber method, used widely for measuring soil respiration, has a significant problem namely that the difference in environmental factors, such as CO_2 concentration and wind speed, inside and outside the chamber may influence readings. However the effect of these environmental factors has not been investigated in detail. Therefore, a portable soil respiration measuring system which could regulate temperature, CO_2 concentration, and wind speed in a chamber was developed, and the effects of CO_2 concentration and wind speed on soil respiration were investigated in section 1 (1.1).

Since environmental factors which affect soil respiration, such as wind speed, CO_2 concentration and temperature, fluctuate continuously in natural conditions, soil respiration may be affected by these environmental factors on the forest floor. However, soil

respiration has been measured in a chamber environment in many studies of soil respiration but effects of natural fluctuation of these factors were not taken into account. Therefore, diurnal fluctuation of soil respiration was estimated from natural changes in temperature, CO_2 concentration and wind speed on forest floor in section 2 (2.2).

The objective of chapter 2 is to investigate factors affecting temporal and spatial fluctuation of soil respiration from the forest floor using the portable open-flow measuring system. In section 1, seasonal changes in soil respiration from a Japanese cedar forest floor were investigated in order to discover the relationships between soil respiration rates and other environmental factors such as soil temperature and soil moisture. The effect of thinning on soil respiration was also examined by comparing soil respiration in a intact section and a thinned section of a Japanese cedar forest stand. Seasonal changes in soil surface CO_2 concentration, estimated from soil respiration rates, were also determined (3.1).

Soil respiration, the sum of plant root and microbial respiration, changes spatially and temporally due to many factors, such as environmental conditions and soil characteristics. Thus, soil respiration may fluctuate considerably on a slope because the complicated configuration may produce an imbalance of affecting factors on soil respiration. However, there are few studies that determine the spatial and temporal variability of soil respiration on a forest slope due to limitations in the portability of measurement system. In section 2, the spatial and temporal variability of soil respiration was determined on a Japanese cedar forest slope using the portable open-flow soil respiration measuring system. The sampling points were located in a grid-like pattern on the slope in order to determine the

spatial variability of soil respiration, and seasonal and diurnal change were measured at the points (3.2).

The objective of chapter 3 is to examine the effect of aboveground vegetation on soil respiration. In forest ecosystems, not only microbial respiration but also root respiration may contribute a significant proportion of soil respiration. Therefore, changes in root respiration depending on aboveground vegetation conditions would affect soil respiration. However, it is difficult to know the relationship between root respiration fluctuation and soil respiration because of technical limitations in separating root respiration from soil respiration. The objective of section 1 is to estimate the contribution of root respiration to total soil respiration using some planting pots. It is assumed that differences in soil respiration rate from the pots before and after plant removal (shoot and root) is equal to root respiration. Effect of shoot removal only on soil respiration was also examined (4.1).

In section 2, contribution of root respiration to total soil respiration in a Japanese cedar forest was estimated using the tree felling method. Soil respiration rate was compared between an undisturbed area and the center of an artificial small gap. The root respiration rate was calculated from the difference. In this study, the effect of artificial gap formation on soil respiration was also examined by estimating the soil respiration gradient from the center of the gap into the stand (4.2).

In young forests, changes in aboveground vegetation, such as planting, growing and felling, may change root respiration, thereby affecting soil respiration. Aboveground vegetation may also affect microclimate in forest ecosystems and affect soil respiration indirectly. However, most soil respiration studies have been conducted in the

mature forest ecosystems in which soil carbon cycles are already in dynamic equilibrium. Therefore, the objective of section 3 is to examine effects of vegetation change on soil respiration. To the end, oak and Japanese cedar stands were grown for 3 years from seed and cuttage, respectively, and partially clear-felled one-and-a-half years after planting (4.3).

Chapter 2 Methodological study of soil respiration

2.1 Effects of carbon dioxide concentration and wind speed using the chamber method on soil respiration

2.1.1 Introduction

Soil respiration is a phenomenon which releases carbon dioxide from the soil surface into the atmosphere. It is used as an index of site productivity (Yabuki and Kitaya, 1984) or as a measure of the carbon cycle of a forest ecosystem (Nakadai et al., 1993). The chamber method is used widely for measuring soil respiration. It can be classified into two types, the open-flow system and the closed system. The most important problem in these two systems is that the internal environments of the chambers differ greatly from that of the external environment. The prime environmental factors in the chambers affecting soil respiration are temperature (Seto et al., 1978), CO_2 concentration (Nakadai et al., 1993), ventilation rate (Inoue, 1986), and wind speed (Gyokusen and Saito, 1995). However the effect of these environmental factors have not been investigated in detail because the chamber method for measuring soil respiration is incomplete. In this study, a portable soil respiration measuring system which could regulate temperature, CO_2 concentration, and wind speed in a chamber was developed, and the effects of CO_2 concentration and wind speed on soil respiration were investigated.

2.1.2 The measuring system

A diagram of the measuring system is shown in Fig. 2-1-1. This system is similar to the portable soil respiration measuring system used in the previous study (Gyokusen and Saito, 1995), except

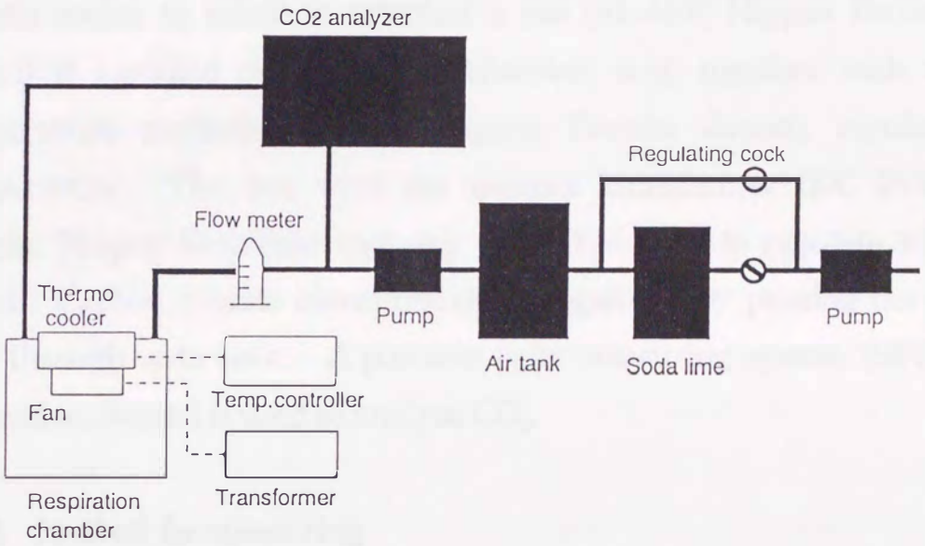


Fig. 2-1-1 Outline of the soil respiration measuring system. Bold line shows the air flow and dotted shows the electric line.

for the addition of a regulator of wind speed and temperature. It consists of a respiration chamber, a CO_2 analyzer, a CO_2 concentration regulator, air tank, air pump, generator, and a wind speed and temperature regulator. Bold lines in Fig. 2-1-1 represent the flow of air, and dotted lines, the flow of electricity. The chamber consists of a 5 mm acrylic thick cylinder 15 cm in diameter and 13 cm in height. A thermo cooler, to which is attached a fan (SL-5FF, Nippon Brower., Japan) is installed on top of the chamber, and, together with the temperature controller (SL-C4, Nippon Brower, Japan), regulates temperature. The fan with the current transformer (DC Power Supply, Nippon Stabilizer Industry, Japan) is used to regulate wind speed. Carbon dioxide concentration is regulated by passing the air flow through soda lime. A portable light measuring system (SPB-3, Shimadzu, Japan) is used to analyze CO_2.

2.1.3 Method for measuring

Soil respiration was measured on the 13 October 1994 in a 28-year-old oak (*Quercus glauca*) forest. After the A_0 layer was removed, the bottom of the chamber was buried about 1 cm into the ground, and air flow rate was maintained at 1.5 $l m^{-1}$. Soil respiration readings become stable five minutes after starting the system. Temperature in the chamber was maintained at 20 ℃ which was close to the temperature outside the chamber, and the CO_2 concentration was increased from 0 ppm to 360 ppm in five gradations. Wind speed was increased from 0 ms^{-1} to 5 ms^{-1} in six gradations at every CO_2 concentration level. Soil respiration was calculated by the following formula using CO_2 concentrations (ppm) flowing in and out of the chamber as C_{in} and C_{out}

$$R = KV(C_{out} - C_{in})\ 273/A\ (273 + T)$$

where, R (mg CO_2 m^{-2} hr^{-1}) is the soil respiration, V(hr^{-1}) is the air-flow rate, A (m^2) is the bottom area of the chamber, T(℃) is the temperature of the air-flow meter, and K is the coefficient 0.00196.

2.1.4 Results and Discussion

Fig. 2-1-2 shows the relationships between the CO_2 concentrations in the chamber and the soil respiration rates at each wind speed. The soil respiration rate decreased with increasing CO_2 concentration, and it increased with increasing wind speed.

Nakadai et al. (1993) noted that decreasing CO_2 concentration gave an impetus to increasing the soil respiration. They supposed that the acceleration in the soil microbial respiration rate (Koizumi et al., 1991) to be one of the causes. Gyokusen and Saito (1995) cited increases in physical diffusion which depended on the CO_2 concentration gradient as one cause. The soil respiration rate in this study changed in proportion to the CO_2 concentration. It was thought therefore, that the change in soil respiration with changing CO_2 concentration was brought about mainly by physical diffusion, because a curvilinear increase in the soil microbial respiration rate with decreasing CO_2 concentration, as reported by Koizumi et al. (1991), was not observed.

The soil respiration rate increased as the wind speed increased. Considering both the increase in the soil respiration rate as the ventilation rate increased (Inoue, 1986) and the change in the soil respiration rate, with or without a wind speed (Gyokusen and Saito, 1995), this result was interpreted as the CO_2 diffusion resistance by the ground as being reduced by wind. Inoue (1986) noted that the soil respiration rate attained equilibrium when the ventilation rate of the chamber exceeded 13 times per hour. However, in this study, the soil

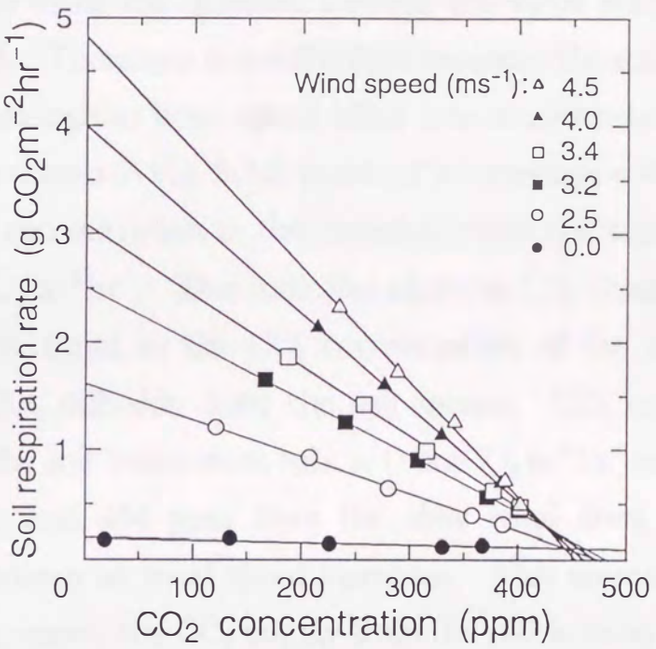


Fig. 2-1-2 Relationships between soil respiration rate and CO_2 concentration at each wind speed. Regression equation: 4.5 ms^{-1}, $y = 4.82 - 0.0106x$ ($r = 1.00$); 4.0 ms^{-1}, $y = 4.00 - 0.00867x$ ($r = 1.00$); 3.2 ms^{-1}, $y = 2.52 - 0.00522x$ ($r = 1.00$); 2.5 ms^{-1}, $y = 0.199 - 0.000201x$ ($r = 0.85$). Temperature in the chamber was maintained at 20 ℃.

respiration rate tended to increase even under 4.5 ms^{-1} of wind speed, and the CO_2 diffusion resistance from the ground further decreased under thus faster wind speeds. In most measurements of the soil respiration rate using the chamber method, the value was affected by the wind speed. Therefore, it is difficult to measure the soil respiration rate without taking the wind speed effect into consideration. On the regression line shown in Fig. 2-1-2, points of intersection with the X axis show the CO_2 concentration in the chamber when the soil respiration rate is 0 $mgCO_2\ m^{-2}\ hr^{-1}$. This indicates that the CO_2 concentration in the chamber is equal to the CO_2 concentration of the soil surface, because the CO_2 diffusion from the soil causes. CO_2 concentration values when the soil respiration rate is 0 $mgCO_2\ m^{-2}\ hr^{-1}$ are 990, 475, 482, 473, 461, and 454 ppm from the slow wind level, showing a decreasing tendency as wind speed increases. This means that if the wind speed increases, the CO_2 supply from the soil is delayed, and the soil surface CO_2 concentration decreases. However when the wind speed is 0 ms^{-1}, C_{out} may not be used as the CO_2 concentration value in the chamber because the air in the chamber was not moved and the CO_2 concentration in the chamber is not uniform. Soil surface CO_2 concentration is an important factor affecting the growth of forest floor vegetation (Bazzaz and Williams, 1991). This research demonstrated a new method of measuring soil surface CO_2 concentration by changing the CO_2 concentration in the chamber.

In this study, it was confirmed that the wind speed and the CO_2 concentration greatly affect soil respiration. The chamber method is used widely to measure soil respiration. However wind speed in the chamber had not been considered as an important factor. In particular, in the closed system, there is almost no wind in the chamber, whereas in the open-flow system, wind speed changes owing to differences in the

measuring machines. Therefore, it is important to consider the effect of wind speed on soil respiration values when measuring soil respiration. Concerning the effects of CO_2 concentrations, it also has been confirmed that soil respiration is underestimated under the closed system because CO_2 concentration in the chamber is very small due to the CO_2 absorption medicine. Whereas it is overestimated in an open-flow system as the CO_2 concentration in the chamber is more than ambience. From these results, it can be seen that wind speed and CO_2 concentration must be specified clearly when soil respiration is measured by the chamber method.

2.2 Estimation of soil respiration from fluctuation of CO_2 concentration, wind speed and temperature on the soil surface in a oak (*Quercus glauca*) forest

2.2.1 Introduction

Temporal change in soil respiration is influenced mainly by two principal environmental factors, temperature and moisture (Singh and Gupta, 1977). The strong effect of temperature (Kirita, 1971d; Anderson, 1973; Chiba, 1975; Sakai and Tsutsumi, 1987), soil moisture (Carlyle and Than, 1988; Holt et al., 1990), and both factors combined (Schlentner and Van Cleve, 1985; Pajari, 1995) have been reported. The effect of these two factors varies depending on geographical location and season. It is supposed that in a temperate environment like Japan, fluctuation in soil respiration is mainly influenced by soil temperature (Chiba and Tsutsumi, 1967; Seto et al., 1978; Hagihara et al., 1984; Sakai and Tsutsumi, 1987; Simono et al, 1989).

Soil respiration also influenced other environmental factors, such as CO_2 concentration and wind speed. Nakadai et al. (1993) and Gyokusen and Saito (1995) reported that soil respiration decreases with increasing CO_2 concentration in the chamber. Inoue (1986) reported an increase in soil respiration rate as the ventilation rate increased. Deference in the soil respiration rate with and without wind speed in the chamber has been also reported (Gyokusen and Saito, 1995). Hanson et al. (1993) and Ohashi et al. (1995) reported that under field conditions, the increase in wind speed stimulated CO_2 diffusion from the soil due to the disruption of the boundary layer over the forest floor. Therefore, in natural conditions, continuous fluctuation of environmental factors, such as temperature, CO_2 concentration and wind speed, on the forest floor may cause fluctuations in soil respiration.

However, in many studies of soil respiration using a chamber method, these environmental factors were often stabilized and soil respiration was measured in a stable environment without consideration of natural fluctuations of the factors.

The objective of this study was to estimate soil respiration fluctuation from natural fluctuation in temperature, CO_2 concentration and wind speed on a oak (*Quercus glauca*) forest floor. It had already reported that soil respiration rate decreased with increasing CO_2 concentration, and increased with increasing wind speed in a chamber (Ohashi et al., 1995). Here, two equations that included temperature CO_2 concentration and wind speed as explanatory variables were formulated from the relationship between soil respiration and each factor in order to estimate soil respiration.

2.2.2 Methods

Measurement was carried out in a 28-year-old oak (*Quercus glauca*) forest in the nursery of Kyushu University, Fukuoka prefecture, south-west Japan. Masa soil, a horticultural soil, covered the study site 1 m in depth and an organic horizon was 10 cm. Undergrowth was sparse. Mean annual air temperature and precipitation in 1998 was 18.9 ℃ and 1866 mm, respectively (Fukuoka Local Meteorological Observatory, 1996).

CO_2 concentration, wind speed and soil temperature on the forest floor

Diurnal change in wind speed and soil temperature 5 cm above the forest floor was measured at 10-minute intervals for a week in summer (August 30～September 5, 1998), autumn (November 28～December 4, 1998), winter (February 20～February 23, 1999) and spring (May 18～May 24, 1999), respectively. All data was recorded by

data logger (LG-C1, Log, Japan).

An electric anemometer (V-01-3, IET, Japan) was used to measure wind speed. A 30 cm×30 cm wooden board 3 mm in thick was attached on a tripod 30 cm in height and a hole was made on the center of the board to allow the sensor of the anemometer to pass through the hole. The tripod was fixed on the forest floor so that the point of the sensor was fixed 5 cm above the floor. To avoid the sensor becoming wet, a 40 cm×40 cm vinyl sheet was put on the wooden board. Soil surface temperature was measured using a thermistor thermometer (LG-C1, Log, Japan). The thermometer sensor was fixed on the soil surface and its cord was covered by a thick hose to avoid being gnawed by rats. CO_2 concentration was measured by an infrared gas analyzer (GMW22, Vaisala, Japan). Twenty holes, 5 mm in diameter, were made on the side of a 30 cm×80 cm×40 cm plastic case on the forest floor. Ambient air was sucked in the case by a pump and sent to the sensor of the gas analyzer in a static chamber after being dried with silica.

Relationship between soil respiration and environmental factors, CO_2 concentration, wind speed and temperature

Diurnal change in soil respiration and soil surface temperature was measured hourly from 7:00 to 16:00 in order to examine the relationship between soil respiration and soil surface temperature. Measurement of diurnal change was carried out once a season on a fine day, summer (September 1, 1998), autumn (December 2, 1998), winter (February 24, 1999) and spring (May 22, 1999). Soil respiration was measured using the open-flow portable measuring system developed by this laboratory (Gyokusen and Saito, 1995; Ohashi et al., 1995). The chamber consists of a 3 mm acrylic thick cylinder, 10 cm in diameter

and 13 cm in height. Wind speed in the chamber was maintained at 1.0 ms^{-1} using a fan in the chamber. CO_2 concentration in the air flowing in and out of the chamber was measured by infrared gas analyzer (SPB-H3, Shimadzu, Japan). Air flow rate through the chamber was maintained at 1.5 lm^{-1}. Soil respiration was measured twice; first, with CO_2 concentration in the chamber maintained at about zero ppm and then, without CO_2 regulation (CO_2 concentration was about 450 ppm). Soil respiration was calculated respiration when CO_2 concentration in the chamber was exactly 400 ppm from the straight line between the two measuring points (Ohashi et al., 1999b). Soil surface temperature was measured at the same time as soil respiration using a thermistor thermometer (SL5-FF, Chino, Japan).

Relationship between soil respiration and CO_2 concentration at different wind speeds was investigated in each season, summer (August 22, 1999), autumn (December 3, 1998), winter (February 23, 1999) and spring (May 22, 1999). All measurements were carried out between 11:00 to 15:00 in order to minimize the effect of diurnal change in temperature (Edwards and Sollins, 1973; Hanson et al., 1993). Soil temperature during measurement varied less than 2 ℃ in all seasons. CO_2 concentration in the chamber increased from 0 ppm to 600 ppm in five gradations. Wind speed increased from 0 ms^{-1} to 5 ms^{-1} in six gradations at each CO_2 concentration level. CO_2 concentration in the chamber stabilized 10 minutes after change in the level and soil respiration readings was taken 5～7 minutes after change in wind speed. CO_2 concentration was regulated by passing the air flow through soda lime (Ohashi et al., 1995). CO_2 concentration flowing out of the chamber was presumed to be CO_2 concentration in the chamber (Ohashi et al., 1995). The fan with a current transformer (DC Power Supply, NISC, Japan) was used to regulate wind speed. Relationship

between wind speed and voltage was measured by electric anemometer (V-01-3, IET, Japan) in the laboratory.

2.2.3 Results

Temporal changes in CO_2 concentration, wind speed and soil temperature on the forest floor

Diurnal changes in soil surface temperature, ranging from 25.1 ~31.7℃, 13.7~19.2℃, 6.6~16.4℃ and 19.9~28.4℃ in summer, autumn, winter and spring, respectively, increased in the daytime and decreased at night (Fig. 2-2-1). The clearest change was observed in summer, with maximum and minimum values in 14:00 and 6:00, respectively. Mean soil surface temperature in each season was 29℃, 16℃, 11℃ and 24℃ in summer, autumn, winter and spring, respectively, indicating a maximum in summer and a minimum in winter.

Fig. 2-2-2 shows diurnal changes in CO_2 concentration and wind speed in each season. The clearest changes were observed in summer but no clear fluctuation was observed in autumn and winter. Higher CO_2 concentrations was observed at lower wind speeds and there was a negative proportional relationship between CO_2 concentration and wind speed ($P < 0.001$). CO_2 concentration, ranging from 540~800 ppm, 480~630 ppm, 440~570 ppm and 470~750 ppm in summer, autumn, winter and spring, respectively, decreased in the daytime and increased at night. Mean CO_2 concentration in each season was 680 ppm, 570 ppm, 480 ppm and 580 ppm in summer, autumn, winter and spring, respectively, indicating a maximum in summer and a minimum in winter. Wind speed, ranging from 0~0.5 ms^{-1} in all seasons increased in the daytime and decreased at night. Mean wind speed in each season was 0.14 ms^{-1}, 0.15 ms^{-1}, 0.11 ms^{-1} and 0.16 ms^{-1} in summer,

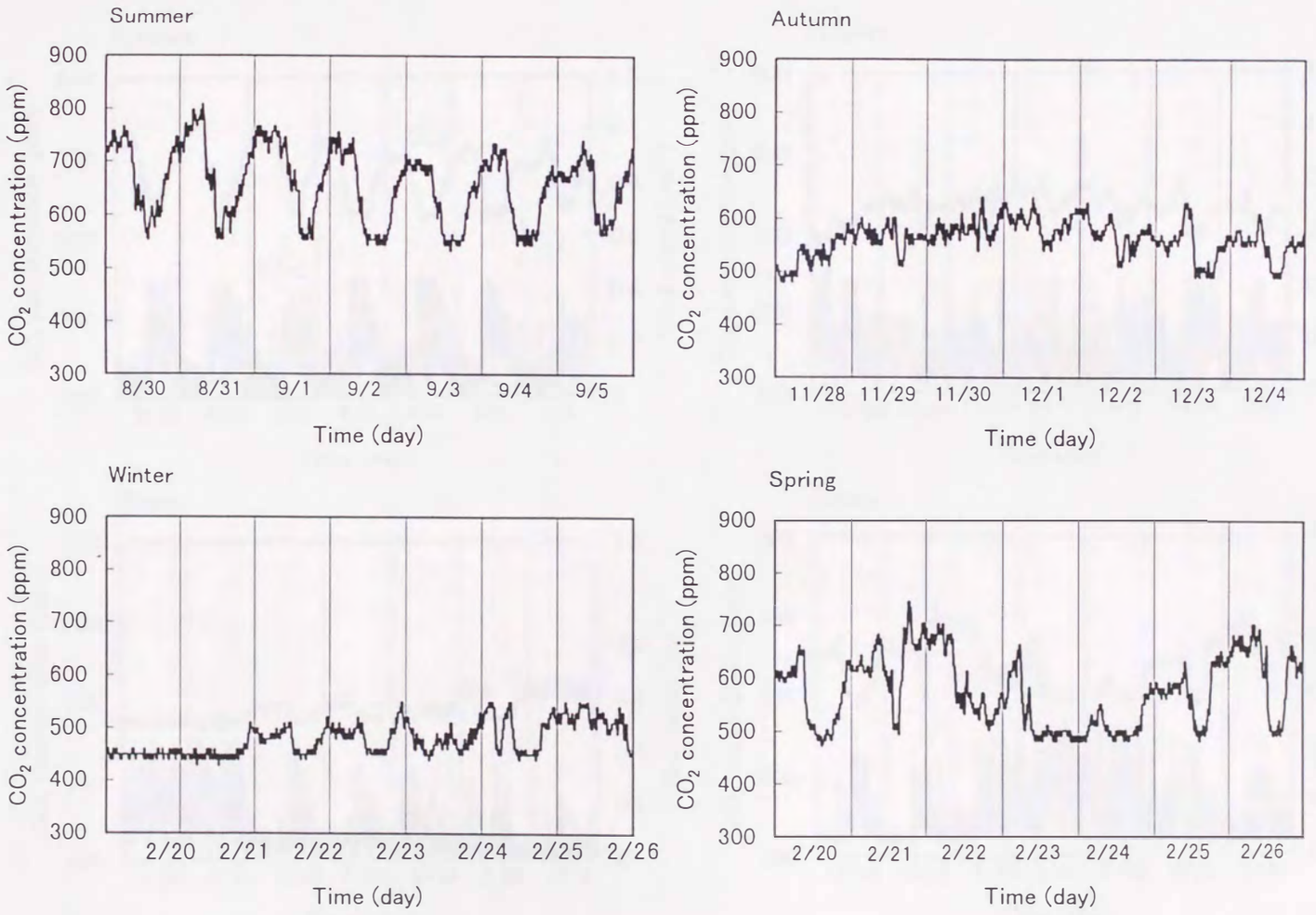


Fig. 2-2-1 Daily change in soil surface temperature.

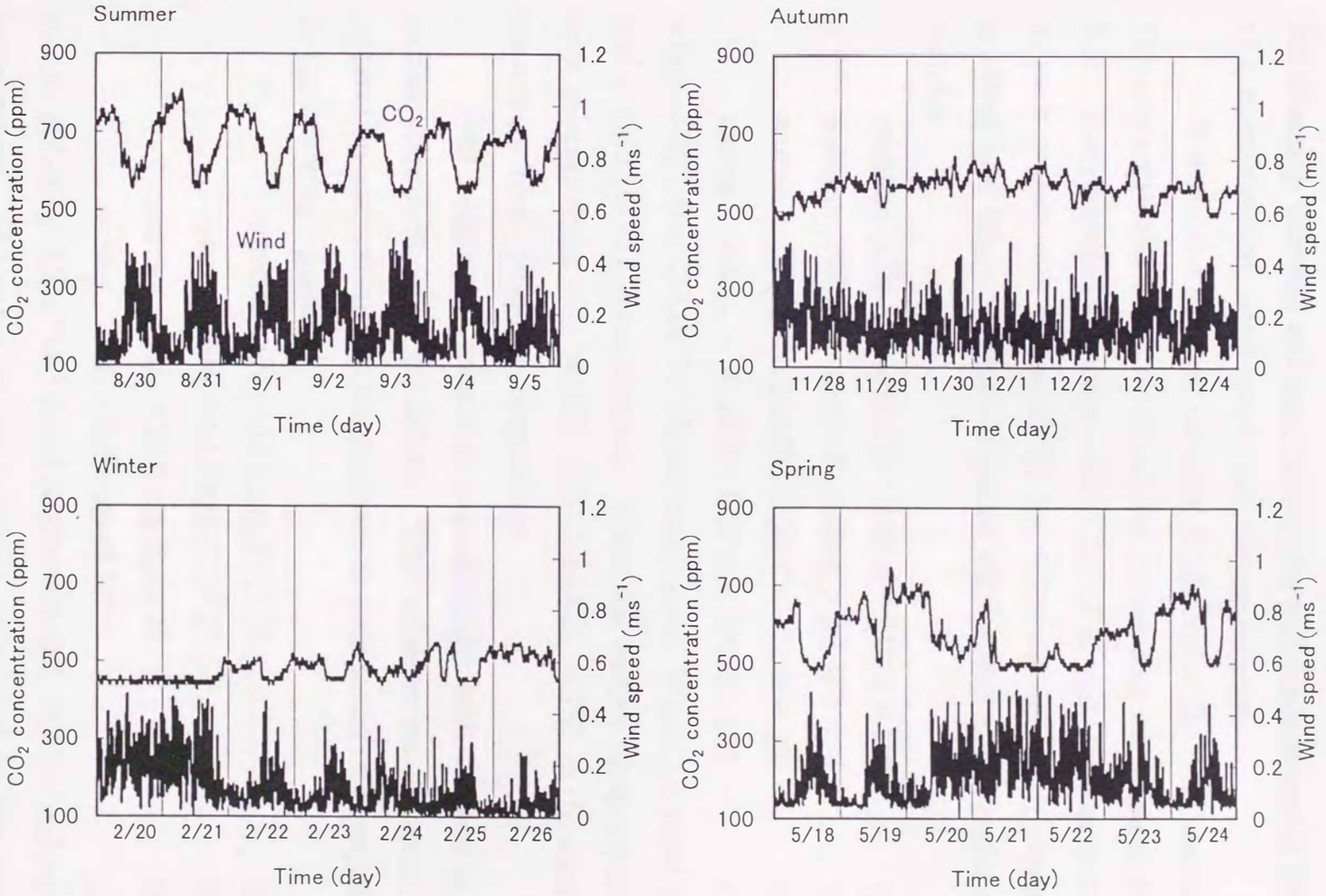


Fig. 2-2-2 Daily change in CO_2 concentration and wind speed.

autumn, winter and spring, respectively, indicating no clear differences.

Relationship between soil respiration rate and environmental factors, CO_2 concentration, wind speed and soil temperature

Soil respiration rate decreased proportionally with increasing CO_2 concentration, and it increased with increasing wind speed (Fig. 2-2-3). The relationship between soil respiration and CO_2 concentration in each season was expressed by the following equations using the gradient and intercept which includes wind speed as an explanatory variable

summer ; $SR_{C\cdot W} = -(0.04W + 0.48)C + 212W + 456$ (1_a)

autumn ; $SR_{C\cdot W} = -(0.03W + 0.30)C + 169W + 274$ (1_b)

winter ; $SR_{C\cdot W} = -(0.07W + 0.24)C + 122W + 129$ (1_c)

spring ; $SR_{C\cdot W} = -(0.12W + 0.27)C + 193W + 231$ (1_d)

where, $SR_{C\cdot W}$ (mg $CO_2 m^{-2} hr^{-1}$) is soil respiration, W (ms^{-1}) is wind speed and C (ppm) is CO_2 concentration. Mean soil surface temperatures in each measurement were 30.6℃, 17.5℃, 12.4℃, 25.7℃ in the summer, autumn, winter and spring, respectively.

Soil respiration increased exponentially with increasing soil surface temperature (Fig. 2-2-4). The relationship between soil respiration and soil surface temperature in each season was expressed by the following equation

summer ; $SR_T = 11.8 \exp(0.12T)$ (2_a)

autumn ; $SR_T = 21.7 \exp(0.14T)$ (2_b)

winter ; $SR_T = 21.2 \exp(0.14T)$ (2_c)

spring ; $SR_T = 8.60 \exp(0.13T)$ (2_d)

where, SR_T (mg $CO_2 m^{-2} hr^{-1}$) is soil respiration and T(℃) is soil surface temperature. Q_{10} value for each season, calculated as the rate of change of soil respiration when temperature increased by 10 ℃, was

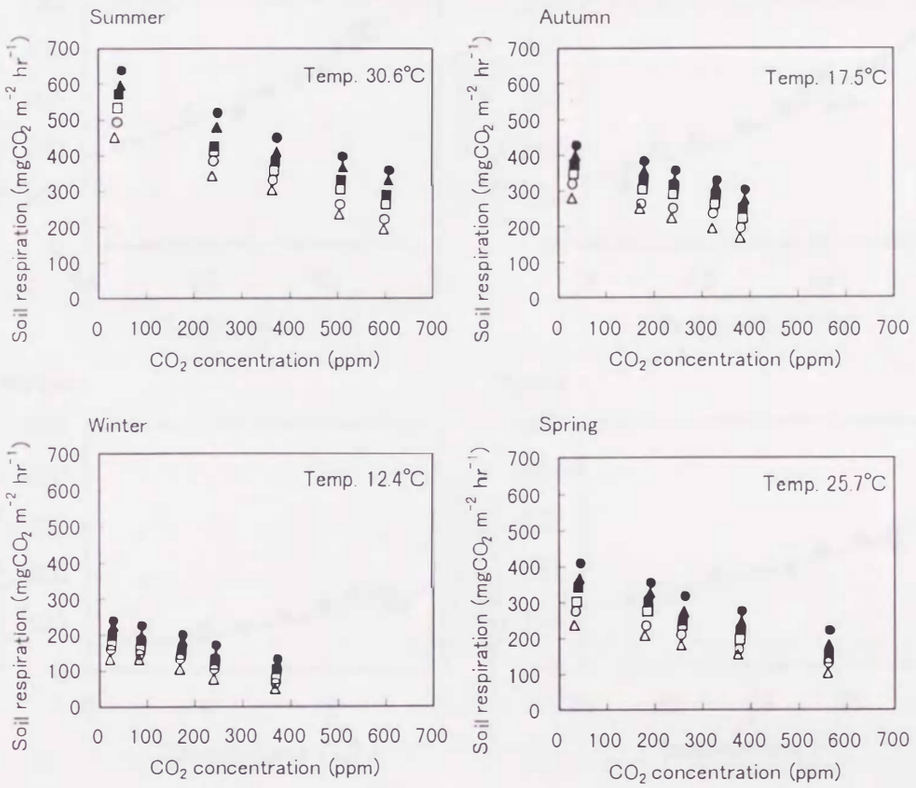


Fig. 2-2-3 Relationship between soil respiration and CO_2 concentration at various wind speed.

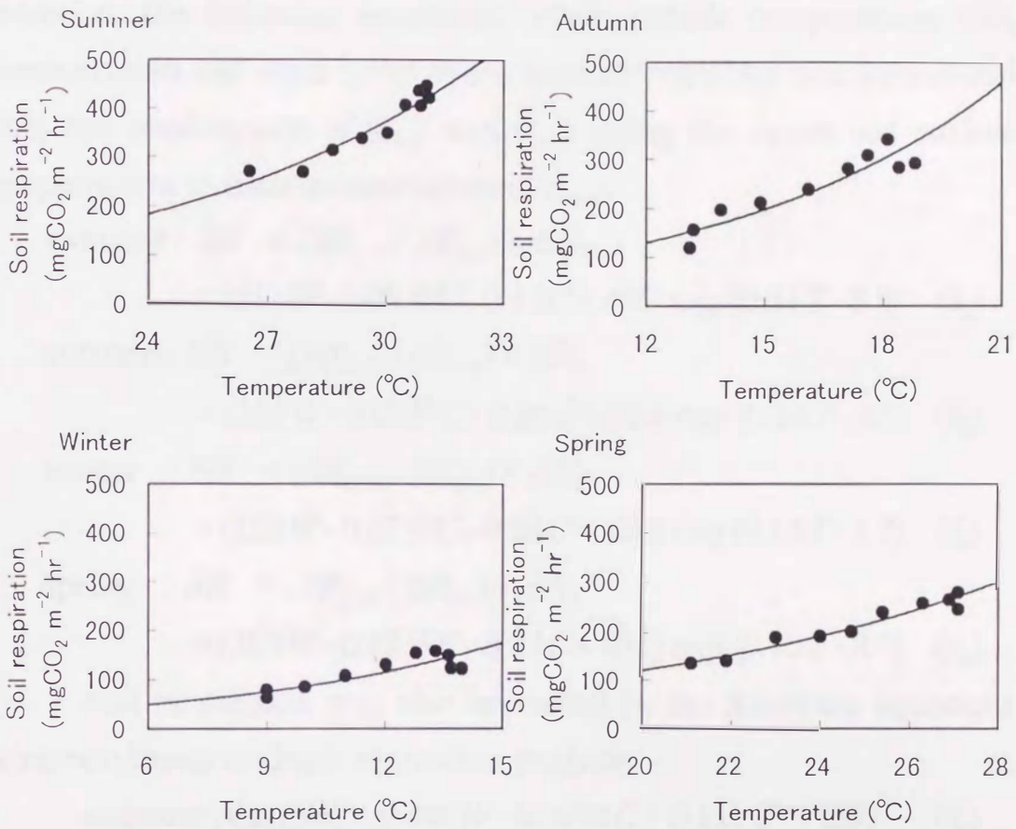


Fig. 2-2-4 Relationships between soil respiration and soil surface temperature.

3.0, 4.1 and 3.7 in the summer, autumn and winter, and spring, respectively.

Since each equation of ($1_{a\text{-}d}$) was made under stable temperature condition, the following equations, which include temperature, CO_2 concentration and wind speed as explanatory variables was formulated from the combination of ($2_{a\text{-}d}$) and ($1_{a\text{-}d}$) using the mean soil surface temperatures in each measurement of ($1_{a\text{-}d}$).

summer ; $SR = (SR_{C\cdot W} / SR_{30.6}) \times SR_T$

$= (211\,W - 0.05\,WC - 0.44\,C + 435) \exp(0.11\,T - 3.5)$ (3_a)

autumn ; $SR = (SR_{C\cdot W} / SR_{17.5}) \times SR_T$

$= (169\,W - 0.03\,WC - 0.30\,C + 274) \exp(0.14\,T - 2.5)$ (3_b)

winter ; $SR = (SR_{C\cdot W} / SR_{12.4}) \times SR_T$

$= (122\,W - 0.07\,WC - 0.24\,C + 130) \exp(0.14\,T - 1.7)$ (3_c)

spring ; $SR = (SR_{C\cdot W} / SR_{25.7}) \times SR_T$

$= (193\,W - 0.12\,WC - 0.27\,C + 231) \exp(0.13\,T - 3.3)$ (3_d)

Soil respiration was also expressed by the following equations using non-linear multiple regression analysis.

summer ; $\mathrm{Ln}(SR) = 0.446\,W - 0.0012\,C + 0.111\,T + 2.67$ (4_a)

autumn ; $\mathrm{Ln}(SR) = 0.356\,W - 0.0012\,C + 0.065\,T + 4.55$ (4_b)

winter ; $\mathrm{Ln}(SR) = 0.664\,W - 0.0020\,C + 0.211\,T + 2.28$ (4_c)

spring ; $\mathrm{Ln}(SR) = 0.526\,W - 0.0012\,C + 0.143\,T + 1.80$ (4_d)

Values estimated from ($3_{a\text{-}d}$) equations and from ($4_{a\text{-}d}$) equations were compared with soil respiration readings measured hourly from 7:00 to 16:00 under high (about 450 ppm) and low (0 ppm) CO_2 concentrations in the chamber. As a result, all values estimated from the two equations are in good agreement with measured values ($r^2 > 0.8$, $P < 0.001$) (Fig. 2-2-5). Subsequently, the equations were used to estimate diurnal changes in natural soil respiration from the fluctuation of temperature, CO_2 concentration and wind speed on the

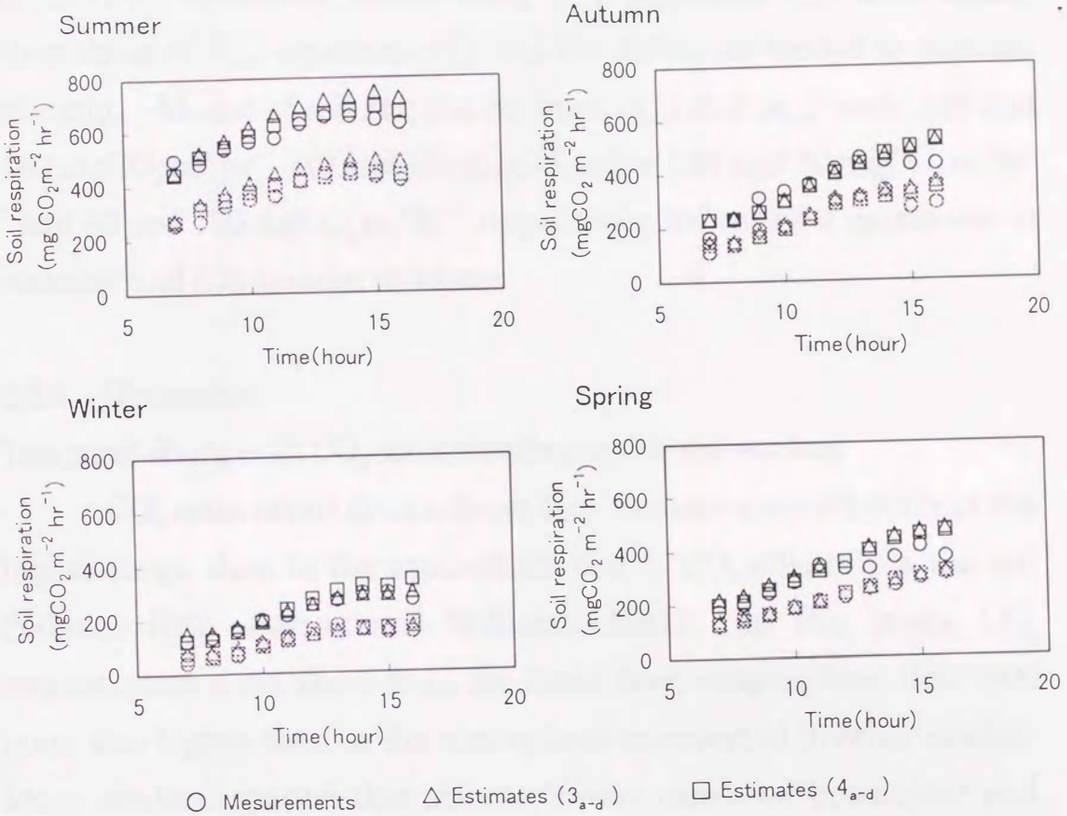


Fig. 2-2-5 Estimates of soil respiration.

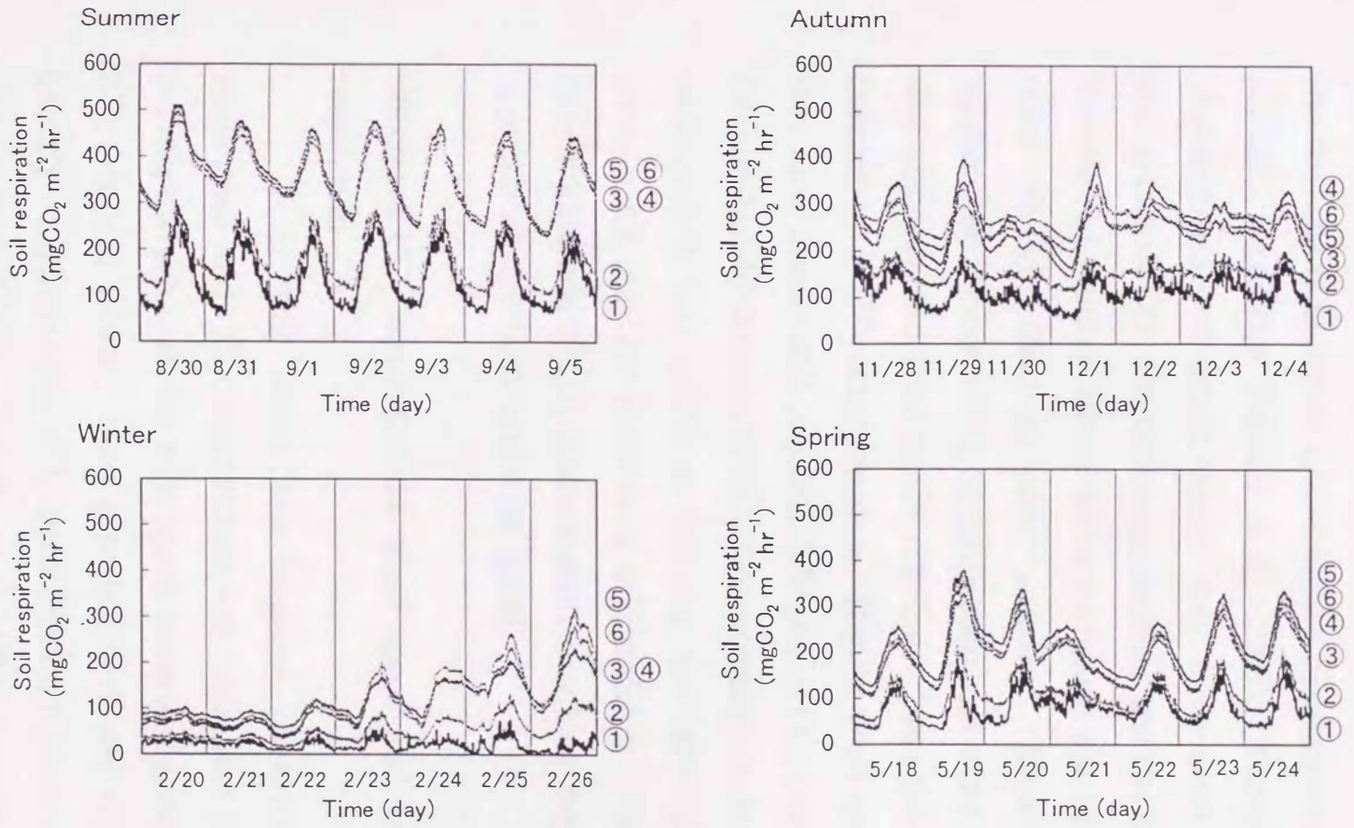
forest floor (Fig. 2-2-1、Fig. 2-2-2). Estimated soil respiration, ranging from 0～305 $mgCO_2m^{-2}hr^{-1}$, increased in the daytime and decreased at night, with the clearest fluctuation being observed in summer (Fig. 2-2-6; ①, ②). Estimated values using (4_{a-d}) equations (②) were higher than those of (3_{a-d}) equations (①) and the difference tended to increase at night. Means of soil respiration from (3_{a-d}) and (4_{a-d}) were 140 and 180 $mgCO_2m^{-2}hr^{-1}$, 110 and 150 $mgCO_2m^{-2}hr^{-1}$, 20 and 50 $mgCO_2m^{-2}hr^{-1}$ and 80 and 110 $mgCO_2m^{-2}hr^{-1}$, respectively, indicating a maximum in summer and a minimum in winter.

2.2.4 Discussion

Temporal changes in CO_2 concentration on the soil surface

CO_2 concentration on a forest floor fluctuates considerably in the higher range than in the atmosphere due to CO_2 efflux from the soil (Yabuki, 1985; Bazzaz and Williams, 1991). In this study, CO_2 concentration 5 cm above from the forest floor, ranging from 440～800 ppm, was higher than in the atmosphere as reported in other studies. Many studies reported that soil respiration increased in summer and decreased in winter (Kirita, 1971d; Anderson, 1973; Chiba and Tsutsumi, 1975; Sakai and Tsutsumi, 1987). Therefore, maximum and minimum CO_2 concentration values in summer and in winter, respectively, may have been caused by seasonal soil respiration.

However, although generally diurnal changes in soil respiration increased in the daytime and decreased at night (Witkamp, 1969; Kanemasu et al., 1974; Grahammer et al., 1991; Gyokusen and Saito, 1995; Osozawa and Hasegawa, 1995; Nakadai et al., 1996), CO_2 concentration on the forest floor decreased in the daytime. Similar findings were also reported by Yabuki (1985), Bazzaz and Williams (1991) and Eguchi et al. (1997). It is considered that the reduction of



① Estimated from 3_{a-d} ② Estimated from 4_{a-d}
③ 3_{a-d} − 1 (C, 400 ppm; W, 1.0 ms^{-1})
④ 4_{a-d} − 1 (C, 400 ppm; W, 1.0 ms^{-1})
⑤ 3_{a-d} − 2 (C, 0 ppm; W, 0.0 ms^{-1})
⑥ 4_{a-d} − 2 (C, 0 ppm; W, 0.0 ms^{-1})

Fig. 2-2-6 Daily change in estimated soil respiration.

CO_2 concentration in the daytime is mainly caused by CO_2 absorption through the photosynthesis of green plants (Yabuki, 1985). As a result, fluctuation in CO_2 concentration within a forest is more intense on fine days than on rainy day, and a greater reduction in CO_2 concentration in the daytime is observed under higher temperature and more intense sunlight conditions (Eguchi et al., 1997). Therefore, in this study, photosynthesis of green plants may have been one cause of the fluctuation of CO_2 concentration because the clearest fluctuation was observed in summer when the temperature was higher and there was more sunlight than in other seasons. Moreover, the negative relationship between CO_2 concentration and wind speed at the study site suggests that wind speed may have been the other cause of the fluctuation in CO_2 concentration. Higher wind speed in the daytime may have accelerated physical diffusion of CO_2 from the forest floor to the air, thereby decreasing CO_2 concentration on the forest floor. Since undergrowth was sparse at this site, the effect of photosynthesis of green plant may not have been so significant. Therefore, such clear daily fluctuation of CO_2 concentration may have been caused by effects of both photosynthesis and wind speed.

Effects of CO_2 concentration, wind speed and temperature on soil respiration

In this study, the negative relationship between soil respiration and CO_2 concentration was expressed using the slope and intercept which included wind speed as an explanatory variable (Fig. 2-2-3). It had already been reported that soil respiration decreases linearly with increasing CO_2 concentration (Gyokusen and Saito, 1995; Ohashi et al., 1995). Nakadai et al. (1993) supposed that acceleration in the soil microbial respiration rate (Koizumi et al., 1991) was one of

the causes. Ohashi et al. (1995) reported that linear change in soil respiration with changing CO_2 concentration was brought about mainly by physical diffusion which depended on the CO_2 concentration gradient. In this study, changes in soil respiration may have been caused mainly by physical diffusion of CO_2, because a linear increase in soil respiration rate with decreasing CO_2 concentration was observed.

In (1_{n-1}) equations, supposing CO_2 concentration is fixed, a linear relationship between soil respiration and wind speed is obtained. This is consistent with other studies, such as Hanson et al. (1993) and Ohashi et al. (1995). Inoue (1986) also reported that soil respiration increased with increasing ventilation rate and Gyokusen and Saito (1995) reported that soil respiration rate changed with and without wind speed in the chamber. Therefore, it is considered that the increase in wind speed stimulated CO_2 diffusion from the soil due to the disruption of the boundary layer over the forest floor (Hanson et al., 1993; Ohashi et al., 1995)

In this study, soil respiration rates increased exponentially with increasing soil temperature (Fig. 2-2-4). Many studies reported the strong effect of temperature on soil respiration (Witkamp, 1969; Kanemasu et al., 1974; Parker et al., 1983; Grahammer et al., 1991; Osozawa and Hasegawa, 1995; Nakadai et al., 1996). The relationship between the two values is often expressed by exponential equation (Kucera and Kirkham, 1971; Anderson, 1973; Hagihara et al., 1984; Sakai and Tsutsumi, 1987; Simono et al., 1989) or linear equation (Gupta and Singh, 1981; Mathes and Schrifer, 1985; Rochette et al., 1991; Lessard et al., 1994). In this study, the exponential relationship was confirmed between soil respiration and soil temperature. Q_{10} values, ranging from 3.0～4.1, were within the higher range of 1.8～4.1 as reported for a variety of temperate forests (Sakai and Tsutsumi,

1987).

Diurnal and seasonal changes in soil respiration

Soil respiration has been estimated using various models, such as those of Schlentner and Van Cleve (1985), Carlyle and Than (1988), Holt et al. (1990) and Raich et al. (1992). However, most of these models estimated seasonal changes in soil respiration and variously used temperature, moisture and precipitation as explanatory variables in the models. In this study, however, daily changes in soil respiration were estimated using new explanatory variables, wind speed and CO_2 concentration, in addition to temperature. The new explanatory variables had already been already confirmed as affecting soil respiration (Nakadai et al., 1993; Ohashi et al., 1995). However, since soil respiration has been measured under a stable environment in a chamber, many studies of soil respiration using chamber methods took no account of the effects of the natural fluctuation in these factors. In this study, soil respiration estimated from the fluctuation of temperature, CO_2 concentration and wind speed on the forest floor increased in the daytime and decreased at night. This pattern may have been caused not only by the fluctuation of temperature but also by the fluctuation of wind speed (Fig. 2-2-1, Fig. 2-2-2). In addition, the obverse fluctuation of CO_2 concentration, increasing at night and decreasing in the daytime, may also have caused the soil respiration fluctuation because soil respiration increased with decreasing CO_2 concentration (Fig. 2-2-3). Similar diurnal change in soil respiration has been reported by Witkamp (1969), Kanemasu et al. (1974), Grahammer et al. (1991), Gyokusen and Saito (1995), Osozawa and Hasegawa (1995) and Nakadai et al. (1996). However, some studies reported nocturnal increases in soil respiration (Witkamp, 1969;

Edwards and Sollins., 1973; Eguchi et al., 1997). Eguchi et al. (1997) showed that increases in root respiration caused nocturnal increases in soil respiration. Witkamp (1969) thought that it resulted from the thermal convection of CO_2 rich subsurface air to the surface. In this study, differences between the estimated values and the measured values tended to be greater in the evening (Fig. 2-2-5). This tendency suggests that fluctuation in soil respiration in the evening may differ from estimated fluctuations. Soil respiration is also affected by occasional rain (Rochette et al., 1991; Kurser, 1989). Therefore, equations formulated using data collected in the daytime on fine days may be of limited use when estimating fluctuations in soil respiration at night or on days that are not fine. It is necessary to investigate effects of physiological activity of roots and effects of other environmental factors, such as precipitation, in order to estimate fluctuations in soil respiration more accurately.

Seasonal change in soil respiration, ranging from $0 \sim 300$ $mgCO_2 m^{-2} hr^{-1}$, increased in summer and decreased in winter. This is seasonally consistent with other studies which reported that seasonal fluctuation in soil respiration is mainly influenced by soil temperature (Chiba, 1975; Simono et al., 1989; Hagihara et al., 1984; Ohashi et al., 1999b). However, estimated values of soil respiration were below the range of $100 \sim 500$ $mgCO_2 m^{-2} hr^{-1}$, as reported for a variety of temperate forests (Singh and Gupta, 1977). Most soil respiration measurements have been conducted using the chamber technique, such as the static CO_2 absorption method and IRGA methods. In static CO_2 absorption methods, CO_2 concentration and wind speed in the chamber fall considerably due to the irreversible binding of CO_2 to the alkali solution in the chamber (Monteith et al., 1964; Kirita and Hozumi, 1966; Kirita, 1971a～d; Buyanovsky et al., 1986; Meier et al., 1993; Robertson et al.,

1995). In IRGA methods, CO_2 concentration in the chamber, 400～500 ppm, is similar to atmospheric concentration and there is often some wind in the chamber due to the air flow through the chamber (Kucera and Kirkham, 1971; Parkinson, 981; Koizumi et al., 1991; Hanson et al., 1993; Ohashi et al., 1999b). Taking these methods into consideration, temperature only was substituted in the equations and the other two factors, wind speed and CO_2 concentration, were fixed at (0.0 ms^{-1} and 0 ppm) and (1.0 ms^{-1} and 400 ppm) similar to those of static CO_2 absorption methods and IRGA methods, respectively. As a result, although the fluctuation pattern was similar to natural conditions, estimated values, 40～510 $mgCO_2 m^{-2} hr^{-1}$, were about twice as high as those of natural, consistent with a report by Singh and Gupta (1977) (Fig. 2-2-6). This suggests that measurement values using the chamber method may overestimate values of natural condition according to wind speed and CO_2 concentration in the chamber. It is important to adjust environmental factors in the chamber similar to external values in order to estimate soil respiration accurately.

Chapter 3 Spatial and temporal variability in soil respiration from a forest floor

3.1 Measurement of carbon dioxide evolution from a Japanese cedar (*Cryptomeria japonica* D. Don) forest floor using an open-flow chamber method

3.1.1 Introduction

Soil respiration or CO_2 evolution from the soil surface has been regarded as important because it represents the sum of soil metabolic activities (Simono et al., 1989; Behara et al., 1990). Recently, understanding the amount and fluctuation of soil respiration has become more relevant because of the need to evaluate the capacity of forest ecosystems to fix carbon, which may be important to the global carbon budget (Houghton and Woodwell, 1989; Oikawa, 1991; Vose et al., 1997).

Seasonal fluctuation in soil respiration from root and soil microbial respiration mainly corresponds to changes in environmental factors, such as soil moisture and temperature (Singh and Gupta, 1977). Nevertheless, influence of these two factors may vary depending on geographical location and season. The strong effect of temperature (Anderson, 1973; Freijer and Bouten, 1991; Lassard et al., 1994), and soil moisture (Carlyle and Than, 1988; Holt et al., 1990), and both factors (Schlentner and Van Cleve, 1985; Pajari, 1995) have been reported. Soil respiration may also be affected by forest management practices. Some reports suggest that clear-felling or artificial gap formation cause the diminution of root respiration, thereby decreasing soil respiration (Nakane et al., 1983; Brumme, 1995; Striegl and Wickland, 1998). Toland and Zak (1994) reported that the

decomposition of dead roots after clear-felling offsets the decrease in soil respiration. Silvicultural practices, then, have the potential to alter the relative contribution of root and microbial respiration to soil respiration. Although thinning is one of the essential practices in forest breeding (Sato, 1983), the effect on soil respiration has not been investigated.

Two-thirds Japan is covered by forests and managed Japanese cedar (*Cryptomeria japonica* D. Don) forests have been highly productive for more than 300 years (Miyajima, 1989; Kawana and Kataoka, 1992). Many studies on aboveground carbon fluctuations have been conducted on Japanese cedar forests (e.g. Yoda, 1971; Kawanabe et al., 1975; Mizunaga, 1994; Tatsuhara and Suzuki, 1995). However, there are only two studies concerning soil respiration in Japanese cedar forests (Hagihara et al., 1984; Simono et al., 1989), even though studies on soil respiration have increased steadily (Raich and Schlesinger, 1992) and various methods to measure soil respiration have been developed (Norman et al., 1992; Bekku et al., 1995; Thierron and Laudelout, 1996). One reason is that most of the wooded areas in Japan are found in steep mountains. Thus, it could be difficult to operate unwieldy or expensive respirometers. Only the static CO_2 absorption method has been used to measure soil respiration in Japanese cedar forests because of its simple construction and low-price (Hagihara et al., 1984; Simono et al., 1989).

However, some reports demonstrated that the static CO_2 absorption method might be inadequate in field measurements (Kucera and Kirkham, 1971; Edwards and Sollins, 1973; Frejer and Bouten, 1991; Nakadai et al., 1993). This method determines the quantity released from the soil with a covered chamber, by irreversibly binding CO_2 to NaOH or soda lime in the chamber. Thus, the difference in

environmental factors inside and outside the chamber may influence readings. It has been confirmed that wind speed and CO_2 concentration in the chamber affect soil respiration rate significantly (Hanson et al., 1993; Nakadai et al., 1993; Gyokusen and Saito, 1995; Ohashi et al., 1995). Thus, it is important to measure soil respiration while regulating environmental conditions in the chamber. To this end, I established a portable open-flow soil respiration measuring system which regulated CO_2 concentration and wind speed in a chamber, and examined the effects of environment factors such as CO_2 concentration and wind speed in the chamber (Gyokusen and Saito, 1995; Ohashi et al., 1995).

In the present study, I evaluated seasonal changes in soil respiration from a Japanese cedar (*Cryptomeria japonica*) forest floor using our portable open-flow measuring system to clarify the relationship between soil respiration rates and other environmental factors such as soil temperature and soil moisture. I also examined the effect of thinning on soil respiration by comparing soil respiration in the intact section and the thinned section of a Japanese cedar forest stand. Seasonal changes in soil surface CO_2 concentration, estimated from soil respiration rates, were also determined.

3.1.2 Study Area

The study area was a 0.9 ha plantation of 9-year-old Japanese cedar in the Forest Research and Instruction Station of Kumamoto Prefecture, located in Kyushu, southwest of Japan (32° 49′ N, 130° 44′ E). The forest is planted on a level topographic site and undergrowth is sparse. Mean annual air temperature and precipitation in this area in 1996 was 16.2 ℃ and 1970 mm, respectively (Kumamoto Local Meteorological Observatory, 1996). The

soil type is a light color humid andosol (Kuroboku) derived from volcanic ash (Inoue, 1979) and there is a thin organic horizon. In March 1992, half of this forest was thinned. The intact and thinned sections had 16,000 and 8,000 trees ha^{-1}, respectively, with trees 6 - 8 m in height. Since tree size, the leaf area index and crown structure in the thinned and intact sections were similar before thinning (Gyokusen, unpublished data), the two sections of this forest plot were the same before thinning. Thus, changes thereafter are considered to have been caused by thinning.

3.1.3 Methods

Soil respiration, soil temperature and soil moisture

I established five sampling points of soil respiration in each of the intact and thinned sections. All samplings were conducted between 9:00 to 15:00 to minimize the impact of diurnal variability (Edwards and Sollins, 1973; Hanson et al., 1993). On March 1996, I verified that 5 sampling points had a coefficient of variation (9.5 %) comparable to 12 sampling points (9.2 %).

I located the sampling points randomly in both sections, with each point at roughly similar distance from surrounding trees. Every sampling thereafter was conducted at the same points and the mean of the five sampling points were calculated. Measurement in all 10 points was carried out once on a fine day at the end of every month for three years, from January 1994, almost two years after thinning, to December 1996.

At each sampling point, I measured soil respiration using the open-flow portable measuring system that we developed (Gyokusen and Saito, 1995; Ohashi et al., 1995). The chamber was 3 mm thick acrylic cylinder, 24.5 cm in diameter and 15 cm in height. The bottom

edge of the chamber was sharpened so it could easily press into the soil. After removing the layer of dead leaves and branches, the bottom edge of the chamber was buried about 1 cm into the ground. Pressure difference inside and outside the chamber was prevented by air flow combination through the chamber (Gyokusen and Saito, 1995). Wind speed in the chamber was maintained at 4.0 ms^{-1} by a fan because higher wind speed provided consistent measurement values (Ohashi et al., 1995). CO_2 concentration in the air flowing in and out of the chamber was measured by an infrared gas analyzer (SPB-H3, Shimadzu, Japan). Each measurement took approximately 10 minutes. Commercial soil respirometers (e.g. Li-Cor, Lincoln, NE) or a closed-dynamic method obtain measurement values while CO_2 concentration in the chamber increase by air circulation through the system (Norman et al., 1992; Garcia et al., 1997). On the other hand, the open-flow system regulates CO_2 concentration in the air flowing into the chamber during measurement. Under field conditions, soil respiration decreases linearly with increasing CO_2 concentration (0 – 450 ppm) in the chamber (Nakadai et al., 1993; Gyokusen and Saito, 1995; Ohashi et al., 1995). Therefore, I measured soil respiration twice; first, with the CO_2 concentration in the chamber maintained at about zero ppm and then, without CO_2 regulation (CO_2 concentration was about 450 ppm). I calculated soil respiration when CO_2 concentration in the chamber was exactly 400 ppm from the straight line between the two measuring points. The intersection points with the X axis, when soil respiration was zero $gCO_2\ m^{-2}\ s^{-1}$, were taken as the CO_2 concentration of the soil surface, since soil respiration would cease as CO_2 concentration in the chamber reached the CO_2 concentration of the soil surface (Gyokusen and Saito, 1995; Ohashi et al., 1995).

I calculated the soil surface CO_2 concentration using the formula in CO_2 weight per unit volume (Eguchi et al., 1997),

$$C = M \times C_0 \times 10^{-3} \times 273 / 22.4 / (273 + T)$$

where, C (g m^{-3}) is the calculated CO_2 concentration, C_0 (ppm) is the measured CO_2 concentration, T (℃) is the temperature of soil surface, and M (g) is the molecular weight of CO_2, 44 g.

Soil surface temperature was simultaneously measured using a thermistor thermometer (SL5-FF, Chino, Japan) at each point as soil respiration was measured. Soil cores (20 cm^2 × 5 cm) were taken at 10 cm depth immediately adjacent to each sampling point at the end of each measurement. Cores were oven-dried at 105 ℃ for 48 hours and soil moisture content were determined gravimetrically.

Statistical analysis

Soil respiration, soil surface temperature and soil moisture were compared between years and between the thinned and intact sections using ANOVA. Monthly difference in soil respiration, soil temperature and soil moisture between the two sections were compared by *t*-test. To examine the correlation of soil respiration rates (n = 5) with temperature (n = 5) and soil moisture (n = 5) in each section, non-linear regression analyses was used. Comparison of regression lines between soil respiration rate and soil temperature were examined by ANCOVA. Significance for all statistical analyses was accepted at $\alpha = 0.05$.

3.1.4 Results

Seasonal changes in soil respiration and soil surface temperature

Soil respiration rates, ranging from 0.05 to 0.78 gCO_2 m^{-2} hr^{-1} and 0.03 to 0.61 gCO_2 m^{-2} hr^{-1} in the thinned and intact forest plots, respectively, increased in summer and decreased in winter (Fig. 3-1-1).

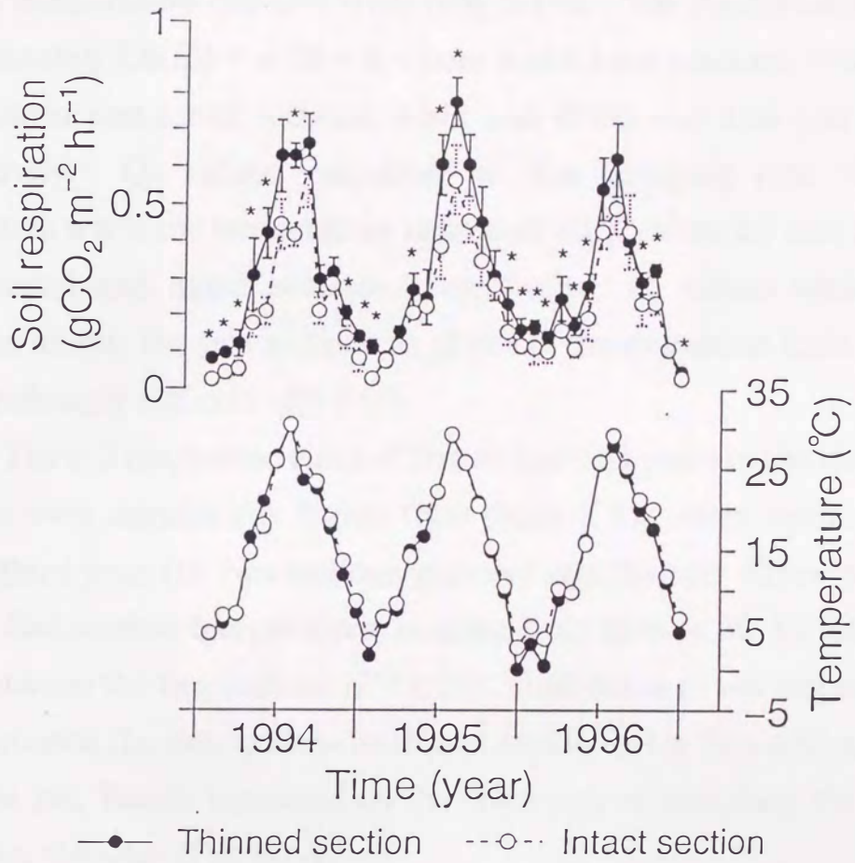


Fig. 3-1-1 Seasonal changes in soil respiration and soil surface temperature. Vertical bars indicate ± S.D. Asterisk means significantly different between the two sections at the 0.05 level.

The maximum values were recorded from July to August, while minimum values were recorded from December to February.

Soil respiration rates (*Rs*) significantly correlated with soil surface temperature (*Ts*) ($P < 0.05$) (Fig. 3-1-2). The relationship was approximately $\mathrm{Ln}(Rs) = a(Ts) + b$, where a and b are constant values in the thinned and intact sections, 0.071 and 0.090 and 4.49 and 3.75, respectively. Q_{10} values, calculated as the changing rate of soil respiration when the temperature increased 10 ℃, were 2.0 and 2.5 in the thinned and intact sections, respectively. Q_{10} values were not different among the two sections as slopes of the regression lines were not significantly different ($P < 0.05$).

The soil respiration rates of first and second years in the thinned section were significantly higher than those of the intact section, but by the third year, the two sections were not significantly different ($P < 0.05$). Soil surface temperature, ranging from zero to 30 ℃, differed little between the two sections ($P < 0.05$). Difference in soil respiration rates between the two sections increased rapidly in the first and second summer, but, hardly increased on the third year of sampling, the fifth year after thinning (Fig. 3-1-3).

Annual soil respiration rates

Correlation equations between soil respiration and soil surface temperature (Table 3-1-1) were used to calculate daily mean soil respiration from daily mean temperatures (Kumamoto Local Meteorological Observatory, 1994 - 1996). Since diurnal changes in soil respiration were negligible at this study site (Gyokusen and Saito, 1995), daily soil respiration was estimated from daily mean soil respiration and cumulated to calculate annual soil respiration.

Annual soil respiration rate in thinned and intact forest sections,

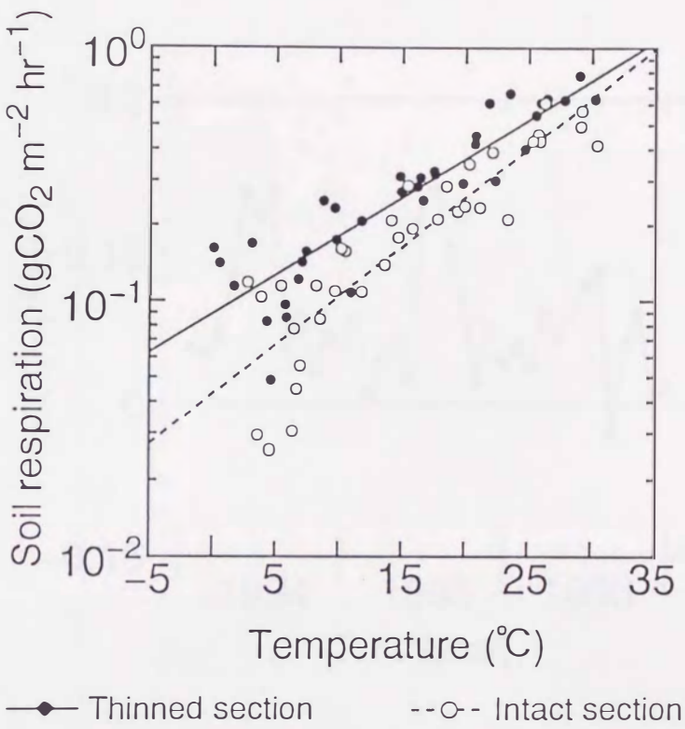


Fig. 3-1-2 Relationship between soil respiration (*Rs*) and soil surface temperature (*Ts*). Regression equation for the thinned section was Ln(*Rs*) = 0.071 (*Ts*) − 2.41 (r^2 = 0.89) and for the intact was Ln(*Rs*) = 0.090 (*Ts*) − 3.15 (r^2 = 0.79).

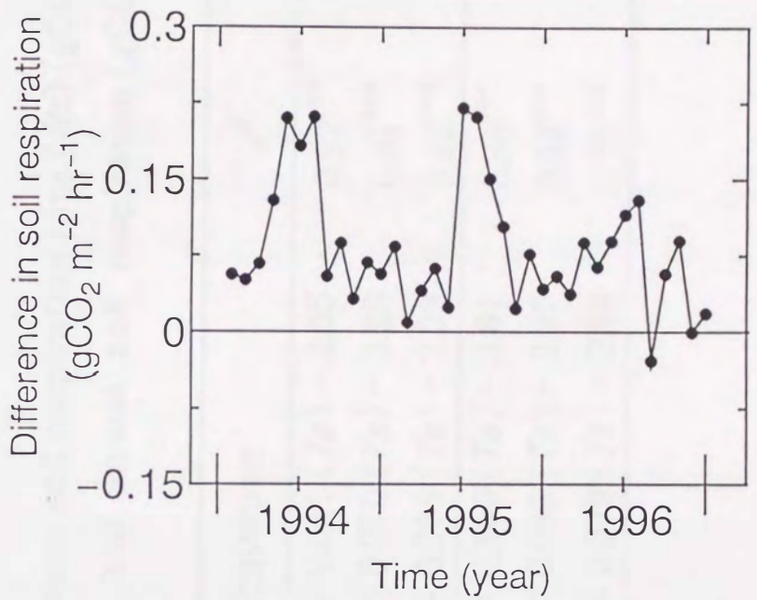


Fig. 3-1-3 Difference in soil respiration rates between thinned and intact sections.

Table 3-1-1 Correlation equations between soil respiration rate (*Rs*) ($gCO_2\ m^{-2}\ hr^{-1}$) and soil surface temperature (*Ts*) (℃), and annual soil respiration ($gCO_2\ m^{-2}\ yr^{-1}$) from the thinned and intact section.

Section	Year	Equation	r^2	Annual soil respiration
Thinned	1997	Ln (*Rs*) = 0.081 (*Ts*) − 2.65	0.92^{***}	1240
	1998	Ln (*Rs*) = 0.070 (*Ts*) − 3.28	0.87^{***}	1330
	1999	Ln (*Rs*) = 0.065 (*Ts*) − 2.38	0.69^{***}	2460
Intact	1997	Ln (*Rs*) = 0.106 (*Ts*) − 3.61	0.88^{***}	1280
	1998	Ln (*Rs*) = 0.088 (*Ts*) − 2.95	0.82^{***}	1310
	1999	Ln (*Rs*) = 0.079 (*Ts*) − 2.98	0.78^{***}	2210

*** Significant at the 0.001 level.

highest in 1995 and lowest in 1996, ranged from 2570 to 3060 gCO_2 m^{-2} yr^{-1} and 1830 to 2170 gCO_2 m^{-2} yr^{-1}, respectively. Mean of annual soil respiration rates from the thinned and intact sections were 2860 and 1950 gCO_2 m^{-2} yr^{-1}, respectively.

Seasonal changes in soil surface CO_2 concentration

Soil surface CO_2 concentration for the three years, ranging from 0.8 to 3.9 g m^{-3}, varied seasonally from year to year (Fig. 3-1-4). A tendency to increase in summer and decrease in winter was observed. In summer, CO_2 concentration in the thinned section exceeded that of the intact section, but in winter, variation between the two treatments was not observed. Soil surface CO_2 concentrations fluctuated and ranged from about two to six times higher than ambient atmospheric CO_2 concentrations.

3.1.5 Discussion

Soil respiration and effect of environmental factors

Annual soil respiration rates from our study area (minimum 1830 to maximum 3060 gCO_2 m^{-2} yr^{-1}) were within the range 1360～3450 gCO_2 m^{-2} yr^{-1}, found in temperate forests (Anderson, 1973; Bowden et al., 1993; Nakane et al., 1996). It was lower than generally reported in tropical forests, 5130～5300 gCO_2 m^{-2} yr^{-1} (Kursar, 1989; Maggs and Hewett, 1990; Lamade et al., 1996), a little higher than in boreal forests, 1750 gCO_2 m^{-2} yr^{-1} (Toland and Zak, 1994).

Our results were within the range of previous researches using static CO_2 absorption method in Japanese cedar forests at 2440 gCO_2 m^{-2} yr^{-1} (Hagihara et al., 1984), and 1710～1800 gCO_2 m^{-2} yr^{-1} (Simono et al., 1989). The reason for this may have been an interaction of factors in the chamber in the static CO_2 absorption method. In static CO_2

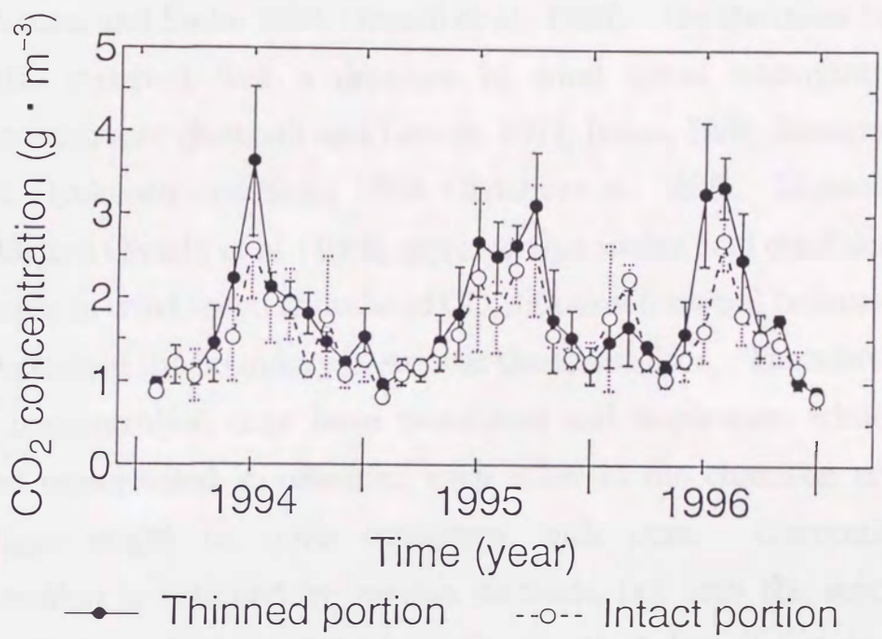


Fig. 3-1-4 Seasonal changes in soil surface CO_2 concentration. Vertical bars indicate ±S.D.

absorption methods, CO_2 concentration and wind speed in the chamber fall considerably because of irreversibly binding CO_2 to alkali solution in the chamber. It was reported that a decrease in CO_2 concentration may stimulate the respiratory activity of microbes (Koizumi et al., 1991) or CO_2 physical diffusion from soil (Ohashi et al., 1995), and thereby lead to an overstatement of soil respiration rate (Nakadai et al., 1993; Gyokusen and Saito, 1995; Ohashi et al., 1995). On the other hand, it is also reported that a decrease in wind speed understates soil respiration rate (Kimball and Lemon, 1971; Inoue, 1986; Hanson et al., 1993; Gyokusen and Saito, 1995; Ohashi et al., 1995). Hanson et al. (1993) and Ohashi et al. (1995) reported that under field conditions, the increase in wind speed stimulated CO_2 diffusion from soil because of the disruption of the boundary layer over the forest floor. Therefore, since CO_2 concentration may have overstated soil respiration while wind speed understated it, offsetting each other in the chamber, previous findings might be quite consistent with ours. Currently, soil respiration is obtained by various methods, not only the static CO_2 absorption method and the open-flow method, but also static IRGA method (Bekku et al., 1995), soil commercial respirometers (Norman et al, 1992; Thierron and Laudelout, 1996) and others. Thus, in comparing measurement values obtained using different methods, consideration of differences in environmental conditions in the chambers is necessary.

Soil surface CO_2 concentration fluctuated considerably in the higher range than in the atmosphere (Fig. 3-1-4), consistent with other studies (Yabuki, 1985; Bazzaz and Williams, 1991; Eguchi et al., 1997). Ohashi et al. (1999a) reported that wind speed also fluctuates continuously on a forest floor. Thus it can be presumed that soil respiration is affected by aspects of CO_2 concentration and wind speed

on a forest floor. However, many studies of soil respiration took no account of the two factors. Formulating an equation that included CO_2 concentration and wind speed as explanatory variables would allow more accurate estimation of natural soil respiration.

Seasonal change in soil respiration is influenced by two principal environmental factors, temperature and moisture (Singh and Gupta, 1977). The effect of these two factors, however, varies depending on geographical location and season. The strong influence of moisture has been reported in a *Pinus radiata* forest (Carlyle and Than, 1988) and in a tropical woodland (Holt et al., 1990) in Australia, whereas the influence of both factors has been reported in four mature forests in Alaska (Schlentner and Van Cleve, 1985), and a scots pine forest in Finland (Pajari, 1995). In this study, soil respiration rates increased exponentially with soil temperature (Fig. 3-1-3), whereas soil moisture did not have a significant effect ($P < 0.05$). Similar findings have been reported in many other forests, such as deciduous forests (Anderson, 1973; Sakai and Tsutsumi, 1987), evergreen broadleaf forests (Kirita, 1971), temperate mixed forest (Freijer and Bouten, 1991; Lassard et al., 1994), and northern hardwood forests (Toland and Zak, 1994).

Q_{10} values, a convenient index in comparing the sensitivity of soil respiration with soil temperature, tend to be large in cooler regions compared with warm regions (Townsend et al, 1992; Kirschbaum, 1995). In this study, Q_{10} values were within the range of 1.8~4.1, as reported for a variety of temperate forests (Fung et al., 1987; Sakai and Tsutsumi, 1987; Hanson et al., 1993) and similar to the mean of Q_{10} values for soil respiration, approximately 2.0 (Sakai and Tsutsumi, 1987; Townsend et al, 1992).

Townsend et al. (1992) expected that temperate systems would

produce a large soil carbon efflux within a century as a response to global warming and the exponential increase in soil respiration with temperature could persist for a long time until limited by carbon availability. If so, understanding the factors that affect temperature sensitivity of soil respiration under field condition is necessary to predict and adapt to the response of ecosystems to global warming. Kirschbaum (1995) reported that Q_{10} values obtained by field measurement were affected by many other factors and that, even at the same sites, they might be different when measured in different years. In this study, however, Q_{10} values were not significantly different either between thinned and intact sections and over years ($P < 0.05$). This may be because soil moisture, the most important factor affecting Q_{10} values (Chiba, 1975; Kirschbaum, 1995), did not vary significantly between the two sections or over years ($P < 0.05$).

Q_{10} values in the thinned section (2.0) tended to be lower than those in the intact section (2.5). Comparing annual Q_{10} values, thinned section values (2.3 in 1994, 2.0 in 1995, 1.9 in 1996) were lower than intact section values (2.8 in 1994, 2.4 in 1995, 2.2 in 1996). Since root and microbial respiration has different temperature sensitivities, a difference in the root and microbial ratio to soil respiration would cause variations in the temperature sensitivities of soil respiration rates (Kirschbaum, 1995). In this study, greater soil respiration in the thinned section compared with the intact section may suggest a difference in the root and microbial ratio to soil respiration. Nutrient status might also affect the temperature sensitivities of soil respiration. The effect of soil organic C and N on soil respiration has been reported (Singh and Gupta, 1977; Maggs and Hewett, 1990). Holland et al. (1997) demonstrated that CO_2 and N in the biosphere are highly interactive and not independent of each other. These reports suggest

that nutrient status not only relates to soil respiration directly, but also to many other parts of the C cycle in the ecosystem, such as photosynthesis, and thereby eventually affects temperature sensitivities indirectly. In this study, the death of roots due to thinning may have caused variation in nutrient status between the two sections.

Effect of thinning

It is considered that the difference in the soil respiration rates between the thinned and intact sections was caused by thinning, because this plantation stand at a level topographic site with tree size, leaf area index (LAI) and crown structure in both sections of the stand being the same before thinning. Thus any subsequent changes were likely to have been caused by the intervention.

Although thinning is one of the main technique in silviculture (Sato, 1983), most investigations have concentrated on clear-felling and artificial gap formation. Nakane et al. (1983) and Striegl and Wickland (1998) observed a decrease in soil respiration rate after clear-felling. Brumme (1995) reported that when a gap 30 m in diameter was made, soil respiration was lowest in the center of the gap. In our study, soil respiration rates in the thinned section were higher than those of the intact stand (Table 3-1-1), even though half the number of trees have been cut. This suggests that thinning may affect soil respiration quite differently from other forest management techniques, such as clear-felling or artificial gap formation.

Since there was little difference in environmental factors, such as soil temperature and moisture, between the two sections, two explanations are possible for the high soil respiration in the thinned section. One reason may be the acceleration of microbial respiration following decomposition of dead roots due to thinning. Some studies

observed that root decomposition increased after clear-felling (Ewel et al., 1987; Hendrickson et al., 1989; Nakane et al., 1983; Nakane et al., 1996). Toland and Zak (1994) reported that acceleration of microbial respiration by clear-felling offset the decrease in soil respiration. The other explanation may be the increased development of the roots of remaining trees. Clear-felling caused diminution of root respiration, and consequently often decreased soil respiration (Nakane et al., 1983; Brumme, 1995). Thus, in this study, soil respiration may have decreased but only immediately after thinning before measurement were taken. However, when measurements were taken, almost two years after thinning, as seen in the rapid increase in the LAI after thinning (Gyokusen, unpublished data), the development of the root systems of remaining trees caused the recovery of root respiration to the same or even greater level as that of the intact section.

The difference in soil respiration rates between the thinned and intact sections increased in the first and second summer, but, hardly increased at all in the third year (Fig. 3-1-3). Gyokusen (unpublished data) observed that four years after thinning, LAI in the thinned section was equal to that of the intact section. Toland and Zak (1994) presumed that more than five years may be needed until all dead roots decompose in clear-felling forest. Therefore five years after thinning, or in the third year of this study, the abatement of the thinning effect and the complete decomposition of almost all dead roots may have reduced further microbial respiration and root development. Further studies are required to determine completely the effect of thinning on forests of different age, density and other parameters. It was also necessary to distinguish soil microbial respiration from root respiration especially in the thinned section, which may be necessary to completely understand changes in CO_2 fluctuation in the soil after thinning.

Although higher soil respiration was observed in the thinned section, it cannot be concluded that the carbon fixing capacity of this ecosystems was reduced by thinning, because thinning may also stimulate the photosynthesis of an individual tree. Therefore, it is necessary to clarify the carbon balance between carbon assimilation by photosynthesis and carbon loss through respiration. This study suggests that forest management such as thinning may have the potential to change the carbon balance of the ecosystems. Soil respiration is the second largest flux in the global carbon cycle (Raich and Schlesinger, 1992; Striegl and Wickland, 1998). Thus, even a small change in soil respiration could alter global carbon budget substantially. Understanding the effects of silvicultural practice on soil respiration is important in establishing effective forestation techniques helpful not only for timber production, but also in addressing environmental problems such as global warming.

3.2 Spatial and temporal variability of soil respiration in a Japanese cedar (*Cryptomeria japonica* D.Don) forest floor using an open-flow chamber method

3.2.1 Introduction

Soil respiration, the sum of plant root and microbial respiration, changes spatially and temporally due to many factors, such as environmental conditions and soil characteristics. Spatial change in soil respiration in forest ecosystems has been observed mainly on slopes because the complicated configuration produces an imbalance of factors affecting soil respiration, such as soil nutrients and aboveground vegetation. Shimada et al. (1998) reported larger soil respiration at lower sites than at other sites on a slope of a Japanese cedar and cypress forest. They conjectured that the high soil respiration caused by high soil organic matter. Simono et al. (1989) reported higher soil respiration on the upper part of a slope in a young Japanese cypress forest due to differences in soil moisture conditions. Hanson et al. (1993) measured seasonal patterns of soil respiration at four topographically distinct locations in an upland oak forest in Tennessee and observed an isolated period when valley-bottom locations had reduced soil respiration relative to other topographic sites. They reported that lower soil respiration was consistent with the reduced fine root density and elevated coarse fraction percentage. Since spatial variability of soil respiration can be observed easily on slopes, high spatial variety may be observed in many Japanese forests because most wooded areas are found on steep mountains.

Many reports have estimated soil respiration rate from a forest from 2～10 measurement points. (Maggs and Hewett, 1990; Jurik et al., 1991; Edwards and Sollins., 1973; Schlentener and Van Cleve, 1985).

However, Rochette et al. (1991) reported that the number of measurements required to estimate soil respiration in a wheat crop was estimated at from 30 to 190 per ha. This indicates that a large number of measurement points may be needed in order to estimate the average value of soil respiration in a Japanese forest because soil respiration may have high spatial variability. Therefore, determination of spatial variability of soil respiration is important in deciding the number of measurement required.

Soil respiration may also fluctuate temporally due to environmental factors, such as soil moisture and temperature (Singh and Gupta, 1977). Many studies observed seasonal changes in soil respiration due to the strong effect of temperature (Kirita, 1971d; Anderson, 1973; Chiba and Tsutsumi, 1967; Mathes and Schriefer., 1985; Sakai and Tsutsumi, 1987), and soil moisture (Carlyle and Than, 1988; Holt et al., 1990). There are fewer reports of diurnal changes in soil respiration because the static chamber method, which has been used widely, needs several hour to carry out measurements (Nakadai et al., 1996). However, using the IRGA method, some studies reported that diurnal changes in soil respiration increased in the daytime and decreased at night, corresponding to temperature (Witkamp, 1969; Kanemasu et al., 1974; Parker et al., 1983; Grahammer et al., 1991; Osozawa and Hasegawa, 1995; Nakadai et al., 1996). Further, no clear fluctuation was observed in some forests due to the absence of a significant diurnal change in environmental factors inside the forest (Kirita, 1971; Kursar, 1989; Gyokusen and Saito, 1995). Nocturnal increases in soil respiration was also been reported (Witkamp, 1969; Edwards and Sollins., 1973; Eguchi et al., 1997) because of the daily change in root respiration (Eguchi et al., 1997) and of the thermal convection of subsurface air to the surface (Witkamp, 1969). Therefore,

since soil respiration fluctuates not only spatially but also temporally, variability of both should be determined simultaneously in order to study soil respiration fluctuation under field conditions. However, there are few studies which determine spatial and temporal variability of soil respiration on Japanese forest slopes due to limitations in the portability of measurement systems.

The objective of this study is to determine the spatial and temporal variability of soil respiration on a Japanese cedar (*Cryptomeria japonica* D. Don) forest slope using a portable open-flow soil respiration measuring system (Gyokusen and Saito, 1995; Ohashi et al., 1995). The sampling points were located on a grid on the slope in order to assess the spatial variability of soil respiration. Seasonal and diurnal change were measured.

3.2.2 Study Area

The study area was a 1.6 ha area plantation of 38-year-old Japanese cedar in the Fukuoka Prefecture Forest Research and Extension Center, located in Kyushu, southwest Japan (Fig. 3-2-1). Mean annual air temperature and precipitation in this area in 1997 was 15.3 ℃ and 2663 mm, respectively (Fukuoka Local Meteorological Observatory, 1997). The forest, with trees 6-8 m in height in 1991, had 2762 trees ha^{-1} and intact management, with no thinning and no cleaning, from the beginning in order to maintain high density. The forest was planted on a 430 ~ 550 m high slope altitude and undergrowth was sparse. The salient geological feature was a crystalline schist, composed mainly of sericite schist and there was a 30 cm A horizon (Sasaki et al., 1996).

At this study site, a measurements plot 60 × 40 m in area was established. The slope of the plot was an average of 35° in a range

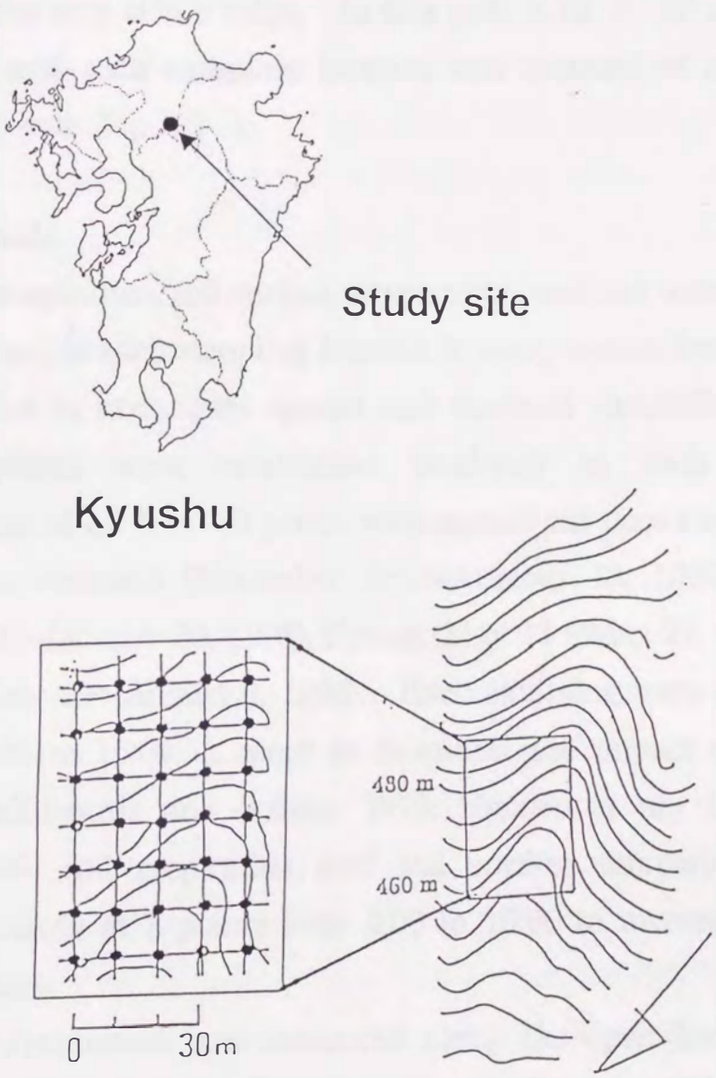


Fig. 3–2–1 Location of study site and measurement points.

from 22° to 47° (Sasaki et al., 1996). The west side of the plot was a valley and the east side a ridge. In this plot, a 10 × 10 mesh was established and each sampling location was situated at one of 35 interaction points (Fig. 3-2-1).

3.2.3 Methods

Soil respiration, soil surface temperature and soil water content were measured at each sampling location in every season from 1997 to 1998 in order to investigate spatial and seasonal variability. Four sampling points were established randomly in each location. Measurement at all 4 × 35 points was carried out once on fine days each season, Autumn (November 3～November 13, 1997), Winter (January 22～January 30, 1998), Spring (May 13～May 21, 1998) and Summer (July 29～August 6, 1998). Each sampling were conducted between 9:00 to 15:00 in order to minimize the impact of diurnal variability (Edwards and Sollins, 1973; Hanson et al., 1993). In August 1998, soil respiration and soil surface temperature was measured hourly at 3 points from 5:00 to 15:00 to investigate their diurnal change.

Soil respiration was measured using the open-flow portable measuring system developed by the author (Gyokusen and Saito, 1995; Ohashi et al., 1995). The chamber was a 3 mm thick acrylic cylinder, 24.5 cm in diameter and 15 cm in height. Air flow rate through the chamber was maintained at 1.5 $l m^{-1}$. Wind speed in the chamber was maintained at 1.0 ms^{-1} using a fan which was installed on top of the chamber to make CO_2 concentration in the chamber uniform (Hanson et al., 1993). CO_2 concentration in the air flowing in and out of the chamber was measured by infrared gas analyzer (SPB-H3, Shimadzu, Japan). Soil respiration rate was calculated when CO_2 concentration

in the chamber was exactly 400 ppm as a result of CO_2 concentration regulation (Ohashi et al, 1995; Ohashi et al, 1999b). Soil surface temperature was measured using a thermistor thermometer (SL5-FF, Chino, Japan) at each point at the same time as soil respiration. Three soil cores (20 cm^2 × 5 cm) were taken at 10 cm depth in each location at the end of the measurement at the location. Cores were oven-dried at 105 ℃ for 48 h and soil moisture content was determined gravimetrically.

3.2.4 Results

Spatial variability

Soil surface temperature for each measurement period ranged from 13.6～21.2℃、22.3～27.3℃、8.2～16.2℃ and –0.6～2.1℃ in spring, summer, autumn and winter, respectively. Soil moisture content for each measurement period ranging 32～96% did not vary seasonally. Soil respiration for each measurement period ranged from 66～468 $mgCO_2 m^{-2} hr^{-1}$, 136～559 $mgCO_2 m^{-2} hr^{-1}$, 33～334 $mgCO_2 m^{-2} hr^{-1}$ and 10～123 $mgCO_2$ in spring, summer, autumn and winter, respectively. Although there were 12 mm, 12 mm and 40 mm precipitation during autumn (12 November), winter (22 January) and spring (16 May) measurements, respectively, soil respiration, soil temperature and soil moisture content did not vary before or after precipitation (*t*-test、$P > 0.05$).

Coefficient of variation (CV) for the 35 measurement locations was 41%, 32%, 33% and 58% in spring, summer, autumn and winter, respectively. Mean CV for the 4 measurement points at a location was 25%, 22%, 23% and 48% in spring, summer, autumn and winter, respectively. Since CV for the locations was greater than CV at a location, spatial variability of soil respiration on this slope was

expressed by the contour line of mean soil respiration in each location (Delta Graph ver. 4.0)(Fig. 3-2-2). As a result, high and low soil respiration were observed at the study site, but distribution changed seasonally. High respiration appeared in the center of the study area in spring and spread in a southerly direction in summer. In autumn and winter, high and low soil respiration appeared randomly. Both soil temperature and soil moisture did not have a significant effect on the distribution of soil respiration ($P > 0.05$).

Temporal variability

Diurnal changes in soil respiration and soil temperature, ranging from 201~234 $mgCO_2 m^{-2} hr^{-1}$ and 24~25℃, respectively, were not observed clearly at 3 sampling points, whereas seasonal change at the same points, ranging from 39~241 $mgCO_2 m^{-2} hr^{-1}$ and 1~24℃, respectively, increased in summer and decreased in winter (Fig. 3-2-3). Soil respiration rate increased exponentially with increasing soil temperature (Fig. 3-2-4), whereas soil moisture did not have a significant effect ($P < 0.05$). The relationship between soil respiration (Rs) and temperature (Ts) was approximately Ln (Rs) = a (Ts) + b, where a and b are constant values at each point, from 0.029 to 0.109 and from 21 to 107, respectively ($P < 0.05$). Q_{10} values, calculated as the changing rate of soil respiration when the temperature increased by 10 ℃, were an average of 2.3 in a range from 1.3 to 3.0 (Fig. 3-2-5).

3.2.5 Discussion

Coefficient of variations of soil respiration

Coefficient of variations (CV) of soil respiration among measurement locations, raging 30~60%, were similar to those of bare soil, 20~70% (Dugas, 1993) and of agricultural fields, from 20~69%

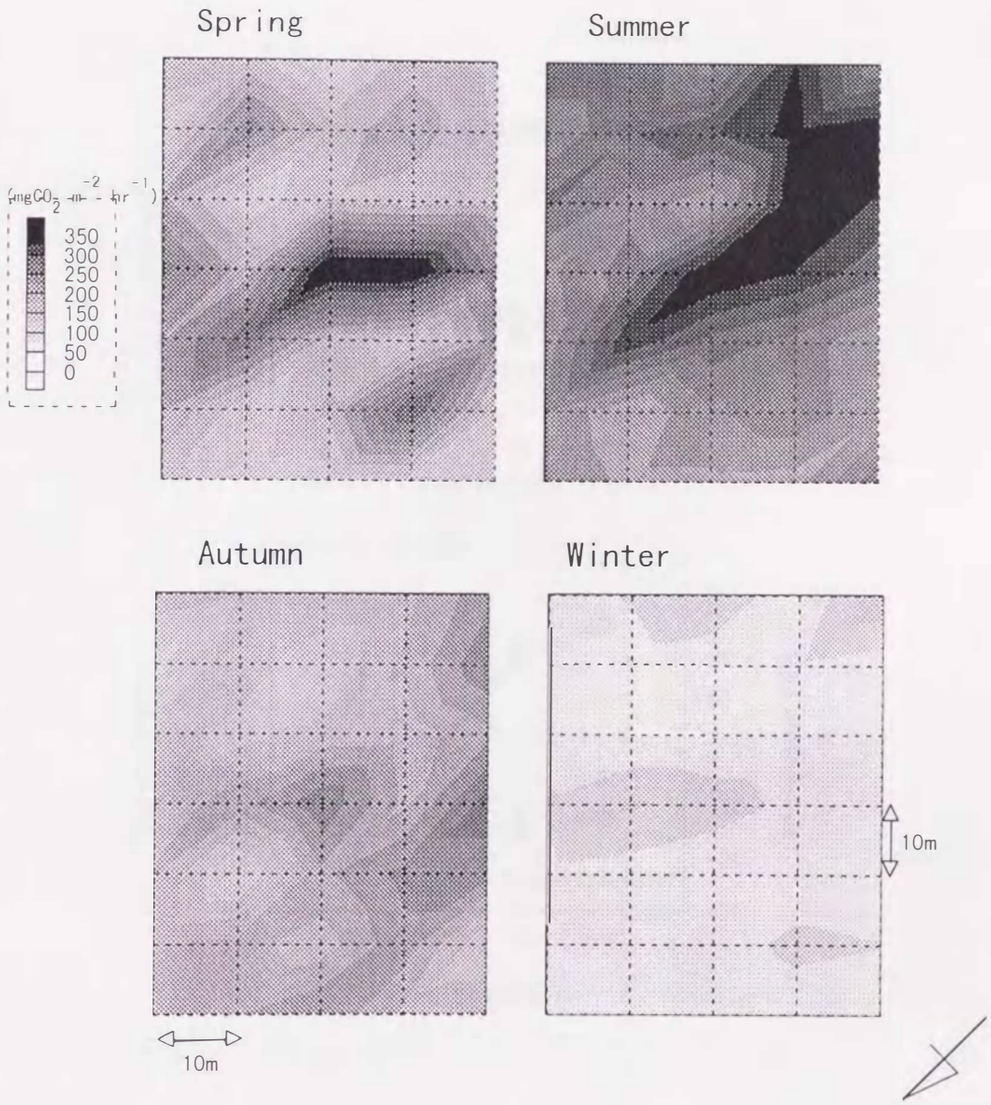


Fig. 3-2-2 Spatial variability in soil respiration.

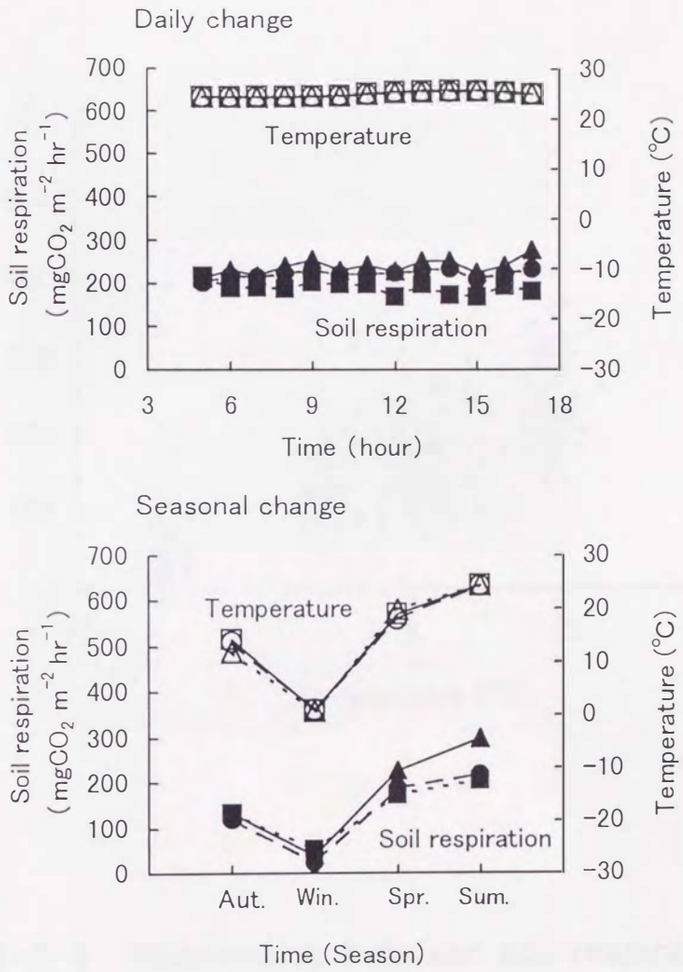


Fig. 3-2-3 Temporal changes in soil respiration.

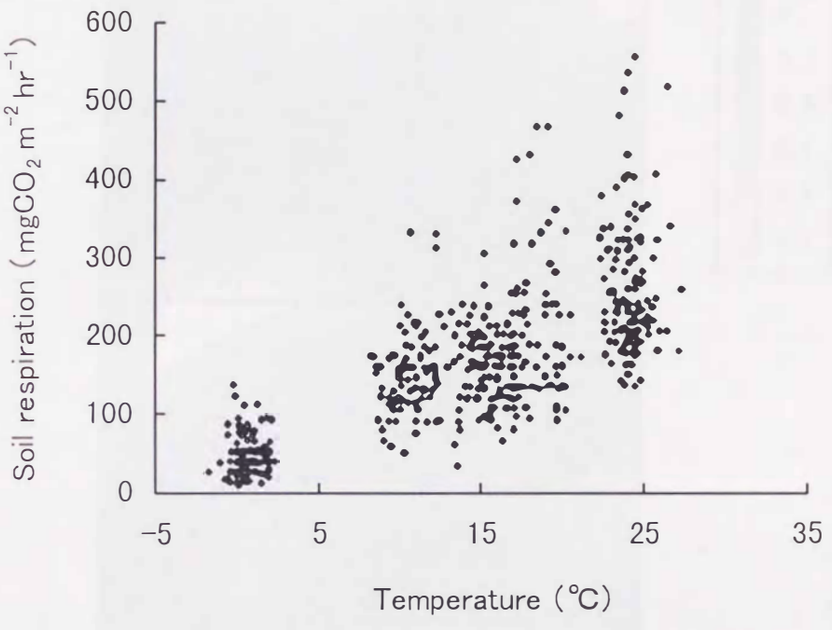


Fig. 3-2-4 Relationship between soil respiration and soil surface temperature.

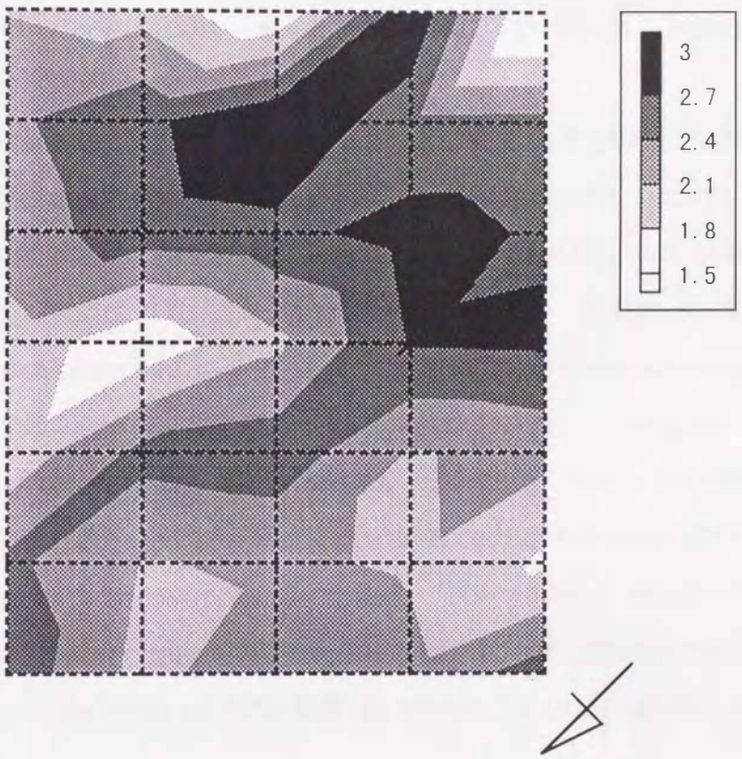


Fig. 3-2-5　Spatial variability of Q_{10} value.

(Rochette et al., 1991). However, CV values at this study site were much higher than those of a Japanese cedar plantation planted on a level topographic site, at 9% (Ohashi et al., 1999b). The difference in CV may have been due to differences in the topographical survey. At this study site, the slope may have caused an imbalance of factors affecting soil respiration, such as soil nutrient status and environmental conditions.

Rochette et al. (1991) reported that CV was highest in May and decreased gradually towards the end of the growth season. They considered that the decrease in CV was caused by a smaller quantity of organic matter oxidized to CO_2 later in the season. In this study, lower CV values were observed in summer and autumn, when decomposition of organic matter was active. Thus, since most of organic matter decomposed from spring to summer, CV may have decreased in summer and autumn. However, Japanese cedar, a evergreen tree, has litterfall randomly throughout the year. Therefore, it is necessary to investigate seasonal changes in the quantity of soil organic matter and the decomposition rate of litterfall in order to understand seasonal change in CV.

The number of measurements (n) required to estimate average soil respiration of a plot within 10 % of its actual value (α=0.05) was obtained for normally distributed samples using the following equation (Snedecor and Cochran, 1967).

$$n = \{t_\alpha s / (0.1m)\}^2$$

where t is the Student's statistic tabulated for the desired confidence interval level and degrees of freedom of the sample, and m and s are the mean and standard deviation of soil respiration in each season. Rochette et al. (1991) estimated the number of measurements in a wheat crop as 30～190 per ha from this equation. At this study site,

the number of measurements required to estimate soil respiration was estimated at 45, 28, 30 and 93 in spring, summer, autumn and winter, respectively, and 50 on average. Therefore, 140 (35×4) measurements in each season may have been enough to estimate soil respiration at this study site. Carlyle and Than (1988) also carried out a large number of measurements, 45 within a 0.09 ha study site, in order to estimate soil respiration in a *Pinus radiata* stand. However, soil respiration has often been estimated from fewer measurements, 2～10, regardless of the forest topographical survey (Kirita, 1971d; Anderson, 1973; Jurik et al., 1991; Edwards and Sollins, 1973; Schlentener and Van Cleve, 1984). It may be important to examine spatial variability of soil respiration in order to estimate the average soil respiration from a forest.

Factors affecting spatial variability in soil respiration

The distribution pattern of soil respiration changed seasonally at this study site (Fig. 3-2-2). In this study, the spatial variability of soil respiration included diurnal variation of soil respiration. However, since diurnal variation of soil respiration was much lower than spatial variability at this study site (Fig. 3-2-3), some other factor may have caused the distribution of soil respiration.

Laboratory and field experiments have shown that spatial variability of soil respiration depends on soil aeration (Yabuki and Kitaya, 1984; Liebig et al., 1995), soil organic matter (Seto et al., 1978; Seneviratne and Van Holm, 1998), soil nitrogen content (Kowalenko, 1978; Seneviratne and Van Holm, 1998; Johnson et al., 1994), soil phosphorus nutrition (Keith et al., 1997) and soil pH (Sparling and West, 1990). However, in natural ecosystems, effects of these factors are not always observed. For example, Maggs and Hewett (1990)

reported that soil respiration did not differed between two rainforests although soil nutrient status (P and Ca) was different. Vose et al. (1997) reported there was no significant effect of N addition on soil respiration in a ponderosa pine forest. At this study site, soil pH, carbon and nitrogen concentration and soil profile at all locations were examined from 1991 to 1995 (Sasaki et al., 1996). However, none of these soil properties had significant effect on soil respiration. This points to the exist of other factors than soil properties which may control soil respiration distribution.

Root density may be one factor. Hanson et al. (1993) observed in isolated periods when valley-bottom locations had reduced soil respiration relative to other topographic positions in an upland oak forest in Tennessee. They concluded that considered one cause of lower soil respiration was reduced fine root density in valley-bottom locations. A linear relationship between soil respiration and root biomass was also reported by Katagiri (1988) and Behara et al. (1990). In this study, each sampling s locations pots would have had an individual root density because the distance from surrounding trees was inconsistent. Thus, differences in root density may have caused the differences in soil respiration. It is necessary to examine root density at each location in order to understand soil respiration distribution more clearly.

Soil moisture conditions also may also be another cause. A strong relationship between soil moisture and soil respiration has been reported by many researchers (Singh and Gupta, 1977; Carlyle and Than, 1988; Holt et al., 1990). Simono et al. (1989) reported higher soil respiration on the upper part of a slope in a young Japanese cypress forest due to differences in soil moisture conditions. Here, soil moisture content did not effect on spatial distribution of soil respiration. However, soil moisture conditions deep below the soil surface, such as

groundwater, could not be represented by soil moisture content in this study, at a depth of 10 cm from the soil surface. Thus, soil moisture conditions in deep soil may have affected soil respiration. Aerts and Ludwig (1997) reported the effect of changes in the water-table on soil respiration. In this region, there was only 14 mm of precipitation in the a month before autumn and winter measurements. This suggests dry conditions at the study site in autumn and winter measurements. However, in spring and in summer, 323 mm and 152 mm precipitation was recorded, respectively, during the month before measurements (Fukuoka Local Meteorological Observatory, 1997 and 1998). Therefore, occurrence, expansion and fluidity of the water table may have occurred in these seasons and may have caused appearance of high soil respiration (Fig. 3-2-2).

Temporal changes in soil respiration and annual soil respiration

Diurnal changes in soil respiration often correspond to temperature, increasing in the daytime and decreasing at night (Witkamp, 1969; Kanemasu et al., 1974; Parker et al., 1983; Grahammer et al., 1991; Osozawa and Hasegawa, 1995; Nakadai et al., 1996). In this study, a small fluctuation in soil respiration may have been caused mainly by small temperature fluctuations. Similar findings have been reported by Kirita (1971d), Kursar (1989) and Gyokusen and Saito (1995). The closed forest crown and the north-west direction of the slope may have decreased sun-light streaming into the forest and maintained stable a temperature in this area.

Seasonal changes in soil respiration increased in summer and decreased in winter. Similar findings have been reported in many other forests, such as deciduous forests (Anderson, 1973; Sakai and Tsutsumi, 1987), evergreen broadleaf forests (Kirita, 1971d), temperate

mixed forest (Freijer and Bouten, 1991; Lassard et al., 1994), and northern hardwood forests (Toland and Zak, 1994). Soil respiration increased exponentially with increasing soil temperature and Q_{10} values were within the range of 1.3~3.0, as reported for a variety of temperate forests (Fung et al., 1987; Sakai and Tsutsumi, 1987) and was similar to the mean of Q_{10} values for soil respiration, approximately 2.0 (Sakai and Tsutsumi, 1987; Townsend et al., 1992).

Correlation equations between soil respiration and soil surface temperature were used to estimate annual soil respiration at each location. Daily mean soil respiration was calculated from daily mean temperature using the equations (Fukuoka Local Meteorological Observatory, 1997 and 1996). Since diurnal changes in soil respiration were small at this study site, daily soil respiration was estimated from daily mean soil respiration and totaled to calculate annual soil respiration. Annual soil respiration from each location was an average of 1657 $gCO_2\ m^{-2}\ yr^{-1}$ in a range from 1127 to 2429 $gCO_2\ m^{-2}\ yr^{-1}$. This was within the range from 1360 to 3450 $gCO_2\ m^{-2}\ yr^{-1}$, found in boreal forests and temperate forests (Anderson, 1973; Bowden et al., 1993; Toland and Zak, 1994; Nakane et al., 1996) and lower than generally reported in tropical forests, from 5130 to 5300 $gCO_2\ m^{-2}\ yr^{-1}$ (Kursar, 1989; Maggs and Hewett, 1990; Lamade et al., 1996).