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Soil Respiration Following Alternative Site Preparation Treatments in a Boreal Mixedwood Forest

By

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DECLARATION

The research presented in this thesis was carried out by the author, and has not been previously submitted for credit toward any other degree or diploma.

The work of other authors included in this thesis have been appropriately cited.

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November, 1995.

ABSTRACT

The effects of experimental site preparation on CO_2 evolution and on planted black spruce (*Picea mariana* (Mill.) B.S.P.) seedling growth were studied one year after the site preparation treatment, during the 1994 growing season (June-October) and again in May and June of 1995 on a boreal mixedwood site. Treatments included: uncut forest, cut forest without site preparation, cut and mixed where organic matter to a depth of 20 cm was mixed with mineral soil, and cut and screefed where the top organic layer was removed. Carbon dioxide evolution was determined once a month in the field by infra-red gas analyzer (IRGA) and by the soda-lime trap technique. Soil temperature and moisture contents were measured once a month during the 1994 growing season and for two months in 1995. Concentrations of organic matter, PO_4^{3-}-P and NH_4^+-N were also determined after treatment. Interactions of temperature, moisture and organic matter on CO_2 evolution were studied under controlled laboratory conditions.

Carbon dioxide evolution from the cut treatment plots was not significantly different from that of the uncut plots. Carbon dioxide evolution from the cut and mixed plots was significantly higher than from the cut and screefed plots. Evolution of CO_2 varied seasonally. The IRGA proved to be a better method for determining CO_2 evolution than the soda-lime technique due to its convenience and efficacy. Highly significant relationships among CO_2 evolution, soil organic content, soil P and moisture contents were found. It was concluded that site preparation treatments had a significant effect on CO_2 evolution by modifying the organic matter and moisture contents of the soils. Height of planted black spruce seedlings, however, did not vary significantly during the first two years after the treatments.

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1. INTRODUCTION

To achieve silvicultural success, tree planting in the boreal forest is often preceded by site preparation. Site preparation involves the manipulation of forest site conditions in order to favour the survival, growth and development of desirable vegetation (Towill et al. 1991). It enhances the establishment of natural or artificial regeneration by reducing competing vegetation. Site preparation methods are generally divided into four types: i) mechanical (e.g. mixing, screefing, mechanical cutting of competing plants etc.); ii) chemical control of weeds using herbicides; iii) prescribed burning; and iv) a combination of the above (Daniel et al. 1979). Site preparation may affect soil moisture, temperature, aeration, pH, organic matter content, nutrient availability and soil microbial diversity (Dobbs and McMinn 1973; Paul and Clark 1989; Weber 1990; Toland and Zak 1994). Changes in soil respiration and organic matter decomposition have been shown to influence the growth of planted seedling (Brand 1990).

Carbon dioxide (CO_2) evolution from the forest floor is considered to be one of the most useful parameters for determining the rate of soil respiration and organic matter decomposition (Towary et al. 1982; Toland and Zak 1994). Decreased soil respiration (CO_2 evolution) was reported immediately after prescribed burning and clearcutting in coniferous forests in Finland (Pietikåinen and Fritze 1995) and Ontario (Weber 1990). For a better understanding of effects of site preparation treatments on soil respiration, it is important to understand the relationship between decomposition, nutrient release and site productivity.

Following site preparation, many factors can directly or indirectly affect CO_2 evolution

by modifying the physical and chemical properties of soil; as well, prevailing microclimatic conditions may be affected (eg. temperature, moisture, pH, and aeration) (Singh and Gupta 1977; Van Cleve and Sprague 1971; Weber 1985). Temperature and moisture were found to be the most important factors influencing soil respiration (Van Cleve and Sprague 1971; Singh and Gupta 1977; Ellert and Bettany 1992; MacDonald et al.1995). Interactions of temperature and moisture on soil respiration have been reported by Bunnell et al. (1977). Weber (1990) reported that forest composition influenced the evolution of CO_2 from forest soil.

McMinn and Hedin (1990) have suggested that soil mixing can facilitate the re-establishment of soil organisms following clearcutting and thereby enhance the growth of both planted black spruce (*Picea mariania* (Mill.) B.S.P.) seedlings and competing vegetation in British Columbia's forest. Screefing (removal of organic layer) combined with the use of herbicide was also considered to discourage the establishment of competing vegetation. However, these treatments have been seldom applied in a boreal mixedwood and their effects on soil respiration and subsequent seedling growth are little known. Following clearcutting of a boreal mixedwood forest in northwestern Ontario two experimental site preparation treatments were applied in 1993 by the Canadian Forest Service: 1) soil mixing by incorporating surface organic layers into underlying mineral soil; and 2) organic matter removal by screefing.

Soil respiration, determined by measuring CO_2 evolution, gives a good indication of the degree of organic matter decomposition, nutrient release and hence the site quality (Towary et al. 1982; Weber 1990). Changes in soil respiration and its relationship with soil organic matter,

moisture and temperature due to the site preparation, have not been widely studied in the boreal forest. Solving these problems are vitally important to the maintenance of site quality and productivity.

The objectives of the present study were to 1) determine the effects of site preparation treatments on soil CO_2 evolution in relation to changes in soil temperature, moisture, organic matter content and pH; 2) study the effects of variable temperature, moisture and organic matter of soil on CO_2 evolution under controlled conditions; 3) compare the soda-lime and infra-red gas analyzer techniques as methods for measuring CO_2 evolution; and 4) study the growth response of planted black spruce seedlings following the site preparation treatments.

It was hypothesized that 1) soil metabolism, as measured by soil respiration will vary following the site preparation treatments resulting from soil modification in soil temperature, moisture and organic matter content; 2) site preparation treatment will create a certain microenvironment which, in turn, will influence CO_2 evolution and black spruce seedling growth.

2. LITERATURE REVIEW

2.1. Soil respiration and organic matter decomposition

Soil respiration is defined as the uptake of O_2 and release of CO_2 by living organisms in soil (Anderson 1982). The CO_2 evolution may be due to microbial, root or faunal respiration. In addition, CO_2 evolution may also result from nonmetabolic reactions such as chemical oxidation of soil minerals (Bunt and Rovira 1954). Root respiration may constitute as much as 50% of the total amount of CO_2 evolved from the soil (Tesarova et al. 1979; Hendrickson and Robinson 1984).

The measurement of CO_2 evolution from forest soils has been accepted as a comparative index of soil respiration and also for the overall assessment of relative biological activity (Reiners 1968; Weber 1990; Toland and Zak 1994). The activity and the relative size of the soil microflora can be obtained from the correlation between CO_2 evolution and other properties such as soil enzyme activity or soil ATP content (Sparrow and Doxtader 1973).

Organic matter decomposition results in soil respiration. During humus decomposition, microorganisms convert the carbon (C) in organic materials to CO_2 and complete the biological C cycle. The order of ease of decomposition of organic matter is as follows: sugar, starches and simple protein > crude protein > hemicellulose > cellulose > fats, waxes > lignin (Brady 1990). Generally, three distinct simultaneous stages occur in organic matter decomposition. Firstly, organic substances are metabolized by specific microbial enzymes (such as pectinase involved in the decomposition of the polymers of pentoses in hemicellulose) with CO_2, water, energy and heat as the major products . Secondly, new biological tissues are formed from the synthesis of microbial cells. Thirdly, certain end-products of the breakdown such as available nutrients are

released into the soils for plants to absorb (Alexander 1967). Carbon dioxide evolution from soil has also been correlated with nitrogen (N) and sulfur (S) mineralization (MacDonald et al. 1995) and with nitrification (Pietikåinen and Fritze 1995).

Soil microorganisms (all heterotrophs) play an important role in organic matter decomposition and in the release of nutrients and energy in soil systems (Alexander 1967). Fungi are responsible for initiating the activity but Actinomycetes maintain the attack over a prolonged period (Paul and Clark 1989). Also, as Pietikåinen and Fritze (1995) reported, clearcutting and prescribed burning cause decreases in soil respiration and in soil fungal and total microbial biomass. Reductions in the number of microorganisms and in respiratory rate after prescribed burning was found in a Minnesota jack pine (*Pinus banksiana* Lamb) forest (Ahlgren and Ahlgren 1965).

Under field conditions, soil respiration is affected by edaphic and microclimatic factors such as temperature, moisture, vegetation cover and soil depth (Heal et al. 1981; Stohlgren 1988). Weber (1990) reported that CO_2 evolution rates in aspen (*Populus tremuloides* Michx.) forest were higher than that in jack pine stands because the latter had resistance to decomposition. This resulted in slower nutrient and organic matter turnover.

2.2. Soil respiration in relation to soil physical and chemical properties

The relationship of chemical and physical parameters (such as organic matter content, moisture-holding ability, and base status) of the soil to microbial activity has been the subject of a number of reviews (Davey and Danielson 1968; Smith and Peterson, 1982). Particle size distribution of soils affects soil respiration by increasing the surface area which results in an enhancement of the microbial population and the ability of organisms to ingest food (Swift et al. 1979).

2.2.1. Soil pH

The hydrogen ion concentration, expressed as pH, in the soil solution affects the rate of organic matter decomposition through its effect of microbial growth and activity (Alexander 1967). Mutatkar and Pritchett (1966, 1967) reported that the decomposition of organic matter was enhanced by reduced acidity. Actinomycetes were most active in terms of cellulose decomposition at pH 6-7 (Szegi 1964). The type of microorganisms participating in the decomposition of cellulose was strongly affected by acidity due to the effect of pH on microbial enzyme activity during the reaction (Alexander 1967).

Not only does pH affect the growth rate and enzymatic potential of individuals making up the microbial population, it also controls the type of microorganisms involved in the C cycle of any habitat. Typically, decomposition proceeds more readily in neutral than in acid soils. Consequently, the treatment of acid soils with lime accelerates the decay of plant tissues and soil organic matter (Alexander 1967). Other factors (temperature or moisture) being equal, C mineralization is most rapid in neutral to slightly alkaline soils. Liming acid soils increased C

volatilization (Alexander 1967). Bååth et al. (1981) found that increased CO_2 evolution shortly after application of fertilizer was probably due to a pH increase.

In addition to soil pH, which is directly responsible for organic matter decomposition by affecting microbial activity, the maintenance of favourable pH is also an important factor. Stotzky (1966) reported that certain 2:1 type clays (e.g. montmorillonite and vermiculite) stimulated soil respiration while other 2:1 type clays (e.g. pyrophylite and vermiculite-mica mixtures) and 1:1 type clays (kaolinite and halloysite) did not. The clay minerals that stimulated soil respiration had a greater buffering capacity than those that did not. Consequently, clay maintained the stability of soil acidity at a level suitable for sustained growth. However, Van Cleve and Sprague (1971) found that soil pH associated with different vegetation types didn't affect forest floor respiration as much as temperature and moisture. Acidity was not the major determining factor in the decomposition of cellulose in mull and mor soils (Went and Dejong 1966).

2.2.2. Soil aeration

Soil aeration regulates moisture and oxygen (O_2) supplies in the soil, which, in turn, determine the population and activity of microorganisms and invariably stimulates soil respiration (Brady 1990; Pritchett and Fisher 1987). Rates of O_2 diffusion in dense subsoils are lower than in loose subsoils (Bertrand and Kohnke 1957). Compact and wet soils have lower O_2 content and lower microbial activity compared with dried and less compact soils because air supply controls the type of oxidation induced by microorganisms (Epstein and Kohnke 1957).

2.2.3. Cation exchange capacity

Cation exchange capacity (CEC) is a major factor in determining the balance cations and H-ions in the soil solution. As a result, CEC plays an important role in potential soil fertility, soil acidity (pH) and soil buffering capacity. These properties, in turn, affect many microbial activities such as decomposition of substrates, production of exoenzymes and microbial metabolites in the soil (Stotzky 1966). Estermann et al. (1959) found increased degradation rate due to the concentration of the charged clay surface. Soil carbohydrate adsorption in clay and interaction with metals such as iron, aluminum and copper were found to greatly increase the resistance of polysaccharides to microbial attack and consequently resulted in slower decomposition. Polysaccharides involved in soil aggregation can be protected from further decay until cultivation or other forces expose the surfaces to microbial attack (Paul and Clark 1989).

In conclusion, higher respiration rates were associated with high alkalinity and greater cation exchange capacity (Davey and Danielson 1968).

2.2.4. Organic matter content

Organic matter content affects soil respiration. A decrease of soil respiration rate was found (on a per gram basis) from L to H layers and was related to the chemical composition of the organic matter (Van Cleve and Sprague 1971). This suggests that relatively newly deposited materials (L layers) have the highest content of readily available energy for microbial activity.

3. Soil respiration in relation to microclimatic factors

The soil respiration rate is controlled largely by factors such as temperature and moisture which vary seasonally and diurnally, and with soil depth.

2.3.1.Temperature

Soil respiration is influenced by temperature (Reiners 1968; Van Cleve and Sprague 1971). Witkamp (1969) found that temperature is a controlling factor influencing annual respiration cycles of the forest floor. Rates of CO_2 evolution from the entire soil profile under a pine forest floor were highly correlated with temperature (Witkamp and Frank 1969). Soil temperature was responsible for 43% of the variation of soil respiration in uncut forest and 58% of the variation of soil respiration in the cut plots (Toland and Zak 1994). Bowden et al. (1993) reported that soil temperature accounted for 80% of the variation in daily soil respiration rate. Toland and Zak (1994) reported an exponential relationship between soil temperature and soil respiration. Increased microbial metabolism resulted in increased enzymatic, hence temperature-dependent decomposition processes. The rate of CO_2 evolution from soils doubled for each 10^0C increase in temperature below 40^0C (Q_{10} of 2)(Wiant 1967; Moore 1986; Singh and Gupta 1977; Swift et al. 1979). Van Cleve and Sprague (1971) found that the average Q_{10} of a L layer in the laboratory over a temperature range of 5 to 20^0C was 3. In the F and H layer, the respiration rate increased with temperature for a Q_{10} of 2 over a temperature range of 5 to 15^0C. However, the Q_{10} decreased sharply at high temperatures (above 50^0C) which were harmful to most of soil organisms (Bunt and Rovira 1954). Elkan and Moore (1960) found that the highest rate of CO_2 evolution occurred at 39^0C and the lowest at 10^0C.

Gordon et al. (1986) reported that soil temperature and moisture increased after harvesting, which was attributed to increased insolation and reduced evapotranspiration in an interior Alaska white spruce (*Picea glauea* (Moench) Voss) forest. Also, clear-cutting increased soil respiration especially in midsummer. In a jack pine ecosystem in eastern Ontario, Weber (1985) found that CO_2 evolution increased in the spring in response to ambient warming and decreased in late fall as seasonal temperatures declined. Weber (1990) reported that the interaction of maximum temperature and mean moisture content accounted for 98% of variation of soil respiration in a young aspen (*Populus tremuloides* Michx. and *P.grandidentata* Michx.) ecosystem of eastern Ontario. A comprehensive study of the interaction between temperature and CO_2 evolution from litter (L), fermentation (F) and humus (H) layers was performed by Boois (1974) in the Netherlands. No correlation between respiration and soil temperature in the litter layer was found. Also, there was no significant difference in the rate of respiration between summer and winter seasons. This might be due to the fact that in the L layer, the large amount of new substrate after autumn leaf-fall might offset temperature-induced decrease in respiration during winter.

2.3.2. Moisture

Temperature is the principal factor controlling microbial activity. Van Cleve and Sprague (1971) studied respiration rates in the forest floor of birch (*Betula papyrifera* Michx) and aspen stands in interior Alaska and found, based on partial regression coefficients, which temperature was 2 to 5 times more significant than moisture in affecting soil respiration. However, when precipitation is not evenly distributed throughout the year, soil moisture can be the limiting factor (Schlesinger and Hasey 1981; Waring and Franklin 1979). Moisture may enhance the rate

of soil respiration by affecting microbial activity and the decomposition of organic matter (Witkamp 1969). It has been shown that soil water content has a stimulating effect on the metabolic rates of soil organisms and the living roots of the plants (Coleman 1973). Soil moisture also affects O_2 availability in a microbial community. High soil moisture can cause a decrease in microbial activity by reducing O_2 supply in soil pores (Bunnell et al. 1977). Respiration of the soil microflora is usually highest at 60% to 80% water-holding capacity of the soil (Alexander 1967). Douglas and Tedrow (1959) noted that CO_2 evolution is negatively affected above and below an optimal soil moisture content. Combined effects of temperature and moisture were more significant than when considered individually (Bunnell et al. 1977; Moore 1986; Witkamp 1969). Boddy (1983) found that at high soil temperatures and high moisture, CO_2 evolution remains stable or decreased. This was attributed to a decline in the rate of O_2 diffusion to a concentration insufficient to meet the demand for microbial respiration. Van Cleve (1971) also observed similar sensitivity of respiration to temperature changes at high moisture content (100-250%). Moisture changes had little effect on soil respiration at low temperature (below 5^0C), but, respiration was quite sensitive to moisture at temperatures between 10 and 20^0C. In the arctic soil of northern Alaska, Douglas and Tedrow (1959) reported that the moisture effect varied with temperature and found a parabolic increase in CO_2 evolution rates with increasing temperature and moisture.

The effect of rainfall on microbial metabolism depends on soil type and on the degree of humus accumulation. Rainfall also affects metabolic rates due to CO_2 displacement in soil pores by rain. Anderson (1973) observed a marked fall in soil respiration during the period of

low rainfall from September to October. It also may have been partially affected by low soil temperature. Soil moisture content is not always consistent with the amount of rainfall. Van Cleve (1971) indicated that rainfall did not cause uniformly higher forest floor water contents or altered CO_2 evolution from soils. Edwards and Sollins (1973) correlated daily fluctuation in CO_2 evolution with litter moisture and found no marked variation when the moisture content was more than 50% of the dry weight of litters.

2.3.3. Seasonal and diurnal variations

Seasonal and diurnal fluctuations in the rate of soil respiration have been reported by many authors (Van Cleve and Sprague 1971). Kirita (1971) found that soil respiration rates showed a marked annual cycle closely associated with the seasonal changes in soil surface temperature. Edwards and Sollins (1973) found seasonal CO_2 evolution ranged from 2.8 g $m^{-2}day^{-1}$ in the autumn to 26.3 g $m^{-2}day^{-1}$ in the summer in forest floors near Oak Ridge, U.S.A. Mid-summer respiration peaks were reported by Weber (1985) and Gordon et al. (1986). In addition, Toland and Zak (1994) found that a large spring CO_2 evolution followed snow thaw.

Makarov (1960) reported maximum values of soil respiration between 9 am and 3 pm These rates were twice the minimum rates. Witkamp (1969) reported minimum rates of CO_2 evolution before predawn and maximum in the afternoon. Witkamp and Frank (1969) found a high rate of soil respiration in the afternoon and a low rate during the night in the litter layer. Witkamp and Frank (1969) have also documented that daily cycles of CO_2 concentration appeared to be controlled by photosynthesis. However, Edwards and Sollins (1973) and Medina

and Zelwer (1972) found that CO_2 evolution rates at the beginning of night were temporarily higher than day time rates especially during the dry period. This might be due to high relative humidity during the night which perhaps favours the activity of microbes. Also, at the beginning of night, the soil was warmer than the air, which may have enhanced evolution of CO_2 from the soil (Medina and Zelwer 1972).

2.3.4. Soil depth

In a grass-woods peat and a thick sedge-*Hypnum* peat, Makarov (1960) found that the intensity of soil respiration at 0-10 cm soil was 7.93 kg CO_2 $ha^{-1}hr^{-1}$ which decreased to 2.33 kg CO_2 ha^{-1} hr^{-1} at 60 cm depth. The high values of soil respiration at 0-10 cm can be explained on the basis that this layer contained the bulk of plant roots and a high density of bacteria. Clark and Coleman (1972) reported that the proportions of the top 5 cm, the 5 to 10 cm segment and the deeper layer of the soil profile, contributing to the daily rates of CO_2 evolution were 75%, 10% and 15% respectively. De Jong et al. (1974) found the highest CO_2 concentration in the top layer of the soil profile during the growing season. Warembourg and Paul (1973) estimated the CO_2 concentration at various depths in the soil profile and found that the amount of labelled CO_2 respired by the roots below 30 cm was small.

There is a close relationship between the hardness of substrate and organic matter decomposition. This may be due to the mechanical role of fungal hyphae in the penetration of plant cuticles (Dickinson 1960). The leaves which are high in total N and sugar and low in cellulose and lignin, are more readily attacked by soil microorganisms and decompose more

rapidly than the tough, heavily cuticularised leaves (King and Heath 1967). These CO_2 evolution rates are lower in jack pine stands compared with those in aspen stands due to the hardness of needles (Weber 1990). It has been suggested that CO_2 evolution was affected by vegetation cover. Singh (1962) reported that faster rates of decomposition in mixed broadleaf forests, as compared to the conifer forests in the western Himalayas, were caused by a broken canopy permitting a greater amount of sunlight to reach the soil surface, hence a higher surface temperature.

2.4. Soil respiration in relation to site preparation treatments

Clear-cutting is widely used in timber harvesting which affects the physical, chemical and biological properties of soil. Differences in the initial site quality, climate and plant species involved in revegetation determine both the duration and the severity of the effect. Most studies showed a doubling or tripling in the biomass of microflora and fauna in the first few years, generally peaking in the second year after clearcutting and sometimes persisting for as long as 5 to 10 years (Weber 1990; Paul and Clark 1989). The input of logging slash should lead to an increase in soil C availability and the amount of substrate available for heterotrophic metabolism in soil. Gordon et al. (1986) reported that soil respiration was enhanced following clearcutting in the white spruce forest of interior Alaska due to increased temperature from insolation and from reduced evapotranspiration. Toland and Zak (1994) proposed two alternative mechanisms to explain the increase in microbial respiration following clear-cutting: (1) the existing microorganisms increase their activity or (2) the microbe population grows due to change in substrate availability and environmental factors. Ewel et al.(1987) found enhancement

of soil respiration in a Florida slash pine (*Pinus elliottii* Englm.) plantation following clearcutting. Similar results were reported by Ewel et al.(1981). The study also indicated that effects of clear-cutting on soil respiration are variable and the response patterns are often related to specific ecosystems. Enhanced soil temperature should further increase microbial activity and the respiration of any remaining live roots (Toland and Zak 1994). However, clearcutting altered soil respiration by enhancing root mortality and resulted in a decrease in root respiration (Weber 1990, Toland and Zak 1994). Toland and Zak (1994) reported no significant difference in CO_2 evolution between uncut and clear-cut areas. Similar results in mixed deciduous forests in Tennessee were found by Edwards and Ross-Todd (1983). Weber (1990) also observed no significant difference in CO_2 evolution from young *Populus tremuloides* Michx. and *P. grandidentata* Michx. stands. This may be due to enhanced microbial respiration offsetting the decreased root respiration. From a study in Finland, total microbial C was found to decrease following clearcutting by 21% and clear-cutting followed by prescribed burning caused a 53 and 67% reduction of total microbial C respectively (Pietikåinen and Fritze 1995). Nakane et al. (1983) reported similar results in a red pine (*Pinus densiflora* Siebold.) forest in Japan.

Several studies have focused on the effect of burning on organic matter decomposition. Weber (1985) found that the highest rate of soil respiration in a jack pine stand in Ontario subject to understorey burning. Temporary decrease of CO_2 evolution may result from draining nutrient and energy reserves of roots after burning for the first two years (Schier et al. 1985). Carbon dioxide evolution may return to the pre-treatment level after the third year (Weber 1990) due to enhanced decomposition of decaying roots. This is also likely due to increased litter deposition following fires, which released nutrients to the forest floors and favoured

microbial activity (Flanagan and Van Cleve 1983; Weber 1990).

Following conventional mechanical harvesting methods, there is a stimulation of microbial activity and an enhancement of the rate of soil respiration (Brady 1990). Such stimulation results from disruption of soil aggregate and better exposure and aeration of their degradable material (Paul and Clark 1989). When compared with humus removal or burning, mixing of the organic layer with the underlying mineral soil increased soil temperature and prevented the usual heating, wet-dry cycles and excessive decomposition of the surface humus. This in turn, provides more suitable temperatures for root growth (McMinn 1974; Salonius 1981, 1983). There is some evidence that microbial activity on organic substrate is stimulated by the presence of clay minerals (Lynch and Cotnoir 1956; Stotzky 1966). The increased soil respiration may be due to a more diverse microbial population operating on the substrate in the mixture of layers (Florence 1965; Salonius 1981). Intermittent drying of the entire organic horizon after harvest and subsequent wetting, drying, freezing and thawing cycles also increased humus decomposition rates (Frater 1980; Van Schreven 1968). This increased decomposition can decrease the thickness of humus layer to the extent that underlying mineral soil may be exposed (Suffling and Smith 1979). The mixture of organic and mineral horizons created a variety of new microhabitats which were quite different from those in the partitioned organic and mineral horizons in the undisturbed forest (Anderson 1973).

Alexander (1967) reported that nitrogenous amendments result in an increase in CO_2 evolution and a greater loss of cellulose, hemicelluloses and other plant polysaccharides. An

enhancement of microbial activity was also found after N fertilization (Van Cleve and Moore 1978). Foster et al. (1980) reported that urea fertilizer stimulates respiration of forest soils due to increased microbial population. In contrast to previous studies, Soderstrom et al. (1983) reported decrease in soil respiration and microbial biomass following N fertilization. Bååth et al.(1981) reported that a changed root structure after fertilization resulted in a decrease of soil respiration. Keyser et al. (1978) suggested that decrease of microbial processes by addition of N was due to inhibition of nitrogenous compounds on ligninolytic enzyme production. In addition, C was less available for microorganisms due to condensation of N-rich compounds and the retention of C in the soil solution (Sauerbeck 1968; Broadbent 1965; Haider et al. 1975). Paul and Clark (1989) concluded that the greater the microbial kill, the more pronounced was the partial sterilization effect on soil respiration.

2.5. Methods of determining soil respiration

Soil respiration can be measured by several methods (Klein 1972; Chaney et al. 1978; Van Cleve et al. 1979; Edwards 1982a; Coxson and Parkinson 1987; Norgron and Anders 1988; Cheng and Coleman 1989; Rochette et al. 1992). Singh and Gupta (1977) categorized these methods into indirect methods and direct methods.

The indirect methods measured CO_2 evolution by related parameters of respiration. For example, Sparrow and Doxtader (1973) measured soil ATP as a parameter to estimate soil respiration. They found that $\log_{10}$ respiration was linearly correlated with $\log_{10}$ ATP concentration. Soil ATP level was also associated with soil respiration rates (Voigt 1965).

Coleman et al.(1976) established a method to predict soil respiration by developing a mathematical model to calculate the effect of soil water and temperature.

The direct methods are more widely accepted and used than the indirect methods. Witkamp and Frank (1969) divided direct methods into two groups: static methods and dynamic methods. The static methods used an inverted air-tight chamber that had a CO_2 absorbent fixed on the surface. After a known period of time, the absorbent is removed and the amount of CO_2 absorbed is measured. The static technique has been used to measure soil respiration for more than 60 years because of its advantages (Lundegardh 1927): it is inexpensive, simple and easy to operate and integrates flux over time. Common static methods involve gravimetric and titrimetric analyses. Two general methods of gravimetric analysis of CO_2 are used in soil respiration research. The first method is alkali absorption where CO_2 trapped in an aqueous solution of alkali (usually KOH or NaOH) is precipitated as $BaCO_3$ by the addition of excessive $BaCl_2$. The precipitate is collected, washed, dried and weighed. This method has been used for both CO_2 and $^{14}CO_2$ analysis (Landa and Fang 1978). However, alkali absorption often underestimated CO_2 output. Further, it is time-consuming to measure a large number of samples by acid titration. Alkali solutions often freezed in the winter, especially when used over the entire 24 hours in temperate regions. Another static method is soda-lime (a mixture of CaO and 20% NaOH and 6% to 18% Water). The soda-lime technique was recommended since it is convenient to handle in the field (Howard 1966; Edwards 1982a). Soda-lime technique eliminates the problems of freezing and spillage of alkali solution. It avoids the use of anhydrone (anhydrous magnesium perchlorate); instead, a correction factor (1.41) is used to obtain a fairly

accurate CO_2 measurement (Edwards 1982a). Titrimetric analysis for CO_2 trapped in either aqueous alkali (Jenkinson and Powlson 1976; Landa and Fang 1978) or nonaqueous solvent (Enoch et al. 1970) thus remains a popular and frequently used method in soil gas exchange research. Cheng and Coleman (1989) modified the substrate-induced respiration technique and proposed a simple titration method to measure CO_2 in a continuous air flow system.

In dynamic methods, fresh air is pumped from surrounding air through inverted chambers (Reiners 1968; Edwards 1982b). The air stream is monitored for CO_2 concentration before and after passing through the inverted chamber using an alkali absorption solution or an infrared gas analyzer. Recently a portable CO_2 analyzer has been developed and successfully used to measure soil respiration in a dynamic closed chamber so that the methods are becoming increasingly more accurate (Norman et al. 1992; Rochette et al. 1992). Edwards and Sollins (1973) reported that soil respiration measurement done by the alkali absorption method was 63% of IRGA value at 20^0C and 90% at 12^0C. Rochette et al. (1992) found that estimates by static methods are usually lower than those by dynamic methods. This might be due to the limitation of CO_2 absorption by NaOH solution, which decreased over time (Freijer and Bouten 1991). Van Cleve et al. (1979) compared four methods for the measurement of soil CO_2 and concluded that the infra-red gas analysis and KOH method had maximum estimates for soil respiration. The lowest respiration value was obtained by gas chromatography. Van Cleve et al. (1979) reported that the minimum sensitivity of the IRGA, Gilson respirometer, gas chromatography and KOH absorption at 25^0C are 0.31, 3.6, 3.8 and 44 $\mu g\ CO_2\ g^{-1}\ h^{-1}$

respectively. Parkinson (1981) improved the field method for measuring soil respiration by redesigning the air chambers and the sampling system. He reported that the difference between CO_2 concentration inside and outside the chamber should be sufficiently small so that any gas leakage will provide negligible errors in the respiration estimation. The chamber shape should be tall and small to ensure that the chamber is always kept steady.

In addition, due to the methodological difference in soil respiration measurement (Schlentner and Van Cleve 1985), there are discrepancies in soil respiration data reported from the ecosystem in similar geographic areas (Table 1). Generally speaking, most of the estimated values of soil respiration fall in the range of 100 to 600 mg CO_2 $m^{-2}h^{-1}$.

Table 1. Some soil respiration values in temperate forest (mg $CO_2 m^{-2} h^{-1}$)

Ecosystem	Place	Rate	Measurement period	Measurement method	Author
Jack Pine Forest	Eastern Ontario Canada	200	May-Nov.	Soda-lime	Weber (1985)
White Spruce Forest	Alaska U.S.A	450-600	May-Oct.	Soda-lime	Gordon (1986)
Aspen Forest	Alaska	550-660			
Paper Birch Forest	Alaska	550-660	Apr-Sept	Soda-lime	Schlentner (1985)
Black Spruce Forest	Alaska	530			
White Spruce Forest	Alaska	630			
Oak Forest	Tennessee U.S.A.	11-109	Mar.-Dec.	IRGA KOH	Edwards (1972)
Mixed Oak Forest	Belgium	20-150	Mar 1966-Dec 1968.2w perio	NAOH Absorption	Froment (1972)
Evergreen Oak Forest	Japan	388-525	Mar.-Mar. yearly mean	Alkali Absorption	Kirita (1971)
Oak Forest	Minnesota U.S.A.	333	Sept.-Sept. yearly mean	IRGA	Reiners (1968)
Oak Pine Forest	Brookhaven U.S.A.	750-830	Summer	IRGA	Woodwell (1966)
Pine Forest	Tennessee U.S.A.	156-183	Mar.-Mar. 2hr mean	Alkali Absorption	Witkamp (1966)
Oak Forest	Wisconsin U.S.A.	7260-7970	Aug,2hr mean	Air Current	Wallis (1957)
Oak Forest	Germany	240		Alkali Absorption	Wolter (1957)
Alder Forest	Sweden	1170-2340	13 Aug.1922-10 Oct.192	Alkali Absorption	Lundegardh (1927)

3. STUDY SITE

The study site was located in the Superior Forest District (B.9) of the Boreal Forest region ($49^0$10' N, $88^0$39' W) (Rowe 1972), approximately 20 km southeast of Black Sturgeon Lake, Thunder Bay District, Ontario, Canada (Fig.1). The vegetation of the area consisted of a 80-year-old productive boreal mixedwood forest, dominated by *Populus tremuloides* Michx. and *Abies balsamea* (L.) Mill., with a lesser component of *Picea glauca* (Moench) Voss, *P. mariana* (Mill.) B.S.P., *Populus balsamifera* L. and *Betula papyrifera* Michx. The forest was cut in the fall of 1992 for the experiment. The uncut area adjacent to the harvested plots was kept as control. The experimental area consisted of four treatment blocks. Each block was subdivided into 10 x 10 m treatment plots, separated by 5 m wide buffer strips (Fig. 2). Three site preparation treatments were applied in the spring of 1993 followed by planting with black spruce in addition to the uncut control area where vegetation was kept undisturbed. These were 1) cut forest without any site preparation treatment; 2) cut and mixed where, following harvesting, soil organic matter to a depth of 20 cm was thoroughly mixed with a rotary mixing machine developed by the Forest Engineering Research Institute of Canada (FERIC) and 3) cut and screefed where the top organic layer was removed.Altogether sixteen 10 x 10 m plots (4 treatments x 4 replicates) were studied.

The soil was classified as a Brunisol (Canada Soil Survey Committee 1978) developed in a deep stone-free silt loam.

Mean total annual precipitation and potential evapotranspiration were approximately 592 mm and 480 mm respectively (Chapman 1953). Monthly means of sunny days, temperature, wind speed and precipitation from May to October are presented in Fig.3 (Environment Canada). The average length of growing season, based on a 5.4^0C index was approximately 153 days, extending from early May to early October. The mean daily temperature was 15.6^0C during the 1994 growing season. Autumn was warm with a 3-month mean temperature of 6.8^0C. The highest mean air temperature was in July followed by June, September, May and October (Figs.3 and 4). Total monthly rainfall was the highest in June followed by August, September, July, May and October in 1994 growing season (Fig.5).

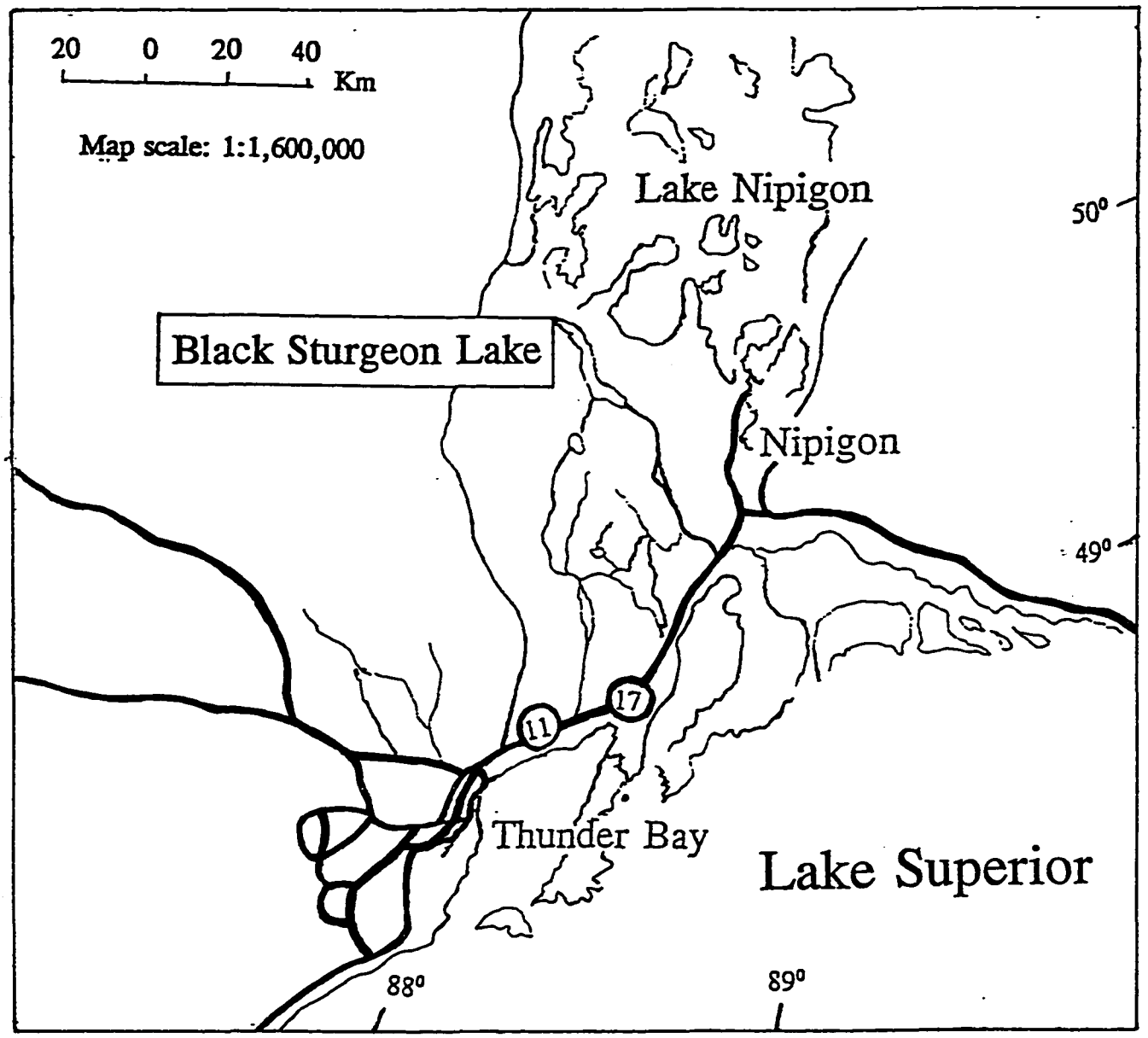

Figure 1. The location of the study site

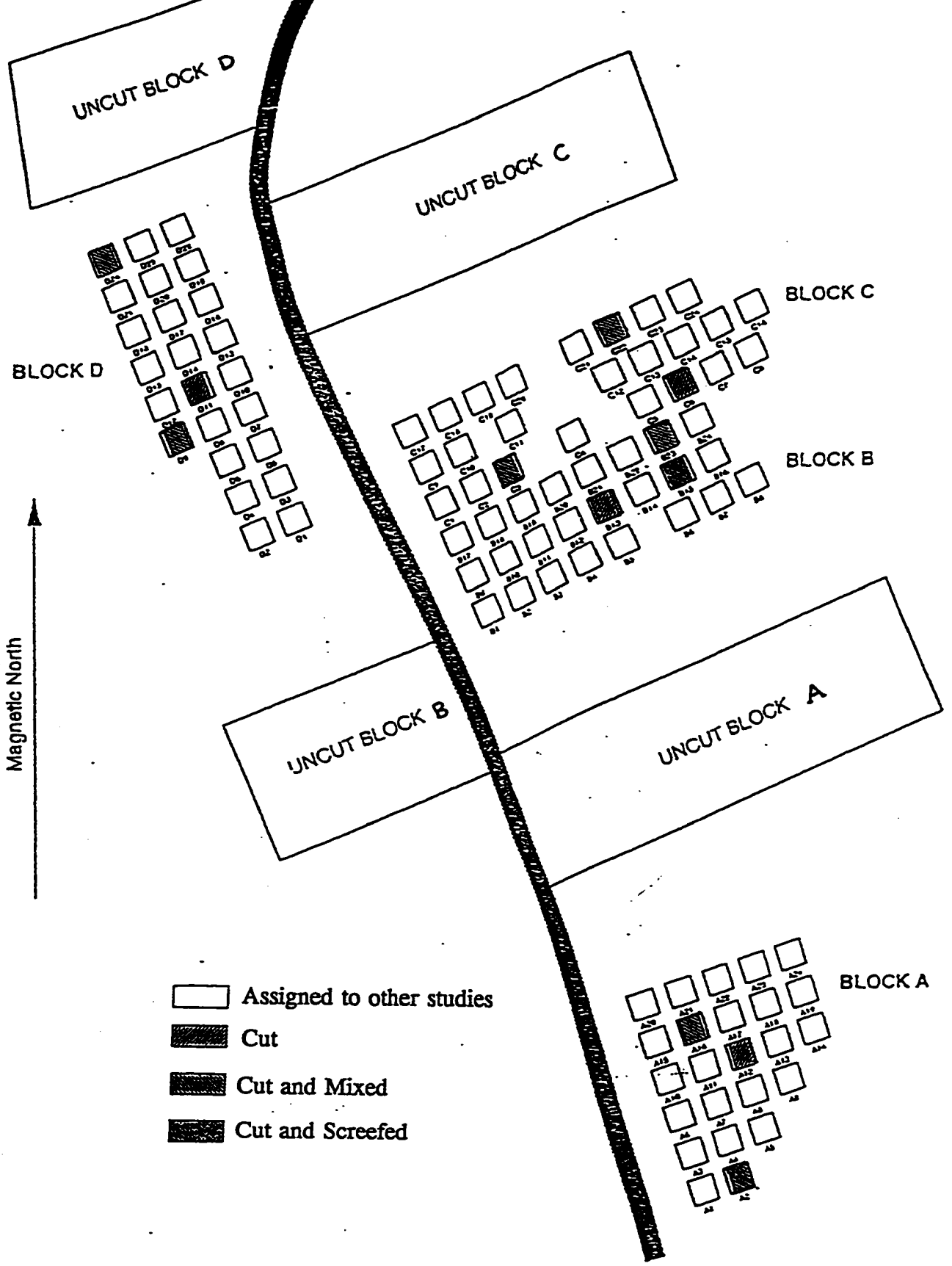

Figure 2. Experimental design of the treatments and replicate plots.

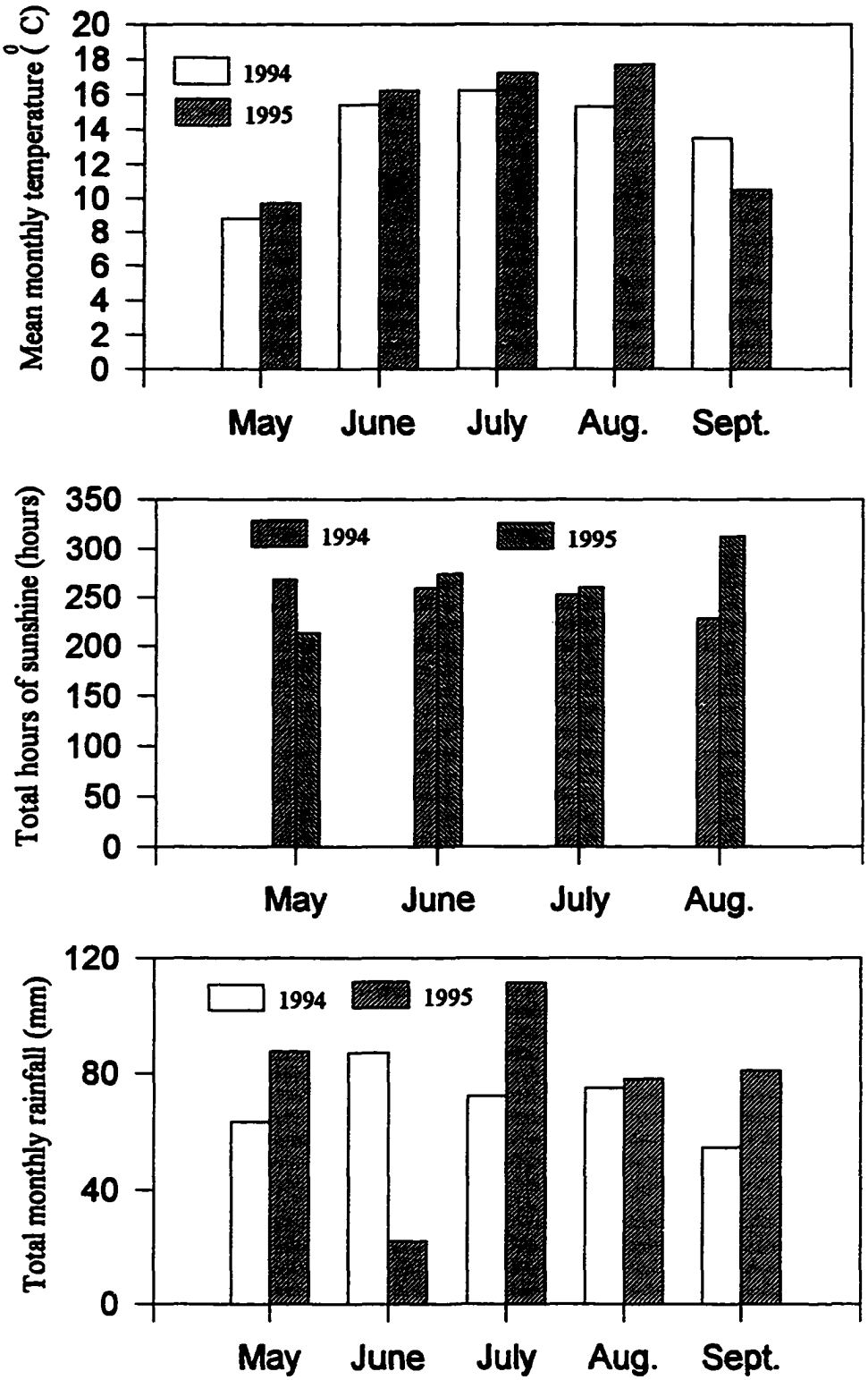

Figure 3. Monthly means of temperature (^{0}C), total hours of sunshine (hours) and total monthly rainfall (mm) in Thunder Bay area in the 1994 and 1995 growing seasons (after: Environmental Canada, Thunder Bay).

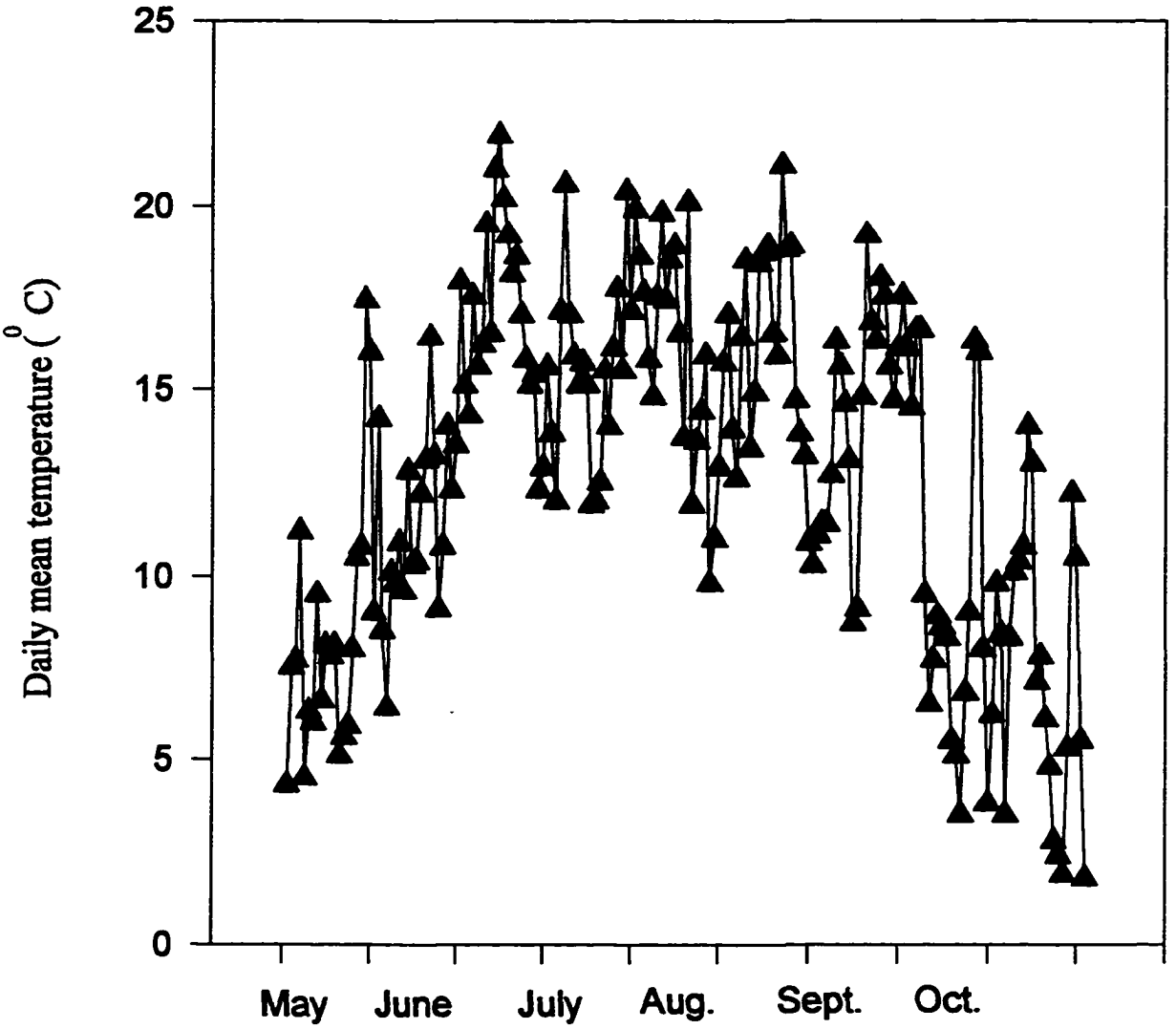

Figure 4. Daily mean temperature (^{0}C) in Thunder Bay area in 1994 growing season (after: Environment Canada, Thunder Bay).

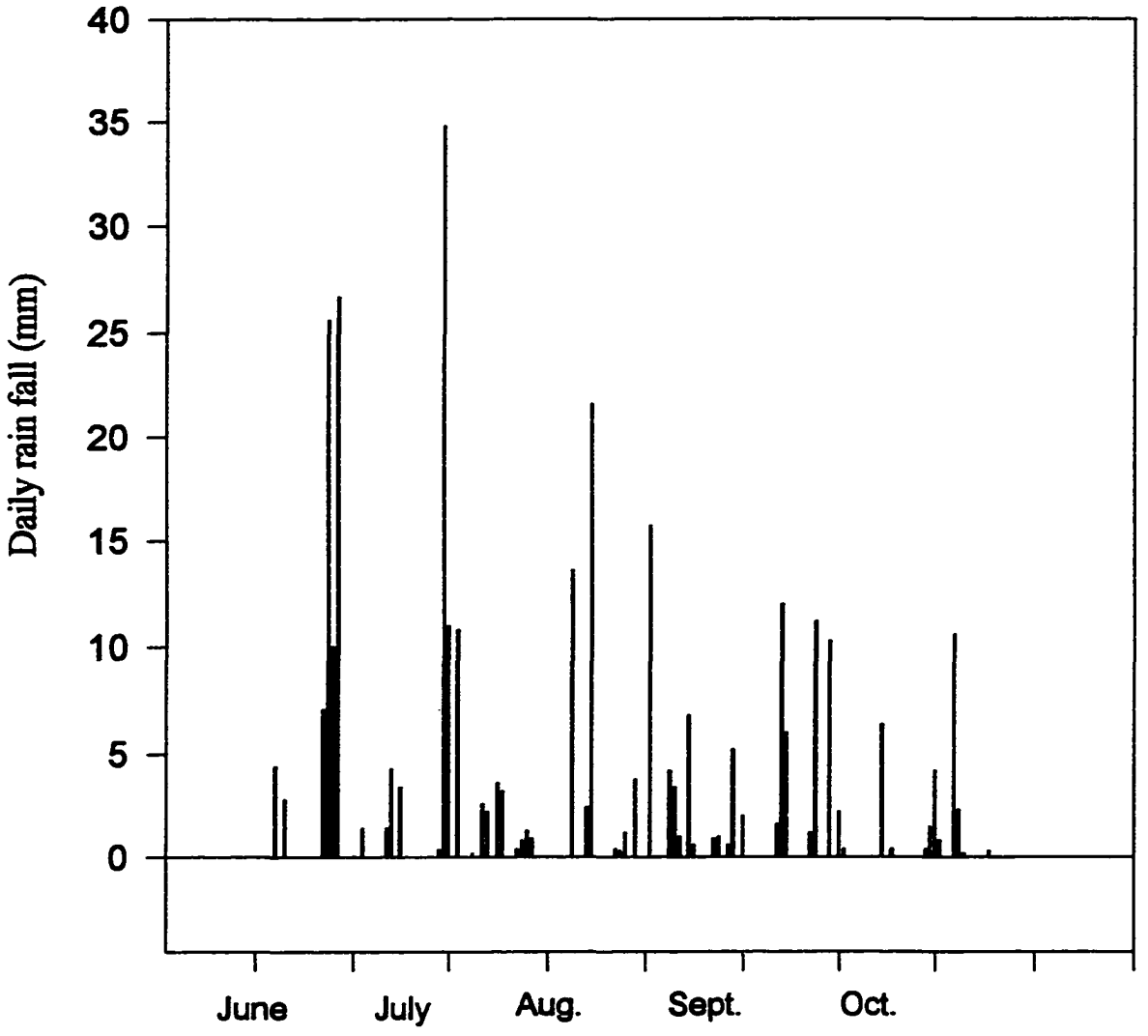

Figure 5. Daily rainfall in Thunder Bay area for 1994 growing season
(after: Environment Canada, Thunder Bay)

4. MATERIALS AND METHODS

Field determination of CO_2 evolution and soil temperature was made once a month during the 1994 growing season and in May and June of 1995. Four measurement stations in each plot were established randomly to determine CO_2 and soil temperature. Four soil samples (0-10 cm) were collected at random from each of the treated and control plots. The samples were put in polythene bags and brought back to the laboratory for measuring soil moisture, organic matter content, soil P, N and pH.

4.1. Carbon dioxide evolution

Carbon dioxide evolution was determined using a portable CO_2 analyzer (infra-red gas analyzer, IRGA; Northtech Control Equipment Inc, Ontario) following Parkinson's (1981) method as well as by soda lime method according to Edwards (1982a).

4.1.1. Infra-red gas analysis (IRGA)

At each station, all the measurements were taken between 11 am and 4 pm with the infra-red gas analyzer (EGM-1) linked to a soil respiration chamber (SRC-1).During the measurement, the shorter pipe of the IRGA was connected with the inlet on the rear panel, while the longer pipe was attached to the exhaust on the top of the EGM-1. The IRGA was switched on for 20 minutes before making any measurement. As the analyzer started up its zero mode, the chamber was held above ground well clear of the soil. The chamber was then inserted in the soil so that the stainless steel perimeter ring was partially embedded to avoid leakage. Measurement of

CO_2 evolution was recorded every 8 seconds. The first 3 sets of readings showed zero for these parameters as a quadratic fit required at least 3 data sets. The readings were recorded when the values were steady. Soil respiration rate was expressed as g CO_2 $m^{-2}h^{-1}$. On completion of the day's measurement, the analyzer was left running with ambient air for a while to ensure that there was no condensation in the unit.

4.1.2. Soda-lime

Approximately 30g soda lime (a mixture of CaO and 20% NaOH and 6 to 18% water) dried at 100^0C for 24 hours was placed in air-tight cans (ca 150 cm^2). At each plot, four opened tin cans were randomly placed in the field beneath a plastic chamber (650 cm^2). The surface of the plastic chamber was covered with aluminum foil in order to reflect sunlight. The chambers were inserted 2 cm into the soil to avoid the air passage. After 24 hours, the soda-lime was capped, brought back to the laboratory, dried at 100^0C for 24h and reweighed. The CO_2 evolution was determined from the increase in the soda-lime mass over a 24-hour period, after subtracting the weight gain in the controls. Mass increases were multiplied by 1.41 to correct the amount of water formed and lost during the bonding of CO_2 to soda lime (Edwards 1982).

4.2. Soil organic matter content

Approximately 15 g of 2mm sieved, oven-dried soil samples were placed in a crucible of known weight. The samples were ignited for 3 hours at 600^0C in a muffle furnace followed by cooling in a desiccator and reweighed to determine the organic matter content by the weight loss method as follows:

$$\textit{Organic matter content}(\%) = \frac{\textit{Weight of oven-dried soil - weight of ignited soil}}{\textit{Weight of oven-dried soil}} \times 100$$

4.3. Soil moisture content

Moisture content of the surface (0-10 cm) soil was measured gravimetrically once a month in the 1994 growing season in each plot. The fresh soil samples were dried at 105^0C for 48 hours and reweighed for determining moisture content as follows:

$$\textit{Moisture content}(\%) = \frac{\textit{Fresh soil weight - oven-dried soil weight}}{\textit{Oven-dried soil weight}} \times 100$$

4.4. Soil temperature

Soil temperature was determined once a month at three levels, On the ground surface, 5 and 10 cm below ground at one location in each plot. Three copper-constantan thermocouples were inserted into the soil at the desired depth and placed in the middle of each measurement plot. A digital temperature sensor (Cole-Parmer Inst.Co.) was used to determine soil temperature.

4.5. Soil pH

Distilled water was added to oven-dried soil samples in the ratio of soil to water at 1:2.5. The pH of the soil solution was determined with a Fisher Acument Model 805 pH meter, using a glass electrode.

4.6. Determination of soil phosphorus and nitrogen

Three soil samples were collected randomly from the combined L, F and H horizons and mineral soils at 0-20 cm depth in each plot. The samples were put in plastic bags and brought into the laboratory. The soils were analyzed for Phosphate-P (PO_4^{3-}-P) and Ammonium-N (NH_4^+-N). The soil samples were oven-dried at 70^0C to a constant weight, passed through a 2-mm sieve and analyzed for N by Indophenol blue method (Anderson 1982). Phosphorus was determined by stannous chloride reduction (Anderson 1982). Three replications were made for each determination.

4.7. Seedling response to the site preparation treatments

The height (from the terminal bud to the base) of seedlings and current-year's leader growth (from terminal bud to terminal bud scale scars) of eight seedlings in each plot (32 seedlings in each treatment) were measured at the end of September 1994 and 1995.

4.8. Effects of soil temperature, moisture and organic matter on CO_2 evolution: a controlled experiment

Fresh humus and mineral soils were sampled from the uncut control mixedwood forest control plots. The samples were collected in the Spring of 1995 and stored at 4^0C until used in the laboratory study. A 3x3x5 factorial experiment was conducted to determine the effects of temperature, moisture and organic matter content on CO_2 evolution. The samples were prepared by mixing appropriate amount of humus with mineral soils to achieve soils with 15%, 28% and 48% organic matter content. The soil samples (100 g) were air-dried, sieved (2-mm), weighed

and placed in the plastic incubation boxes (18 x 13 x 5 cm deep). They were given three moisture treatments (20%, 40% and 60%) by adding distilled water spray. The incubation boxes with soils were placed at 10, 15, 20, 25 and 30^0C in growth chambers (Controlled Environments LTD. Canada) for 24 hours. Carbon dioxide evolution measurements were recorded in three replicated samples for each treatment by IRGA. After the measurement of CO_2 evolution, percent organic matter content of different mixtures of mineral and organic soils were determined by the loss on ignition method. Soil moisture content was determined by gravimetric method. Prior to the factorial experiment, three preparatory tests were performed to determine the amount of organic matter content and moisture required to achieve the desired proportions. Loss of moisture after 24 hour incubation at different temperatures was also determined. Open water pans were placed in the growth chamber to compensate for the loss of water by evaporation.

4.9. Statistical analysis

Analysis of variance (ANOVA) was used to determine the difference in CO_2 evolution among the treatments. Tukey's multiple range test was performed to measure the level of significance. Significant difference of means refers to $P \leq 0.05$.

Multiple regression analysis was applied to the four microclimatic parameters that influenced the soil CO_2 evolution.

5. RESULTS

5.1. Carbon dioxide evolution following the site preparation treatments

The values of CO_2 evolution, as determined by IRGA once a month in the field plots, ranged from 0.11 to 0.99 g CO_2 $m^{-2}h^{-1}$ from June to October 1994 (Fig. 6). The rate of CO_2 evolution decreased in the order of mixed > cut > uncut > screefed plots. Carbon dioxide evolution from the mixed plots was 1.28 times greater, and that from the screefed plots was 0.38 times lower than that from the cut plots in July (Table 2). Compared to the uncut plots, CO_2 evolution was slightly less (0.03 times) in the cut plots. However, Tukey's analysis did not show any significant difference in CO_2 evolution between the uncut and cut plots (Table 2). The value of CO_2 evolution in June 1995 was lower than that measured in June of 1994 (Table 2).

The rate of CO_2 evolution determined by soda-lime technique followed the order of mixed > cut > uncut > screefed plots as above (Table 2). However, the measurements by soda-lime in July were approximately 0.4 times lower than those by the IRGA in uncut and cut plots respectively (Table 2). No significant difference in CO_2 evolution was found among the cut, uncut and mixed plots as determined by the soda-lime method. However, significantly lower rate of CO_2 evolution was determined from the screefed plots compared to all other plots, a trend similar to that obtained by the IRGA.

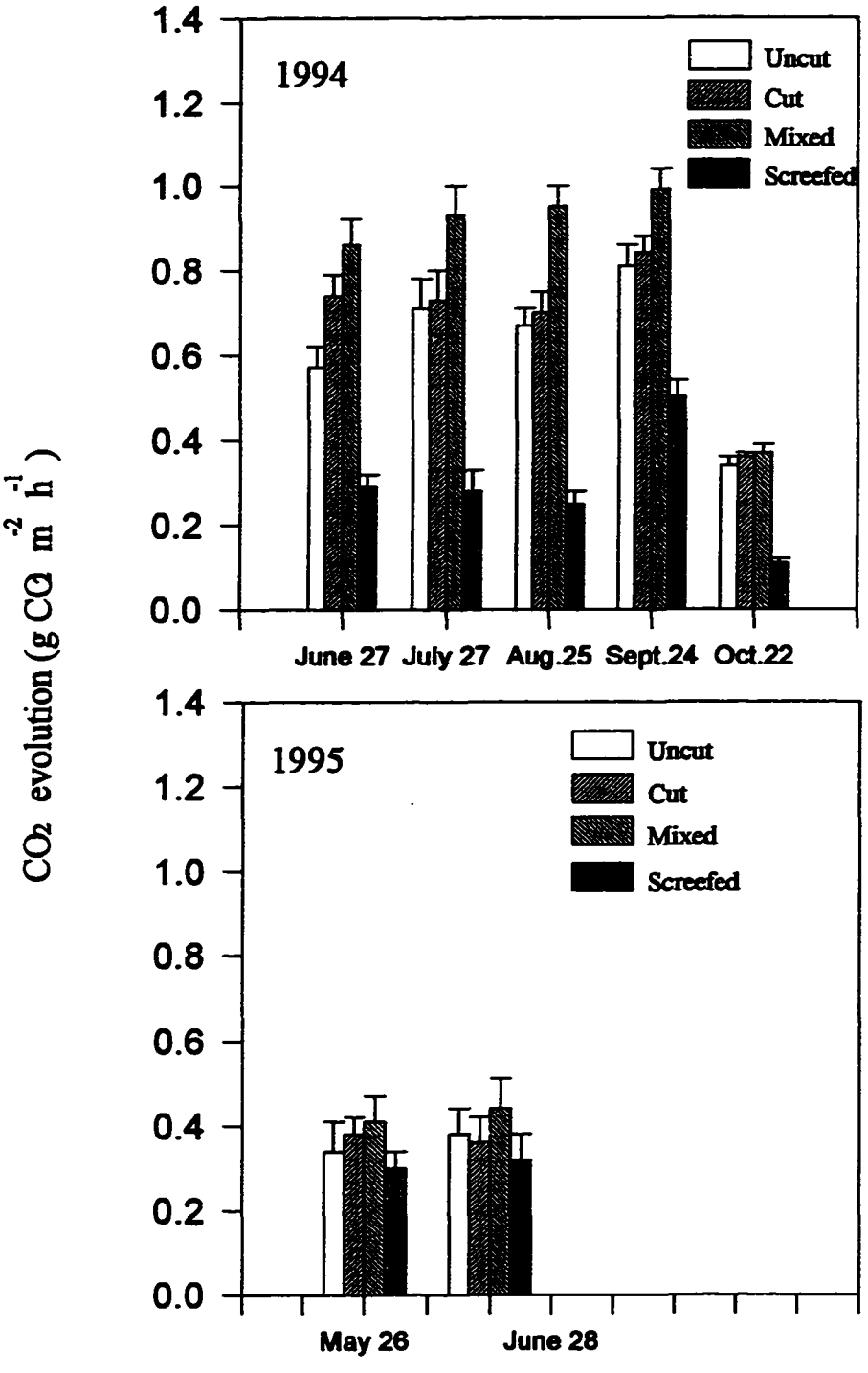

Figure 6. CO_2 evolution (g CO_2 m^{-2} h^{-1}) from soil surface in 1994 and 1995 growing seasons following the site preparation treatments, as measured by the IRGA. Vertical bars indicate standard error of means (n=16).

Table 2. Mean values (±S.E.) of CO_2 evolution (g CO_2 $m^{-2}h^{-1}$) in the 1994 and 1995 growing seasons as determined by soda-lime and infra-red gas analyzer (IRGA).

Methods used	Treatments	1994					1995	
		June 27	July 27	Aug. 25	Sept. 24	Oct. 22	May 26	June 28
Soda-lime*	Uncut	0.28^{a1} ±.02	0.28^{a1} ±.02	0.28^{a1} ±.012				
	Cut	0.29^{a1} ±.01	0.27^{a1} ±.01	0.30^{a1} ±.02				
	Mixed	0.32^{a1} ±.01	0.29^{a1} ±.02	0.30^{a1} ±.01				
	Screefed	0.17^{b2} ±.01	0.18^{b2} ±.01	0.19^{b2} ±.01				
IRGA	Uncut	0.57^{a1} ±.05	0.71^{a2} ±.07	0.67^{a2} ±.04	0.81^{a3} ±.05	0.34^{a4} ±.02	0.34^{a1} ±.07	0.38^{a1} ±.06
	Cut	0.74^{b1} ±.05	0.73^{a1} ±.07	0.70^{a1} ±.05	0.84^{a2} ±.04	0.36^{a3} ±.01	0.38^{a1} ±.04	0.36^{a1} ±.06
	Mixed	0.86^{b1} ±.06	0.93^{b1} ±.07	0.95^{b1} ±.05	0.99^{b1} ±.05	0.37^{a2} ±.02	0.41^{a1} ±.06	0.44^{b2} ±.07
	Screefed	0.29^{c1} ±.03	0.28^{c1} ±.05	0.25^{c1} ±.03	0.50^{c2} ±.04	0.11^{b3} ±.01	0.30^{b1} ±.04	0.31^{c2} ±.06

Note: Unlike letter in a column and unlike number in a row indicate values significantly different at 0.05 level determined by the Tukey-HSD test. * Soda lime method was discontinued after August 1994 since the values were low with higher variance compared to the IRGA method.

Table 3. Summary of ANOVA for CO_2 evolution, soil moisture and soil organic matter for 1994 and 1995 growing seasons

Source of variation	df	F values						
		1994					1995	
		June 27	July 27	Aug.25	Sept.24	Oct.22	May 26	June 28
CO_2 evolution	3	52.94 *	40.21*	95.58**	38.67*	119.4**	34.33*	39.25*
(1)IRGA	3		45.34*					
(2)Soda-lime								
Soil moisture	3	40.41 *	105.8**	130.0**	94.8**	136.7**	93.15**	101.4**
Soil organic matter	3		71.14**					45.3**

Note: * and ** indicate values which differ significantly at 0.05 and 0.01 level respectively.

5.2. Microclimatic factors in relation to CO_2 evolution

5.2.1. Soil temperature

Temperatures at soil surface, 5 cm and 10 cm below ground were significantly greater in the treated plots than in uncut control plots during the 1994 growing season (Fig. 7-9). Surface temperature after clearcutting was increased by 3.2^0C to 5.4^0C. Temperature at 5 cm below ground was increased by 7.9^0C to 9.8^0C, while that at 10 cm below ground was increased by 9.3^0C to 10.2^0C, compared to the uncut plots in July 1994 (Fig. 7-9). However, the range of difference in temperature amongst the treated plots at soil surface in July, was from 0.1^0C to 2.2^0C, which was not statistically significant. Site preparation treatments had little effect on soil temperature. Soil temperature at any of the three levels, among the treated plots (cut, mixed and screefed) did not show significant correlation with CO_2 evolution (Table 7). Temperatures at soil surface, 5 cm and 10 cm below ground in June 1995 were however, significantly lower than those of June 1994.

As most measurements of soil temperature were done between 11 am and 4 pm, usually on sunny days, the temperature was relatively steady. Daily mean temperature, obtained from Environment Canada, was lower than that records on site perhaps due to high fluctuation between day and night temperature (Fig.4). Decrease in soil temperature (12.2^0C) was observed with the increase of soil depth from 0 up to 10 cm in uncut plots in July 1994. The mean air temperature in the 1995 growing season was higher than that in the 1994 growing season (Fig.3).

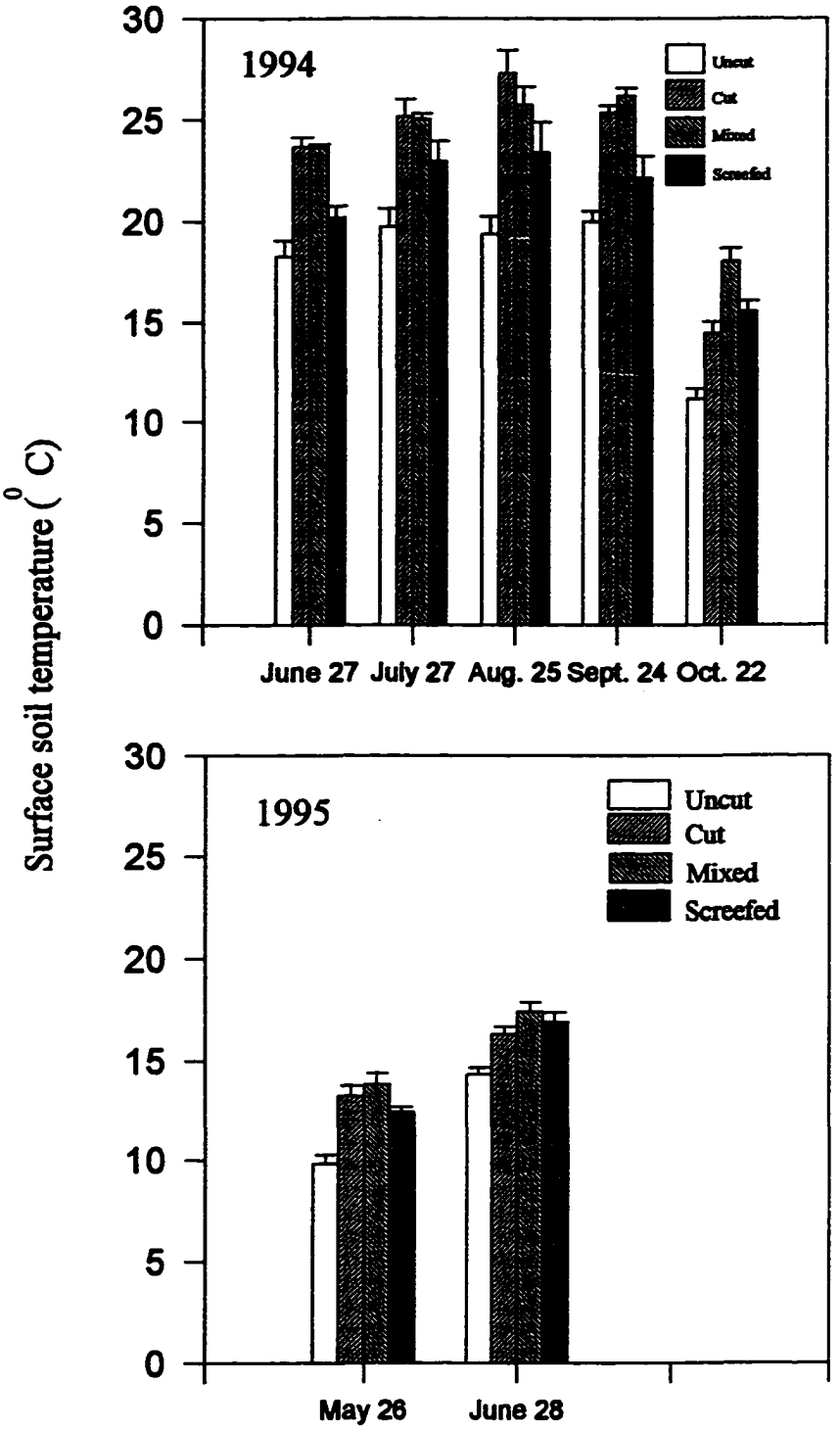

Figure 7. Surface soil temperature (^{0}C) in 1994 and 1995 growing seasons following the site preparation treatments. Vertical bars indicate standard error of means (n=16).

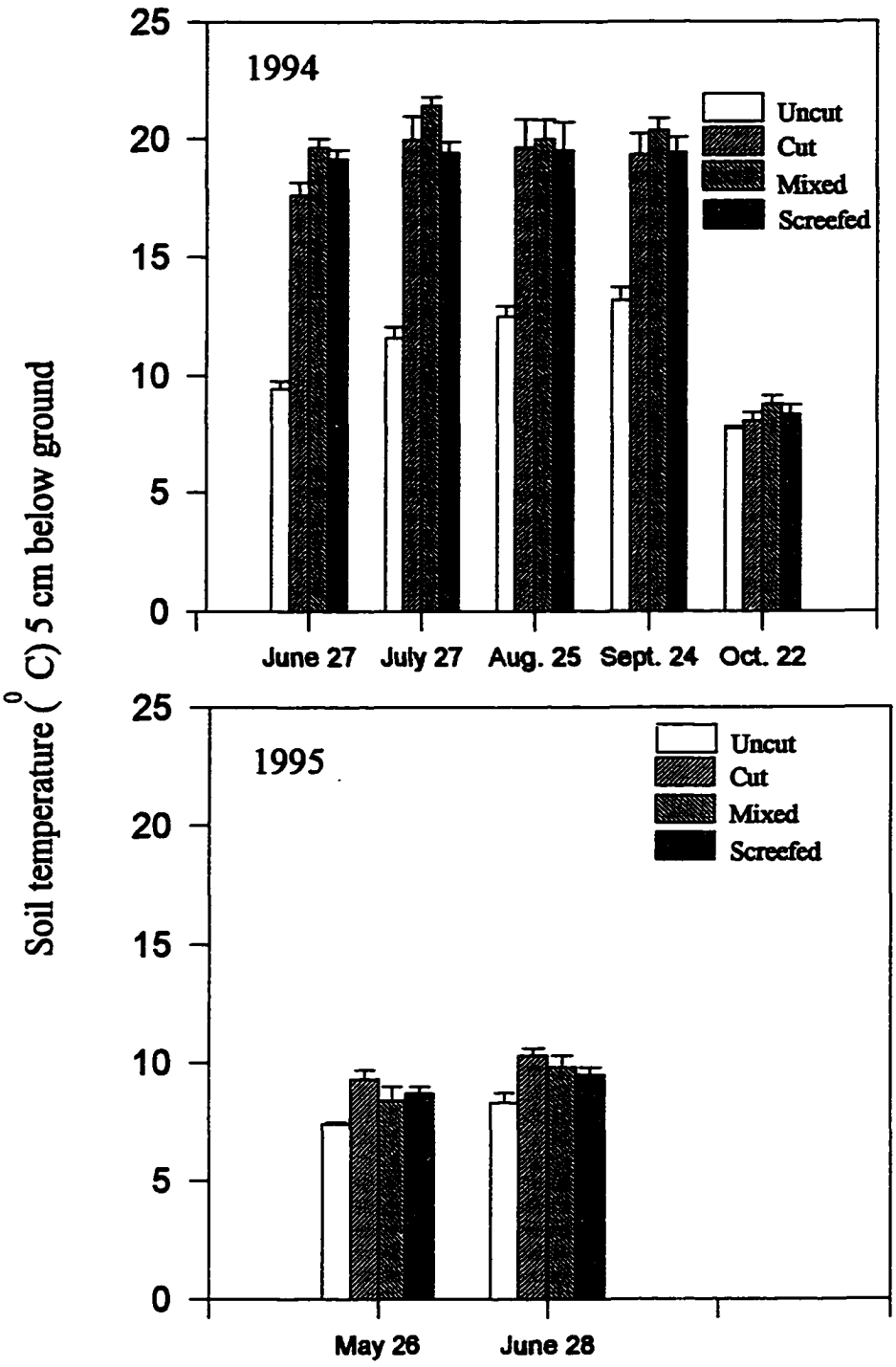

Figure 8. Soil temperature (^{0}C) 5 cm below ground in 1994 and 1995 growing seasons following the site preparation treatments. Vertical bars indicate standard error of means (n=16).

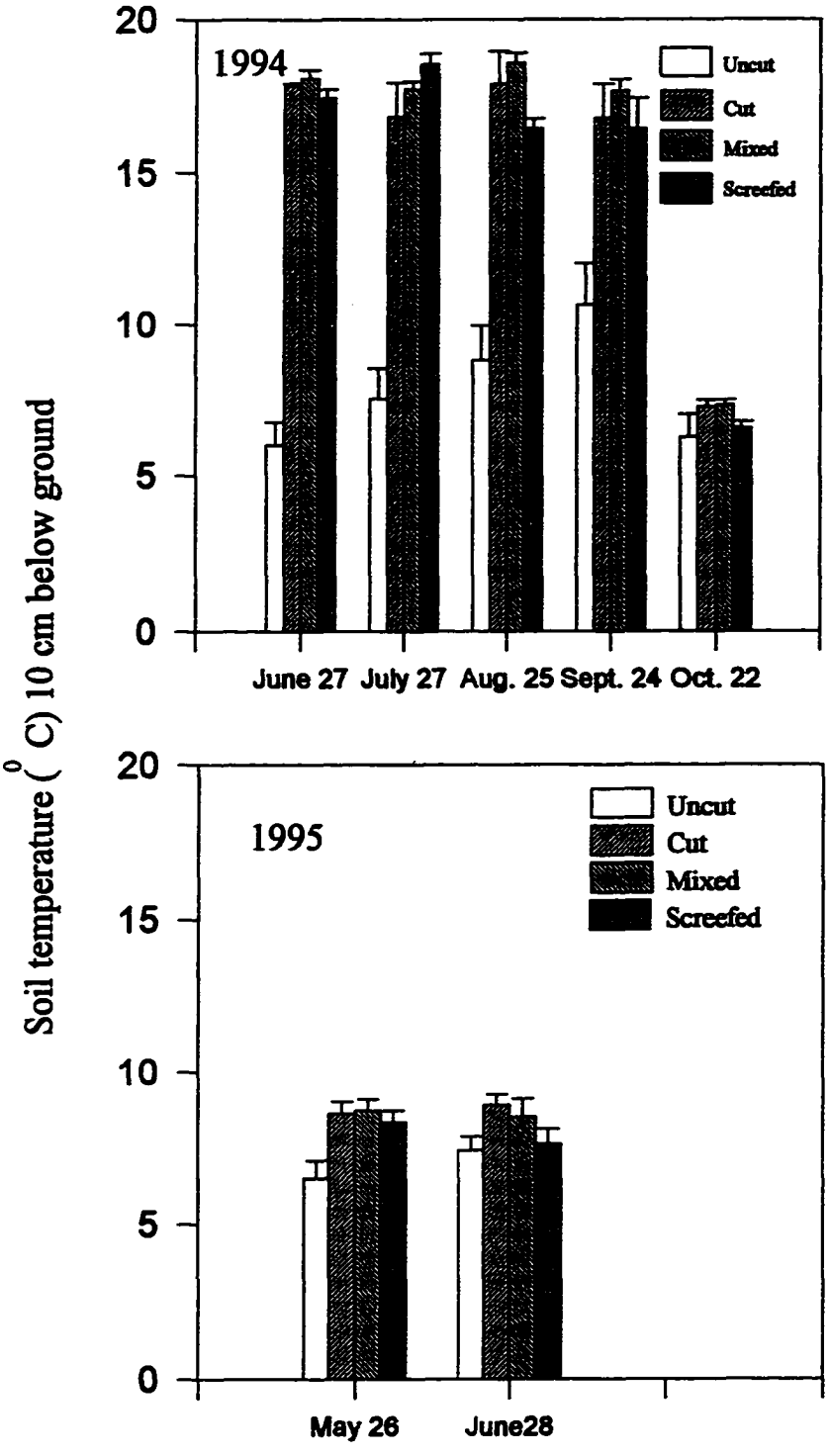

Figure 9. Soil temperature (^{0}C)10 cm below ground in 1994 and 1995 growing seasons following the site preparation treatments. Vertical bars indicate standard error of means (n=16).

Table 4. Summary of ANOVA for soil temperature at surface, 5 cm below ground, 10 cm ground in 1994 and 1995 growing seasons

Source of variation	df	F values						
		1994					1995	
		June 27	July 27	Aug.25	Sept.24	Oct.22	May 26	June 28
Surface	3	48.46*	20.20*	18.95*	37.75*	48.19*	45.41*	32.12*
5 cm below	3	280.44*	95.68**	28.58*	50.89*	3.71	250.12**	43.23*
10 cm below	3	257.5**	91.15**	47.68**	26.61**	2.23	234.12**	38.94*

Note: * and ** indicate values in lines which differ significantly at 0.05 and 0.01 level respectively.

5.2.2. Soil moisture

The soil moisture content of cut, mixed and screefed plots was significantly lower by 20%, 19% and 49% than that of uncut plots (Fig.10). Screefed plots had the lowest soil moisture (about 30%). Soil moisture content was affected significantly by the site preparation treatments (Table 3). However, the difference in soil moisture content between the cut and mixed plots was not significant (Fig.10). Similar trend in soil moisture content was obtained during June 1994 and 1995 (Fig. 10 and Table 3). Monthly totals of rainfall in 1995 were higher than that in the 1994 (Fig. 3).

A positive correlation between soil moisture and soil organic matter content was found (Table 7). Similarly positive correlation between soil moisture content and CO_2 evolution was observed in all the treated plots. The present study showed that moisture content played a more important role than soil temperature in CO_2 evolution (Table 7).

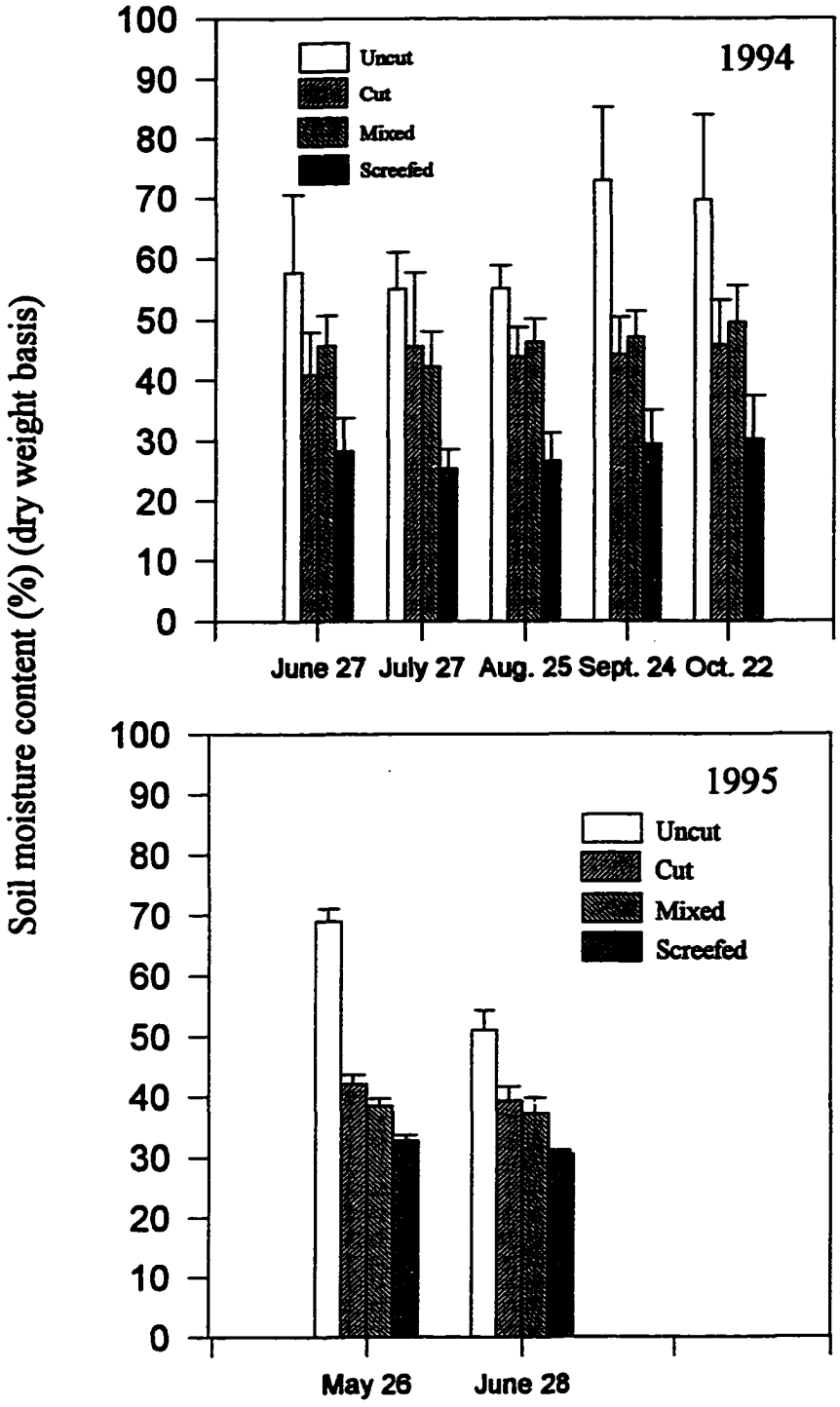

Figure 10. Soil moisture (%) determined once a month in 1994 and 1995 growing seasons following site preparation treatments. Vertical bars indicate standard error of means (n=16).

5.3. Other changes following the site preparation treatments

5.3.1. Soil organic matter

Uncut plots had the highest soil organic matter content and the screefed plots had the lowest (Fig.11). Organic matter content between the cut (25.1%) and mixed plots (22.5%) was not significantly different. A similar trend in soil organic matter content among the treatments was found in 1995 and 1994 (Fig.11). Site preparation treatments reduced soil organic matter significantly (Table 3).

5.3.2. Soil phosphorus and nitrogen

Soil phosphorus (PO_4^{3-}-P) content of mixed and screefed plots was lower (0.9 and 0.5 times) than that of the cut plots. Soil P content of mixed plots was significantly greater (2.2 times) than that of the screefed plots (Table 5 and 6). No significant difference in soil P was found between the cut and the mixed plots (Table 5).

Soil nitrogen (NH_3^+-N) in mixed plots was significantly higher (by 1.4 to 2.7 times) than that of the cut and the screefed plots (Table 5 and 6). A positive correlation was found among soil phosphorus, nitrogen and soil organic matter (Table 7).

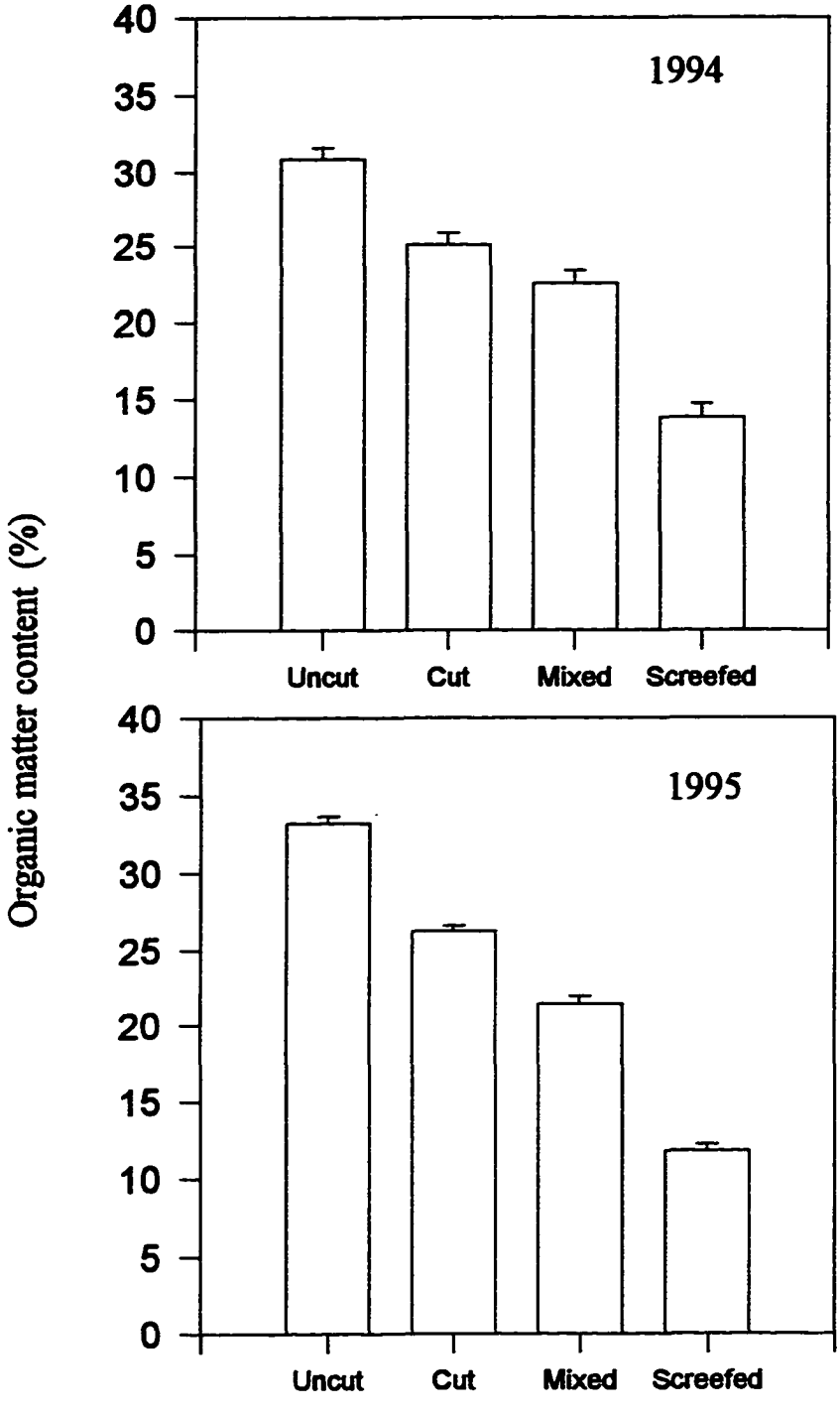

Figure 11. Soil organic matter content (%) of the treated and control plots in 1994 and 1995 growing seasons following the site preparation treatments. Vertical bars indicate standard error of means (n=16).

Table 5. Mean values of soil phosphorus (PO_4^{3-}-P), nitrogen (NH_4^+-N) and pH in the uncut cut, mixed and screefed plots (n=16).

	Uncut	Cut	Mixed	Screefed
PO_4^{3-}-P (mg/100g)	$1.1^a \pm 0.04$	$0.06^b \pm 0.01$	$0.058^b \pm 0.02$	$0.026^c \pm 0.003$
NH_4^+-N (μg/mg)	$8.5^a \pm 1.9$	$4.2^b \pm 2.3$	$6.02^c \pm 2.5$	$2.2^d \pm 0.8$
pH	$5.9^a \pm 0.9$	$5.9^a \pm 1.3$	$5.4^a \pm 1.3$	$5.2^a \pm 0.1$

Note: Unlike letter in a line indicates values significantly different at 0.01 level respectively determined by the Turkey-HSD test.

Table 6. Summary of ANOVA for soil phosphorus (PO_4^{3-}-P), nitrogen (NH_4^+-N) and pH.

Factors	df	p
soil phosphorus (PO_4^{3-}-P)	3	0.000**
soil nitrogen (NH_4^+-N)	3	0.000**
pH	3	0.21

Note: ** refers to $p < 0.01$.

Table 7. Correlation coefficients of CO_2 evolution (CO_2), soil temperature (T_1, T_2, T_3), soil moisture content (M), phosphorus (PO_4^{3-}-P), nitrogen (NH_4^+-N), pH and organic matter content (O.M.) in 1994 growing season.

	CO_2	T_1	T_2	T_3	M	PO_4^{3-}-P	pH	O.M.
T_1	0.09							
T_2	0.28	-.13						
T_3	-0.07	-.22	.79**					
M	0.52**	.09	.38*	.07				
PO_4^{3-}-P	0.64**	.24	.21	-.02	.76**			
pH	0.27	.21	.05	-.18	.49**	.58**		
O.M.	0.56**	.22	.17	.12	.63**	.75**	.64**	
NH_4^+-N	0.60**	.25	.24	.10	.48**	.69**	.27	.51*

Note: * refers to $P < 0.05$; ** refers $P < 0.01$; CO_2 evolution in (g CO_2 m^{-2} h^{-1}); T_1, T_2 and T_3 refer to soil temperature at surface soil, 5 cm and 10 cm below ground (^0C); M refers to soil moisture content (% dry weight basis).

5.3.3. Soil pH

Soils of the treated plots were acidic, pH ranging from 5.2 to 5.9, regardless of the type of treatment (Table 5). Soil mixing, in spite of mixing more acidic organic matter with less acidic mineral soil, did not change soil pH significantly. Similar results were found in the screefed plots (Table 6).

5.4. Seedling response to the site preparation treatments

The planted black spruce seedlings did not respond to the site preparation treatments immediately. A similar trend in the current year's leader growth and seedling height of planted black spruce was found in treated (cut, mixed and screefed) plots in 1994 and 1995, one and two years after the treatments respectively (Table 8). The current year's leader growth in September 1995 was 1.8 times higher than that in September 1994, although these differences were not significant due to high variance. The increase in current year's leader growth of black spruce seedlings ranged from 17.1 cm to 19.5 cm during the second year after the site preparation treatments (Table 8). However, no significant difference in current year's leader growth and height of planted black spruce seedlings among the treatments was found (Table 9).

Table 8. Mean seedling height (cm) and current year's leader growth ± S.E.in the cut, mixed and screefed plots at the end of 1994 and 1995 growing seasons (n=32).

Seedling	Treatment	1994	1995
Height (cm)	Cut	37.9±1.5	55.0±2.7
	Mixed	40.3±1.4	58.1±2.4
	Screefed	38.8±1.0	58.3±3.6
Leader growth (cm)	Cut	8.8±2.8	17.1±1.5
	Mixed	10.0±1.5	17.8±1.02
	Screefed	9.6±0.98	19.5±1.6

Table 9. Summary of ANOVA for the seedling height and current year's leader growth

Factors	df	Year	p
Seedling height	2	1994	0.51
		1995	0.67
Leader growth	2	1994	0.19
		1995	0.47

5.5. Carbon dioxide evolution at different levels of temperature, moisture and organic matter content of soil under controlled conditions

Carbon dioxide evolution increased gradually with the increase of temperature at certain moisture levels (Table 10). However, below 20^0C, temperature had little effect on CO_2 evolution in low organic matter soils with low moisture. The optimum temperature for high CO_2 evolution was between 25^0C-30^0C. The optimum soil moisture range for high CO_2 evolution was from 40% to 60%. At 25^0C and 30^0C, no significant difference in CO_2 evolution was observed between high (60%) and medium (40%) soil moisture contents (Fig. 12c). Soils with medium and high organic matter, an increase of temperature from 20^0C to 30^0C, resulted in a two-fold increase in CO_2 evolution (Table 12). However, when temperature was increased from 20^0C to 25^0C, CO_2 evolution was not proportionately increased at high moisture level between 40% and 60% (Table 10). In soils with low organic matter, a temperature increase from 20^0C to 30^0C had little effect on CO_2 evolution (Table 10).

The relationships among soil temperature, moisture, organic matter contents and CO_2 evolution were developed by the polynomial equations with three independent variables (Table 11). Because of their complexity, the actual polynomial equations were not presented in the graph. However, the three-dimensional response surfaces showing the relationship among temperature, moisture, organic matter content of soil and CO_2 evolution are presented in Fig. 12. Significant interaction among soil temperature, soil moisture and organic matter on CO_2 evolution was observed (Table 13). Therefore, when the predicted equation was applied in the field, the interaction effect among temperature, moisture and organic matter content should be considered.

When soil moisture and organic matter content were kept constant at different levels, the predicted relationship between CO_2 evolution and soil temperature followed an exponential model (Table 11). This model was more realistic under field conditions. Estimated r^2 values in this study were significantly higher than those of the field results. The values of CO_2 evolution under controlled laboratory condition were lower than those obtained under field conditions.

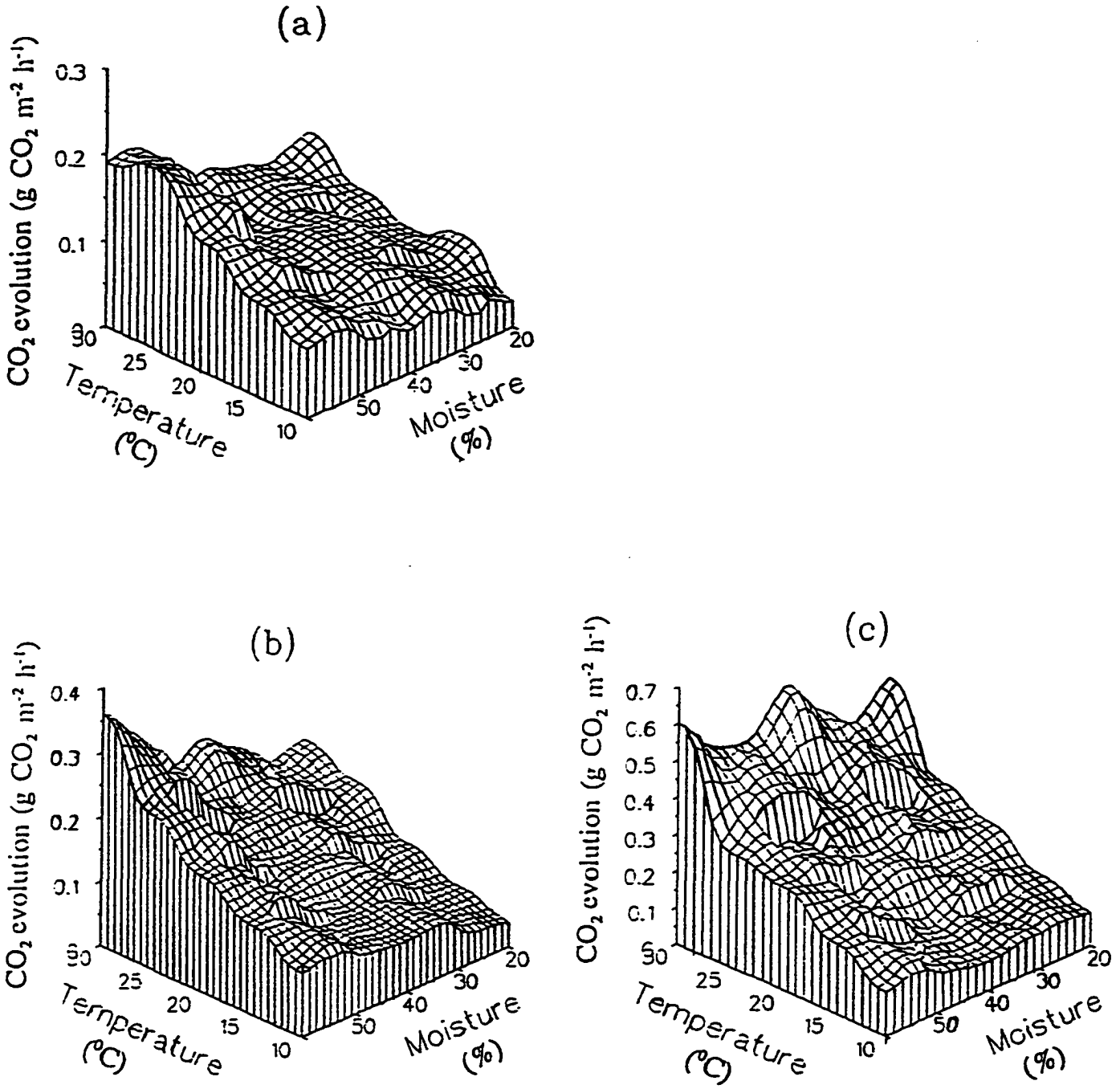

Figure 12 . CO_2 evolution in relation to soil temperature and moisture in different proportions of organic matter and mineral soil mixtures. (a) soil with 15% organic matter; (b) soil with 28% organic matter and (c) soil with 48% organic matter.

Table 10. Carbon dioxide evolution (g CO_2 $m^{-2}h^{-1}$) with varying soil temperature (^0C), moisture (%) and organic matter.

Temperature (^0C)	Moisture (%)	Organic matter content (%)		
		15%	28%	48%
10^0C	20%	$0.04^{1a}\pm0.01$	$0.06^{1a}\pm0.02$	$0.07^{1a}\pm0.02$
	40%	$0.07^{1a}\pm0.02$	$0.07^{1a}\pm0.01$	$0.08^{1a}\pm0.03$
	60%	$0.09^{1a}\pm0.02$	$0.12^{2a}\pm0.02$	$0.12^{2a}\pm0.02$
15^0C	20%	$0.06^{1a}\pm0.02$	$0.08^{1a}\pm0.02$	$0.09^{1a}\pm0.04$
	40%	$0.08^{1a}\pm0.02$	$0.11^{1a}\pm0.01$	$0.12^{1a}\pm0.03$
	60%	$0.09^{1a}\pm0.01$	$0.13^{1a}\pm0.03$	$0.15^{1a}\pm0.03$
20^0C	20%	$0.05^{1a}\pm0.01$	$0.09^{1a}\pm0.02$	$0.21^{2a}\pm0.03$
	40%	$0.11^{2a}\pm0.02$	$0.13^{2a}\pm0.03$	$0.26^{2b}\pm0.04$
	60%	$0.13^{2b}\pm0.02$	$0.18^{3b}\pm0.02$	$0.30^{2b}\pm0.02$
25^0C	20%	$0.08^{1b}\pm0.02$	$0.15^{1b}\pm0.01$	$0.26^{1b}\pm0.04$
	40%	$0.11^{2a}\pm0.03$	$0.19^{2b}\pm0.03$	$0.32^{2b}\pm0.03$
	60%	$0.17^{3b}\pm0.04$	$0.25^{2b}\pm0.05$	$0.32^{2b}\pm0.04$
30^0C	20%	$0.10^{1c}\pm0.02$	$0.21^{1c}\pm0.03$	$0.41^{1c}\pm0.07$
	40%	$0.16^{2b}\pm0.04$	$0.22^{1b}\pm0.04$	$0.53^{2c}\pm0.05$
	60%	$0.18^{3c}\pm0.03$	$0.32^{2c}\pm0.04$	$0.60^{2c}\pm0.02$

Note: Unlike letter in a column and unlike number in a row indicate values significantly different at 0.01 level respectively as determined by the Tukey-HSD test.

Table 11. Carbon dioxide evolution model parameters based on soil temperature and soil moisture by multiple regression

	Field Study			Laboratory Study	
Soils (O.M.)	Predicted equation for CO_2 evolution	R^2	Soils (O.M.)	Predicted equation	R^2
Uncut	CO_2=.08+.05T_2	27.1	48%	CO_2 =0.048 exp (0.083 T_m) (moisture: 62%)	0.71
(31%)	CO_2=-.3+.03T_1+.05T_2-.03T_3+.002M	43.6		CO_2 =0.038 exp (0.09 T_m) (moisture: 44%)	0.74
Cut	CO_2=.3+.023T_2	27.0		CO_2 =0.032 exp (0.085 T_m) (moisture: 21%)	0.88
(25%)	CO_2=.15+.014T_1+.02T_2+.02T_3+.01M	34.4	28%	CO_2=0.064 exp (0.05 T_m) (moisture: 62%)	0.65
				CO_2=0.048 exp (0.052 T_m) (moisture: 44%)	0.73
Mixed	CO_2=.10+.048T_3	45.4		CO_2=0.026 exp (0.069 T_m) (moisture: 21%)	0.78
(23%)	CO_2=.6+.014T_1+.002T_2+.04T_3+.09M	49.3			0.69
			15%	CO_2=0.062 exp (0.037 T_m) (moisture: 62%)	
Scr-eefed	CO_2=.06+.015T_3	16.5		CO_2=0.042 exp (0.044 T_m) (moisture: 44%)	0.75
				CO_2=0.028 exp (0.041 T_m) (moisture: 21%)	0.76
(14%)	CO_2=.18-.02T_1+.02T_2+.01T_3+.001M	25.8		CO_2=-0.227+0.076S+0.05T_m+0.04M	0.73

Note: Carbon dioxide evolution in (g CO_2 m^{-2} h^{-1}); T_1 and T_m, T_2 and T_3 refer to soil temperature at surface soil, 5 cm and 10 cm below ground (^{0}C); M refers to soil moisture content (% dry weight basis). S refers to organic matter content (%).

Table 12. The Q_{10} values on CO_2 evolution (g CO_2 m^{-2} h^{-1})with varying soil temperature, moisture and organic matter contents.

Treatment	Moisture (%)	10-20^{0}C	20-30^{0}C
	21.3	1.25	2
Soil with 15%	41.4	1.57	1.45
organic matter	63.4	1.44	1.38
	21.3	1.5	2.3
Soil with 28%	41.4	1.78	1.69
organic matter	63.4	1.5	1.78
	21.3	3	1.95
Soil with 48%	41.4	3.25	2.04
organic matter	63.4	2.5	2.00

Table 13. Summary of MANOVA for the effect of temperature, moisture and organic matter contents on carbon dioxide evolution.

Source of variation	SS	DF	MS	F	Sig. of F
Error	.13	135	.00		
M	.13	2	.07	67.67	.000
S	.59	2	.30	307.71	.000
T	1.06	4	.27	275.00	.000
M By S	.01	4	.00	1.72	.150
M By T	.01	8	.00	1.62	.120
S By T	.35	8	.04	45.81	.000
M By S By T	.03	16	.00	2.04	.015

Note: S refers to different mixtures of mineral and organic soils; M refers to soil moisture content and T refers to soil temperature.

6. DISCUSSION

6.1. Effects of the site preparation treatments on carbon dioxide evolution

The values of CO_2 evolution ranging from 0.11 to 0.99 g CO_2 $m^{-2}h^{-1}$ for the mixedwood forest in northwestern Ontario, were comparable to those reported by Gordon et al.(1986) who presented seasonal values (0.45-0.60 g CO_2 $m^{-2}h^{-1}$) for a white spruce stand in interior Alaska. In general, the respiration values found in this study were also within the range of CO_2 evolution encountered in other temperate coniferous forests world wide (0.01 to 7.9 g CO_2 m^{-2} h^{-1}). However, the values of CO_2 evolution in cut, cut-mixed and uncut plots of the present study were higher than those reported by Weber (1985) (0.2 g CO_2 m^{-2} h^{-1}) and Gordon et al.(1986) as mentioned above. They probably reflect the differences in site quality. It was suggested that the rate of organic matter decomposition in mixedwood forest was higher than that in pure jack pine and white spruce forests due to slow rate of decomposition of pine needles (Weber 1985; Gordon et al.1986). This might be due to thick organic layer and high moisture content in the mixedwood forest (Sims et al. 1989). A positive correlation between soil organic matter content and CO_2 evolution was found in this study. This is in agreement with Kaiser (1992) who reported a highly significant positive relationship among CO_2 evolution, soil microbial activity, organic matter content and total nitrogen.

Site preparation treatments had an impact on CO_2 evolution. The rates of CO_2 evolution in the mixed plots were significantly higher than those in the cut and uncut plots during the 1994 growing season. This increased CO_2 evolution may have resulted from 1) accelerated activity of the existing microbial population due to better aeration after mixing the organic layer with

the mineral soils; and/or 2) a more diverse population of microbes appearing on the substrate in the mixture of humus and mineral soils (Florence 1965; Foster et al.1980; Salonius 1981). In the present study site, the number of *Pseudomonades* increased greatly after forest harvesting, and the population returned to previous levels one year after the treatments (Appendix 1). The number of *Pseudomonades* was in the order of mixed > cut > screefed plots. The number of *Trichodermas*, which was responsible for ammonification, on the other hand, was reduced greatly after forest harvesting and site preparation treatments and the order of reduction was mixed > cut > screefed (Appendix 2). These results suggest that changes in composition of microbial population have occurred following the site preparation treatments. This increased microbial activity after soil mixing may have stimulated organic matter decomposition and released nutrients, both of which have a positive influence on CO_2 evolution.

The present results were different from those of Keenan et al. (1994) who found that soil mixing resulted in lower microbial activity, in comparison to that of the uncut forest. This might be due to the following: 1) They tested the CO_2 evolution under laboratory conditions (at constant temperature (25^0C) and moisture (78%). Such optimal conditions could not be obtained in the uncut forest. 2) The measurements were made 4.5 years after the treatments. Soil respiration may return to the previous levels, three years after treatments, as reported by Weber (1990). 3) different soil types, soil sampling method and type of infra-red gas analyzer used might have also affected the results. However, the laboratory component of the present study, conducted under conditions of optimum temperature (from 25^0C to 30^0C), high CO_2 evolution was obtained at the similar conditions of moisture with soils with high organic matter content (see 6.3).

Carbon dioxide evolution was lowest on the screefed plots during the 1994 and 1995 growing seasons. This might be due to low microbial activity as evidenced by low population of *Pseudomonades* and lower soil moisture combined with low organic matter content. No significant difference in CO_2 evolution was found between the uncut and cut plots. These findings were in agreement with the results reported by Weber (1990) who explained enhanced microbial respiration, due to increased soil temperature might have offset the reduced root respiration after clearcutting. In uncut plots, high CO_2 evolution resulted from high moisture content under the undisturbed forest canopy, which may have favoured the microbial activity as well as greater root respiration in soil containing higher organic matter content.

6.2. Carbon dioxide evolution in relation to soil temperature and moisture

The high value of CO_2 evolution during the growing season (from June to the end of September 1994) was due to favourable soil temperature (from 16.4^0C to 18.1^0C) which resulted in optimal condition for microbial respiration (Edwards 1973; Weber 1985). These results are consistent with the conclusions reached by Schlentner and Van Cleve (1985) who found the optimum boreal soil temperature for soil respiration was 17^0C. The low October temperature may be responsible for the low CO_2 evolution in that month. Decreased CO_2 evolution during June 1995 in comparison to 1994 might also be due to the lower temperature, which likely resulted from light interception by the competing vegetation developed two years after the site preparation treatments.

Site preparation had no significant effect on soil temperature. For example, surface temperature ranged from 22.9^0C in the screefed plots to 25.13^0C in the cut plots in July. These

results differed from the conclusions made by Weber (1990) and Toland and Zak (1994) who argued that organic matter decomposition may affect the soil microenvironment. Screefed plots were expected to have the highest soil temperatures due to removal of the organic layer, loss of soil water and exposure to sunlight. However, more pioneering grasses, herbs, shrubs and trees particularly aspen and alder were colonized in these areas causing a high degree of light interception. This might have kept the surface protected from the direct solar radiation. Similar results were reported by Bassman (1989) following soil mounding and scarification, and by Orlander (1986) for soil with thick humus layers in Sweden. The relationship between CO_2 evolution and soil temperature was not significant under field conditions. In uncut forest, the relationship between CO_2 evolution and soil surface temperature was rather weak. These results were contrary to the findings of Toland and Zak (1994) who reported that soil temperature below 10 cm was responsible for 58% of variation of CO_2 evolution. The results obtained under controlled laboratory conditions showed that CO_2 evolution was not affected significantly when the change in temperature was less than 5^0C.

Nevertheless, site preparation modified the microclimatic factors such as soil moisture, which might be indicative of greater evaporation after clearcutting. Soils of the uncut plots consistently had higher moisture content than that in the cut and treated plots. Screefed plots had the lowest moisture content. The decrease might be due to the lower moisture-holding capacity of mineral soil in comparison with organic matter and increased thermal conductivity, heat admittance and consequently evaporation of the exposed mineral soil. Although reductions in moisture content due to higher rates of infiltration by soil mixing had been observed in other studies (Ross and Malcolm 1982, Keenan et al. 1994), there was no difference in soil moisture

content between the cut and mixed plots in the present study.

The linear relationship among soil temperature, soil moisture as independent variables and CO_2 evolution was not clear in any of the site preparation treatments. Multiple regression indicated the existence of the interaction effect of soil temperature and moisture on CO_2 evolution. These results suggest that organic matter content accounted for a significant difference in CO_2 evolution following the site preparation treatments. Results under laboratory conditions also showed that CO_2 evolution depended on soil organic matter content.

6.3. Seedling response to site preparation treatments

Seedling growth one and two years following the site preparation treatments was not significantly different among the treatments. This supported the conclusions made by Sim et al.(1990) who reported that black spruce was a slow growing plant, especially during the first several years after planting. In the present study, soil phosphorus (PO_4^{3-}-P) and nitrogen (NH_4^+-N) contents were lower than those reported for white spruce and jack pine sites in central Ontario (Munson et al.1993). The low level of nitrogen and phosphorus due to soil disturbance likely affected seedling growth. Secondly, soil moisture content was decreased by 49% in screefed and 20% in mixed and cut plots, compared to the uncut forest, which might have an adverse effect on seedling growth. These results are in agreement with those of Brand (1990) who argued that slow seedling growth in the first season may be due to water loss from soils, regardless of the treatments. The accelerated evaporation after clearcutting resulted in slow growth and establishment of an adequate root system and utilization of the nutrients from soil solution (Bassman 1989). However, warmer soil temperature after clearcutting is thought to improve root

membrane permeability and favour seedling growth (Tyron and Chapin 1983). Seedling growth is not affected until the roots are exposed to significant drying effect of the site preparation (Tyron and Chapin 1983; Brand 1990).

The increase of current year's leader growth in 1995 was higher than the average range of growth (5 to 13 cm) reported by Arnup et al. (1988). This suggests that there was a trend of accelerated leader growth of black spruce during the second year after treatments. This might be due to 1) more favourable temperature and moisture contents in the 1995 growing season: the temperature and rainfall in May 1995 were higher than those in May 1994; 2) black spruce grows faster during the second and third year than in the first year; 3) perhaps more root development occurs in the second year after planting (Arnup et al. 1988).

6.4. Comparison of soda lime method with IRGA

The amount of CO_2 measured by the soda lime method was significantly less than that determined by the IRGA technique at the same forest sites. Under field conditions, the values of CO_2 evolution obtained by IRGA were 1.5-2 times greater than those obtained by the soda lime method. The reduction in CO_2 measured by the soda-lime methods may be due to the hygroscopic nature of soda lime (Edwards 1982a). No literature is available on a comparative study of CO_2 measurements by soda-lime and IRGA. However, it has been reported that alkali solution, which is one of the static methods absorbed only 60% CO_2 compared to IRGA (Kucera and Kirkham 1971; Edwards and Sollins 1973). Raich and Schlesinger (1992) concluded that the estimates of CO_2 evolution from soils determined by soda lime method were not significantly

different from those obtained by gas chromatography. Van Cleve et al.(1979) reported that IRGA had the highest sensitivity compared to the four other methods of CO_2 measurements, such as, infrared gas analyzer, gas chromatography, KOH absorption and Gilson respirometer. Results of the present study agreed with those of Van Cleve (1979), who reported IRGA, as a dynamic method for determination of CO_2 evolution seemed to have a distinct advantage over the static method in terms of efficiency, accuracy and convenience to operate.

6.5. Carbon dioxide evolution under varying soil temperature, moisture and organic matter

In the experimental study, soil organic matter content proved to be the primary factor affecting the rate of carbon dioxide evolution. The highest CO_2 evolution was found in the soils with high organic matter content at the temperature of 30^0C and with a moisture content of 60%. These results support the conclusions made by Ino and Monsi (1969) who argued that the variation in soil respiration amongst different stands was due to differences in nitrogen and organic content. In addition to organic matter content, an optimum range of temperature was found to be a significant factor in the rate of carbon dioxide evolution. An increase in temperature from 20^0C to 30^0C doubled the rate of carbon dioxide evolution in soil containing high organic matter. However, in low organic soils with low moisture content, CO_2 evolution did not increase with increasing temperature. These findings, are contrary to the results obtained by Brand and Janas (1988) who reported that soil temperature and/ or moisture are much more important factors than soil organic content in influencing CO_2 evolution. In this study, only when soil organic matter was kept constant temperature and moisture became the limiting factors affecting CO_2 evolution.

Soil moisture between 40% and 60% did not result in significant difference in CO_2 evolution when the soil had high organic matter content. In other words, with optimal organic content, increase in soil moisture levels did not enhance CO_2 evolution. This is likely due to the fact that there is an optimal level of soil moisture for microbial activity and further increase in moisture do not result in greater microbial activity. Alexander (1967) reported that with excessively high soil moisture content, O_2 supply to soil microorganisms is inhibited, which inevitably leads to the suppression of microbial activity. The present study showed that maximum CO_2 evolution was obtained in soils with a 40-60% moisture content. Schlentner and Van Cleve (1985) found that the optimum soil temperature and moisture levels for soil respiration were 17^0C and 150% soil moisture respectively. Their results differ from the findings of the present study. This was likely due to the fact that Schlentner and Van Cleve measured temperature directly at soil depth of 10 cm below ground in the field whereas this experiment was carried out under controlled laboratory conditions. Also, the lower CO_2 evolution obtained in the laboratory may be due to the lack of root respiration, compared to the field condition. Soil respiration is a product of temperature-dependent metabolism (MacDonald et al. 1995). Temperatures below 20^0C were less significant in affecting CO_2 evolution in low organic soils. Though the exponential model, similar to Toland and Zak's (1994), to predict soil respiration from soil temperature was developed, the model's ability to simulate the daily fluctuation of microclimatic factors was limited. The polynomial equation provided a better-fit model of simulation of soil respiration as a function of temperature, moisture and organic matter. However, the model's interpretation has little biological significance. In the field, if organic matter and moisture content were kept constant, then perhaps one could predict CO_2

evolution from soil temperature data. This study also explained the weak relationship between temperature and CO_2 evolution in the field during the 1994 growing season as it demonstrated no significant microclimatic change (less than 5^0C) following the site preparation treatments.

In summary, these results indicate the importance of maintaining high organic matter content for soil respiration, therefore, nutrient cycling by organic matter decomposition. Removal of organic matter, as a vegetation control method may cause nutritional deficiency. Similar results were found when removal of organic horizons resulted in deficiencies of nutrients necessary for seedling growth (Brand 1990). Compared to screefing, soil mixing had little effect on soil temperature, but has the potential for sustaining available soil nutrients, maintaining optimum soil water and increasing organic matter decomposition. These factors play important roles in survival and growth of planted seedlings (Herring and McMinn 1980). However, the high cost of soil mixing as a site preparation treatment for enhancing seedling growth may not permit this strategy as an acceptable option.

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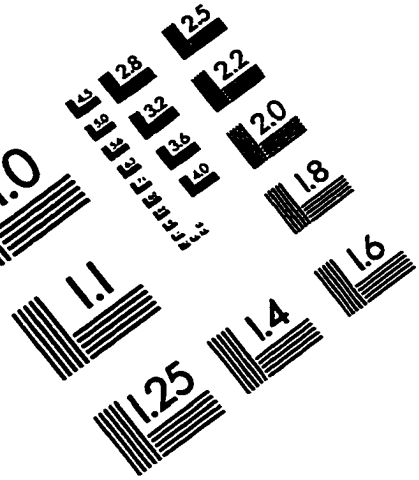
Appendix 1. Populations of fluorescent *Pseudomonades* before and after clear cutting and after silvicultural treatments (M.T. Dumas, pers. com. 1995).

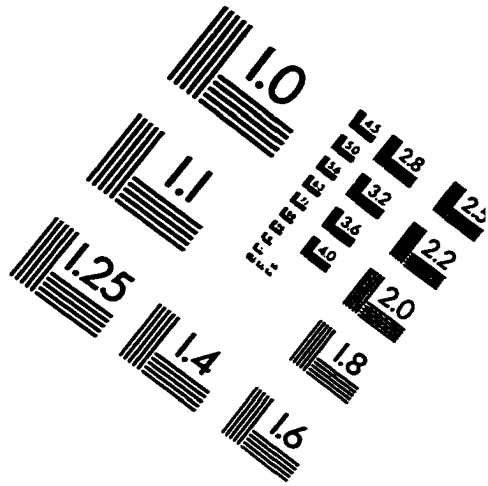
Treatment	Number of *Pseudomonades sp.* ($1x10^3$/g dry soil)		
	Before harvest	After harvest	After treatments
Cut	5.53±1.36	43.50±10.44	10.73±5.8
Mixed	8.10±1.00	43.50±15.34	10.93±2.94
Screefed	7.35±1.6	53.20±7.44	9.99±2.04

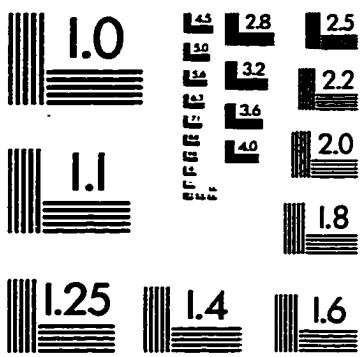
Appendix 2. Number of *Trichoderma* isolated from plots before and after clear cutting and after the various silvicultural treatments (M.T. Dumas, pers. com. 1995).

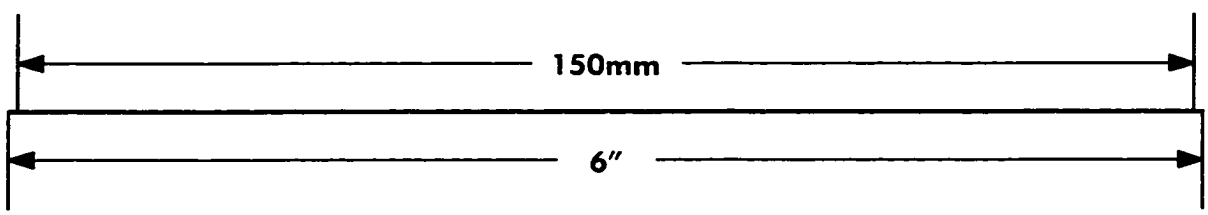
	Number of *Trichodermas sp.* (1x10/g dry soil)		
Treatment	Before harvest	After harvest	After treatments
Cut	20.9±2.47	1.45±0.45	2.15±0.23
Mixed	17.21±5.46	1.5±0.36	10.25±4.8
Screefed	16.45±4.9	1.6±0.5	3.53±0.37

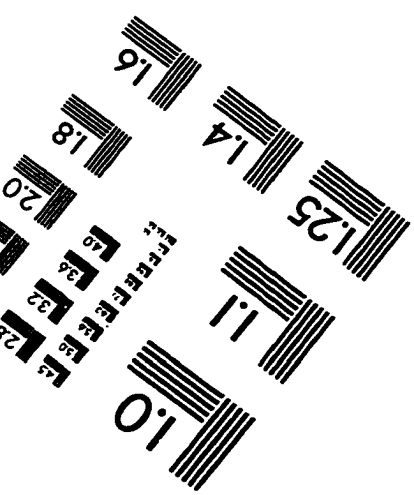
IMAGE EVALUATION
TEST TARGET (QA-3)

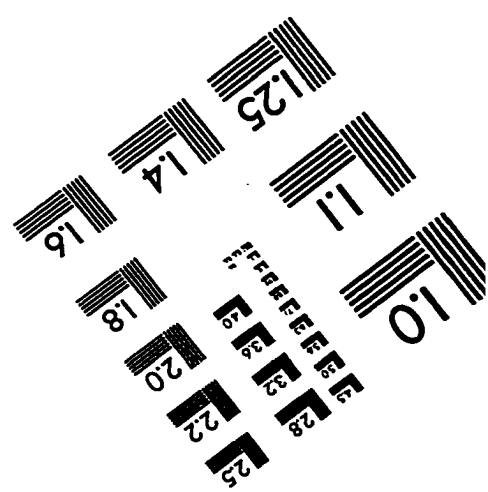












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