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LITTER FALL AND DECOMPOSITION
IN 40-YEAR-OLD RED PINE AND WHITE SPRUCE PLANTATIONS

By

Martina A. Sangari ©

A thesis presented to
the Lakehead University
in partial fulfillment of the requirements
for the degree of M.Sc.
in the Department of Biology

Thunder Bay, Ontario

January, 1993

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DECLARATION

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Martina A. Sangari

January, 1993

ABSTRACT

Litter dynamics of 40-year-old red pine and white spruce plantations, each species planted at three different spacing regimes, were examined during an eighteen-month period (May 1991 - October 1992). Litter decomposition was measured monthly throughout two growing seasons and once during the winter season. The amount and pattern of litter fall was also examined under similar time intervals. Near ground microenvironmental measurements, taken during the 1991 and 1992 growing seasons, were related to the rate of decomposition. Substrate quality (organic constituents) of red pine and white spruce litters and their decomposition rates were examined in a laboratory study. The rate of decomposition increased proportionately to the below ground temperatures and the ground relative humidity. Above ground temperature and soil moisture content did not appear to be related to decomposition. The rates of litter fall and decomposition increased as spacing decreased from wide to medium to close spacings in both red pine and white spruce. Analysis of variances showed that the effect of spacing was dominant in the decomposition process as also demonstrated with temperature, relative humidity, and soil moisture measurements. Species effects were significant in litter biomass and pH measurements. No significant interactive effects between species and spacing were found to be influential. Spacing trends observed on both species for high rates of litter fall and similarly, litter decomposition and accumulation, were close > medium > wide.

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1. GENERAL INTRODUCTION

Rates of plant litter fall and the subsequent decomposition are important factors in understanding forest site productivity. The continued plant litter deposition and decomposition is required to maintain the availability of nutrient elements essential to plants as well as to other living organisms in the soil. In most terrestrial ecosystems, this is a major pathway for material and energy transfer (Spurr and Barnes 1980). More than half of the carbon and energy annually established into the organic pool is contributed through litter fall which is, in many cases, mostly leaf fraction (Ovington 1961). In a Douglas-fir forest, about 80 to 90 % of the nutrient uptake is returned every year through leaf litter fall (Sollins et al. 1980). Furthermore, Waring & Schlesinger (1985) calculated that as much as 87 % of N and P released to the environment comes from the decomposition of plant litter. Therefore, compared to other ecological factors and processes such as precipitation and element fixation, the internal organic cycle releases substantially more essential nutrients to the soil (Aber and Melillo 1991, Hendrickson 1985, Weber 1987).

In a northern boreal environment litter decomposition is mainly a biochemical rather than a physical phenomenon (Persson 1980). Decomposition is performed by soil microorganisms that directly utilize organic matter as an energy source (Bunell et al. 1977, Flanagan and Van Cleve 1983, Heal et al.

1981). The metabolic rate of soil microorganisms depends largely on the environmental conditions. It is related directly to temperature and moisture, and indirectly to soil pH and aeration (Brady 1990, Moore 1986, Singh and Gupta 1977, Witkamp 1966). Temperature regulates the activity of the microbial decomposers; whereas aeration affects the presence of soil microbes.

The rate of decomposition also is affected by the quality of substrate, i.e., physical structure and chemical composition of litter. The resistant substrate of coniferous litter slows the decomposition process which is normally already restrained by low temperature and by the imbalance in annual moisture supply characteristic of boreal coniferous forests (Bonan and Shugart 1989). These phenomena retard growth and activity of major decomposers, slow organic degradation, and ultimately restrict nutrient availability in boreal forests (Bunnell 1981, Swift et al. 1979).

Slow decomposition leads to the conservation of inorganic elements incorporated in organic materials (Bonan and Van Cleve 1992, Olson 1963). The accumulation of organic matter in the forest floor may indicate low productivity of the soil (Bunnell 1981, Bray and Gorham 1964, Meentemeyer et al. 1982). In this case, the unbalanced rates correspond to organic input through litter fall and inorganic output through microbial decomposition. Thus, the dynamics of litter fall and decomposition can determine the nature of organic accumulation in the forest floor.

Rates of litter fall are documented for major forest types of the world, emphasizing certain trees and their environmental factors (e.g. Albrektson 1988, Bray and Gorham 1964, Facelli and Pickett 1991, Meentemeyer et al. 1982, Stohlgren 1988). The production of litter is affected by macroclimate as litter production is linearly related to plant productivity (Barbour et al. 1980). The annual variation of litter fall is thus influenced by annual fluctuations in the length of the growing season and by the distribution of rainfall. Furthermore, for similar climatic regions, factors such as species, spacing, and site quality become important in controlling the rate of litter fall (Rodin and Bazilevich 1969).

Litter accumulation and decomposition have been widely studied, but largely in natural forests. Plantation management has been considered as an alternative to future forest development. This is especially true under the growing conflict between demands for both timber production and nature conservation (Nambiar 1984, Reed 1991). Attempts to increase the commercial values of forests while sustaining the intangible ones have generated a "silvicultural revolution" in many parts of the world (Matthews et al. 1979, White and Waldram 1991). Treatments such as even-aged tree plantation, initial spacing, thinning, fertilization, and site preparation involving litter removal to stimulate germination have been widely applied to increase forest production as well as other desired outputs of forests (Bray and Gorham 1964, Hosick 1991, Sims et al. 1991). However, little work has been done to understand the relationship between litter fall and environmental variables relative to the organic matter dynamics in mature coniferous plantations. These relationships are of vital importance to the maintenance of site quality and productivity.

Within a forest plantation a variety of microenvironments may develop due to tree density, crown coverage, tree size, stand age, growth periodicity (i.e. evergreen or deciduous), amount of branching, and texture of the leaves (Barry and Chorley 1987). These differences in microenvironment can have direct effects on litter decomposition and nutrient release. Studies are still rare on the microenvironmental effects of different species planted at different spacings on forest floor microclimate, litter fall, litter decomposition, and organic accumulation in mature boreal plantations. The Thunder Bay Spacing Trial established four decades ago provided an excellent opportunity to conduct such a study.

Research objectives

The first objective was to study the relationships among litter fall, litter decomposition, and litter accumulation in 40-year-old red pine (Pinus resinosa Ait.) and white spruce (Picea glauca (Moench) A. Voss) stands planted at three different spacings. The second objective was to study litter decomposition and how it is related to near ground microenvironmental factors for different species and spacing combinations.

Research hypothesis

Litter fall and decomposition will vary depending on the species and spacing, and this will result in differential organic accumulations on the forest floor. The species and spacing combination will also create a certain microenvironment which, in turn, will influence the litter decomposition.

2. LITERATURE REVIEW

2.1. Plant litter

In recent years, efforts to measure the rate and composition of litter fall have been growing. Litter fall has been recognized as representing the essential link between organic production and decomposition and, thus, is a fundamental component in a forest ecosystem. Despite substantial nutrient reabsorption before leaf abscission, plant litter remains the dominant pathway for the return of nutrient elements to the soil (Barbour et al. 1980). As much as 87% of N and P released to the environment comes from the decomposition of plant litter (Waring and Schlesinger 1985).

The presence of litter on the forest floor may also have important indirect effects on microbial decomposition, by inducing changes in microenvironmental factors (Facelli and Pickett 1991). Litter contributes to the texture and water storage capacity of the soil and thus can lead to a significant improvement in soil aeration and drainage (Albrektson 1988). Alternatively, the presence of litter with certain chemical properties such as phenolic compounds can result in soil acidity levels that are unfavorable to microbial growth and activity (Bonan and Shugart 1989).

The annual litter fall of coniferous trees generally consists of 40-50 % green parts, 30-40 % perennial above ground parts, and 5-20 % root parts (Rodin and Bazilevich 1969). In northern forests, the fine coniferous litter fall mainly consists of a leaf fraction (60-90%), a limb fraction (9-35%), and a reproductive fraction (1-5%) (Bray and Gorham 1964, Rodin and Bazilevich 1969, Stohlgren 1988, Weber 1987). This leaf to total litter ratio is obviously higher than the ratios (less than 50 %) reported in humid tropical forests (Bray and Gorham 1964, Swift et al. 1979).

The needle fraction is the largest component of coniferous litter, and also is the most readily decomposable fraction due to the physical and chemical properties of needles (Millar 1974, also see Section 2.2). Perennial tissues may contain most of the nutrients stored in the forest biomass, but they also contain large concentrations of structural compounds such as cellulose and lignin. These compounds may shield the more soluble compounds and form organic complexes resistant to decomposition (Aber and Melillo 1991, Foster and Lang 1982). The accumulated elements in the perennial tissue can only explain the long-term nutrient requirements. It is the amount of nutrients in the leaves and also in the fine roots that forms a vital part of the annual nutrient cycle within a forest ecosystem, even though these nutrients comprise only a small portion of the total nutrient capital in the whole biomass (Aber and Melillo 1991). Sollins et al. (1980) calculated that about 80 to 90 % of the nutrient uptake is returned every year through leaf litterfall in Douglas-fir forests. Leaf tissue (through its growth, death, and replacement) is therefore often selected as a parameter indicating the annual nutrient circulation in the ecosystem (Flanagan and Van Cleve 1983, Waring and Schlesinger 1985).

The rate of litter fall varies annually, and a relatively high yearly fluctuation is normally found within seasonal forests. Generally, the ratio of the maximum to minimum annual litter production fluctuates between 1.5 to 3.0 (Bray and Gorham 1964, Millar 1974). Such annual variation is related to leaf, flower, and seed production. Annual litter production, therefore, is ultimately indicative of the variation in yearly productivity of individual plants (Barbour et al. 1980, Facelli and Pickett 1991). Factors that determine primary productivity such as the duration of growing season and evapotranspiration have similarly been found to determine litter production (Meentemeyer et al. 1982).

Hence, the main determinants of litter production macroclimatically are temperature, precipitation, and solar radiation. Factors such as species composition and soil fertility are accordingly important within the same climatic range. Furthermore, at local microclimates litter fall varies with the density and quality of the stand, and also with annual weather conditions (Rodin and Bazilevich 1969).

2.2. Decomposition in relation to litter quality

Litter fall gives an annual addition of organic matter to the forest floor, since it is within a year after abscission that litter becomes subject to the process of decomposition (Waring and Schlesinger 1985). In spite of the complexity of the process, the two most important controls to decomposition are litter susceptibility to microbial attack (i.e., substrate quality) and the prevailing climatic environment, in particular ground temperature and moisture supply (Flanagan and Van Cleve 1983, Heal et al. 1981, Meentemeyer 1978, Stohlgren 1988). The process of decomposition involves soil microorganisms and both physical and chemical mechanisms and results in the reduction of particle size, the transportation of water soluble material, and the transformation of complex organic carbon compounds to smaller and more simple molecules. These processes can either occur simultaneously or successively. The ultimate products of the organic transformation are gaseous carbon and water with the liberation of heat energy into the surrounding environment (Heal et al. 1981, Swift et al. 1979).

Leaching can be a significant aspect of the decomposition process (Nykvist 1961, Yavitt and Fahey 1986). However, in the boreal forest of North America the annual rainfall is relatively light (Bonan and Shugart 1989, Larsen 1980), the winter is characteristically dry, and more than half of the annual rainfall occurs in the summer (Anon. 1991b). Therefore, leaching is not considered to be a significant factor in northern boreal forests (Persson 1980). Similarly, another important part of the decomposition process, fragmentation and mixing, is fairly limited in the northern boreal coniferous environment. Mor humus is generally developed under such conditions (Pritchett and Fisher 1987) which does not encourage the activity of soil fauna. In fact, fauna from the Phyla Arthropoda and Annelida which have significant roles in fragmenting as well as mixing the litter material into the lower layer are adversely affected by dry and acid conditions (Brady 1990, Edwards 1974, Seastedt and Tate 1981, Seastedt et al. 1983). In addition, needle-like leaf anatomy (including the cuticular thickness and trichomes), the high lignin content, and the low macronutrient content work against herbivory. These leaf attributes are characteristic of evergreen conifers and allow conifer litter to last for a number of seasons (Millar 1974).

The fact that leaching and comminution (fragmentation) are fairly restricted in boreal and temperate conifers infers that organic transformation, or microbial catabolism, should have the greatest effect on decomposition processes (Flanagan and Van Cleve 1983, Persson 1980, Witkamp 1966, Yavitt and Fahey 1986).

Several methods have been introduced to measure the dynamics of the decomposition process, including the amount of weight loss, changes in chemical composition, and the release of gaseous and water-soluble materials from the organic matter. Of these parameters, total weight loss is most commonly found in the literature. As a parameter it combines all losses caused by leaching, comminution, and catabolism (Heal et al. 1981). The amount of weight loss, in many cases, is biased towards the weight of the major organic substrates which constitute the material (Swift et al. 1979).

2.2.1. The physical properties of coniferous leaf litter

Coniferous leaves vary from needle-like leaves (as in genus Pinus, Picea, and Abies) through the flattened small leaves (as in genus Cupressus, Thuja, and Chamaecyparis), to the simple angiosperm-like leaves (as in genus Podocarpus). The leaves are characterized by a thick waxy surface which makes them hydrophobic and thus less available to most microbes (Millar 1974). The size of the litter particle determines the ability of organisms to ingest food. It has been shown that feeding rates on fragmented leaves are considerably higher than those rates on intact leaves (Swift et al. 1979). This suggests that the increased surface area can be a stimulus to the microbial population present within the substrate.

The hardness of the substrate is mainly related to the type of organic chemical content of the litter. Since the penetration of plant cuticles by, for instance, fungal hyphae is largely a mechanical rather than an enzymatic process (Dickinson 1960), the toughness of the substrate should be regarded as an important component of litter quality indicating its susceptibility to microbial degradation. Heath and Arnold (1976) have shown that the thin soft leaves from shaded beech and oak are more readilly attacked by soil organisms and decompose more rapidly than the tough, heavily cuticularised leaves from the non-shaded trees of similar species. Soft leaves are high in ash contents, total nitrogen, and sugars, and low in cellulose, tannins, and lignin (King and Heath 1967).

2.2.2. The chemical properties of coniferous leaf litter

2.2.2.1. Organic chemical contents

The chemical composition of litter, both organically and inorganically, determines the availability of the material as food and media for decomposers (Aber and Melillo 1991). Decomposition occurs by the production of microbial enzymes which break the chemical bonds formed during the plant development.

To produce such enzymes, substantial amounts of energy and nutrients are needed for microbial growth and activity. In contrast to plants, microbes are particularly energy-limited (Foster et al. 1980, Flanagan and Van Cleve 1983). Microbial activity has been reported to increase through, primarily, the improved availability of energy-yielding substrates (Flanagan 1986, Moore 1981). In early decomposition stages microbial demand for energy-yielding substances are especially high regardless of the inorganic nutrient supply. In fact, an excessive supply of some inorganic nutrients, for instance potassium chloride (KCl), may suppress microbial activity as reported in the Alaskan taiga (Van Cleve and Yarie, 1986). In the case of nutrient limited substrate or environment, a sufficient addition of inorganic nutrients will increase microbial activity. It was found that in the poor quality substrate of spruce forest soils, addition of energy-yielding substrates, such as sugar compounds, was found to be more influential in stimulating microbial respiration than either moisture additions or temperature improvement from 10°C to 20°C (Flanagan 1986). In fact, the lower the substrate quality, the more potential there is for available nutrients to be released by "energizing" the microorganisms (Foster et al. 1980). It was observed that NO_3^- and PO_4^{3-} increased despite high increases in microbial biomass due to the addition of high energy-yielding substances such as sugar (Flanagan and Van Cleve 1983). As the microbial biomass continues to increase the gain in available nutrients decreases. However, the decrease would never reach a point significantly less than that contained in substrates as long as sufficient energy sources of litter exist to maintain microbial activity. Under such condition, microbial growth and activity need not absorb and immobilize available nutrient pools (Flanagan 1986, Waring and Schlesinger 1985).

The major organic components of coniferous litter are lipids, lignins, and celluloses (Bray and Gorham 1964, Millar 1974, Swift et al. 1979). Organic compounds of low molecular weight and structure such as simple sugars, starches, and simple proteins are generally the first fractions to be attacked (Flanagan and Bunnell 1976, Yavitt and Fahey 1986). These compounds contain the greatest source of energy and can also be taken directly into microbial cells and metabolized internally. Nutrient-rich compounds of crude proteins are second to be decomposed. These large molecules can become resistant to degradation due to the complexity of their three-dimensional structure (Gibson 1984). Moreover, proteins are often found to be condensed with tannins or lignin. The resulting complexes are even more resistant to decomposition, although they may contain energy-rich sub-units (Aber and Melillo 1982, Basaraba and Starley 1966, Fogel and Cromack 1977, McClaugherty et al. 1985). This is one of several negative effects that polyphenolic compounds can have on the process of organic decomposition.

The majority of plant litter consist of large polymers of celluloses and hemicelluloses. These polymers cannot be taken into microbial cells directly unless they have been cleaved into simple sugars by enzymatic activity. Hemicelluloses are slightly easier than cellulose to decompose, as they still contain several basic sugars. Cellulose compounds, which constitute the largest portion of most terrestrial plant litter (Allen et al. 1974), are the next to decompose (Aber and Melillo 1991).

The previously mentioned compounds are all carbon saturated; other carbon compounds which have a hydrogen group instead of a hydroxyl group are partially saturated. These hydrocarbons, known to be hydrophobic, are the next category to decompose (Gibson 1984, Swift et al. 1979). Lipids (including fats, waxes, oils, resins, and cutin) belong to this group. Some other plant compounds with fully unsaturated carbon bonds also have complex structures. Particularly important are phenolic compounds, such as tannins, and the large, amorphous compounds categorized as lignin. Since large amounts of energy and nutrients are required for the decomposers to break the phenolic rings and side chains, these compounds are considered to be the slowest substrate fraction to decompose. Additions of high-quality organic or inorganic substances (such as sugars, N, and P) have been reported to increase the weight loss rate of the lignin fraction (Aber et al. 1991, Kelly and Henderson 1978, Salonius 1972, Van Cleve and Moore 1978). As the decomposition proceeds, more lignin would normally be produced as byproducts. The presence of "new lignin" causes an increase of its relative proportion as the decomposition rate declines (Fox and Van Cleve 1983, McClaugherty et al. 1985).

After approximately a decade, litter accumulation rates will be determined primarily by these repolymerized polyphenols (Berg et al. 1982, Minderman

1968). There also tends to be an inverse relationship between amounts of soluble carbohydrate and protein as one grouping, and lignin and cellulose as the second grouping (Aber and Melillo 1980, Berg et al. 1982, 1984, Heal et al. 1981, Melillo et al. 1982). The rate of decomposition is, therefore, inversely related to the concentration of lignin (Fogel and Cromack 1977, Meentemeyer 1978). For the reasons above, lignin content has typically been used as a major control to determine the rates of decomposition produced by different litter materials.

2.2.2.2. Inorganic chemical contents

The microbial decomposition is not only influenced by the availability of energy obtained from carbon materials, but also by the availability of nutrient elements obtained from the degraded substances (Aber and Melillo 1991, Swift et al. 1979). The nutrient to energy ratio of a substrate determines the rate of organic decomposition and, in turn, the release of nutrient elements to the soil environment (Berg & McClaugherty 1989). In many cases, nutrient-rich litter tends to decompose faster than nutrient-poor litter within a given environment (Fogel and Cromack 1977, Hunt 1988). It is found that the rate of decomposition is negatively correlated with increasing C/N and C/P ratios; but positively and linearly correlated with concentrations of K, Ca, N, and P (Berg and Staaf 1980, Flanagan and Van Cleve 1983, Swift et al. 1979). Melillo et al. (1982) also concluded that as the litter decomposition rate declined, the C/N and C/P ratios narrowed, and lignin concentrations increased.

If the nutrient requirements of microbial growth and activity are not met, as in slow-decomposing boreal forests, a removal of available nutrients from the soil solution may occur (Brady 1990, Waring and Schlesinger 1985). This may lead to nutrient competition between decomposers and other soil microbes eventually resulting in reduced soil productivity. In the case of a nutrient shortage within the litter itself, an increased concentration of inhibitory compounds such as lignin and tannins likely will develop (Rice 1979). Similarly, litter that has high concentrations of cell wall materials (including lignin and cellulose) is often found to be low in nutrient concentration (Del Moral 1972). The rate of decomposition can be influenced not only by the presence and proportion of organic compounds within the litter, but also through those of inorganic nutrient elements.

2.3. Decomposition in relation to environmental factors

The quality of litter has been shown to affect microbial activity necessary for decomposition. Yet, the overall process of decomposition can only be expected if the surrounding environment is favourable. Particularly important is the balance between heat and water operating in microbial metabolism (Flanagan and Bunnell 1974, Moore 1986, Van Cleve and Yarie 1986, Witkamp 1966). Several studies conducted in boreal forests have concluded that no microbial activity occurs until the temperature and moisture interaction exceeds a minimum threshold, regardless of the chemical composition of the litter (Bonan and Van Cleve 1992, Moore 1981, Van Cleve and Yarie 1986). It has also been found that the microbial community in the boreal ecosystem, unlike the trees, is not significantly limited by the supply of nutrients. Instead, it is more likely dictated by the energy provided both by organic quality of substrates and by the heat and water supply required by the microbial community to survive and metabolize (Flanagan and Van Cleve 1983).

The complex interaction between the factors of temperature and moisture contributes to a highly significant effect on the rate of microbial respiration in comparison with the effects found for the individual factors alone (Bunnel et al. 1977, Flanagan and Bunnel 1974, Jenny et al. 1949, Moore 1986, Witkamp 1966, Witkamp and Van der Drift 1961). This interaction is reported to account for as high as 90 % of the variation occuring in the rates of decomposition among subarctic tree species (Heal et al. 1981).

The fact that most forests grow in mesic regions ensures that temperature will be the principal factor controlling microbial activity. However, when precipitation is not evenly distributed throughout the year, soil moisture can instead be the limiting factor (Schlesinger and Hasey 1981, Waring and Franklin 1979). In Finland, when the rainfall is evenly distributed throughout the year, temperature has been reported to be the most important factor in regulating plant litter decomposition rate (Mikola 1960). Whereas in the Pacific Northwest of the

United States, when the summer is considerably dry, moisture becomes the most limiting factor affecting the decomposition of plant litter (Edmonds 1979, 1984, Fogel and Cromack 1977).

Temperature directly affects microbial respiration and thus growth and activitiy. This is mainly due to the fact that microbial metabolisms are enzymatic and therefore temperature-dependent processes. Microbial metabolisms have been shown to increase exponentially with increasing temperatures (Edwards 1975). This relation often shows a Q_{10} value of two in a northern environment, i.e., a doubling microbial activity is shown for every 10^0C increase in temperature (Moore 1981, Singh and Gupta 1977, Swift et al. 1979). Moisture affects the oxygen available to the microbial community. This mechanism involves the blocking action of water films on the pores of soil particles and substrates (Bunnell et al. 1977). Hence, to a certain extent, moisture levels may determine the abundance and composition of the microbial community. Microbes need moisture for their activity (Swift et al. 1979), and it is normally obtained either from the soil solution or the decomposing substrates (Nagy and Macauley 1982). Therefore, their activity may continue even after the water potential of the soil has become limited (Waring and Schlesinger 1985). As with temperature, microbial response to soil moisture is normally parabolic. When soils are moisture saturated, aerobic respiration becomes negligible (Schlesinger 1978). Under such condition, decomposition becomes inhibited, and in the extreme case, peat accumulation can occur (Reiners and Reiners 1970). In the subarctic peat soils, for example, prolonged freezing is accompanied by low quality of both nutrient and energy sources of plant litter, a relatively acidic medium of forest floor, and low populations of mesofauna, in particular arthropods and annelids (Bonan and Shugart 1989, Larsen 1980, Moore 1981).

Besides the climatic factors, the process of decomposition is affected indirectly by edaphic factors. Soil aeration regulates moisture, oxygen, and carbon dioxide supplies within the soil which, in turn, determine the presence and activity of microorganisms (Brady 1990, Pritchett and Fisher 1987). In poorly drained soils, CO_2 may build up and affect the microbial respiration. As the result, anaerobic microbes will replace the existing organisms and bring about changes in earlier soil interactions (Swift 1976).

The majority of aerobic decomposers consist of bacteria, fungi, and actinomycetes. These organisms are mainly found in the upper layer of the soil (Steubing 1973). The presence of this community in the soil is often dictated by the quality of plant litter (Brady 1990, Stohlgren 1988). The influence of litter quality is also demonstrated, in many cases, by the range of soil pH (Flanagan and Van Cleve 1983, Swift et al. 1979). Within a given range, soil pH affects the process of decomposition by limiting the microorganisms present. Bacteria and actinomycetes are most active at medium to high pH values. At low pH, these microorganisms are generally replaced by fungi which can remain active within a wide range of pH values (Brady 1990, Steubing 1973, Witkamp 1966).

The release of high quality inorganic decomposition products is greatly enhanced by the presence of bacteria over other groups of microorganisms. Through the enzymatic transformations performed by bacteria, both elemental reduction and oxidation (e.g. nitrification) are made possible. Consequently, the availability of nutrient elements such as nitrogen, sulphur, iron, and manganese is increased (Brady 1990). The importance of bacteria is also evident in nitrogen fixation where higher amounts of nitrogen are fixed in less acid soils. The amount produced through such fixation is normally higher than that absorbed by mycorrhizal fungi (Dowding 1976, Witkamp and Ausmus 1976). Fungi, however, are capable of continually breaking down the complex organic materials after bacteria and actinomycetes have ceased to function in extremely acid conditions. Therefore, fungi can include the largest portion of decomposing plant litter into their body tissues. This value can be up to 50 %, as compared to about 20 % for bacteria (Brady 1990). Actinomycetes also have a significant role in breaking down the resistant compounds such as cellulose and lignin, especially under medium pH values (Steubing 1973, Swift 1976).

Soil pH values are often species-specific since it is mainly determined by the nature of decomposing organic material contributed by the species (Swift et al. 1979, Van Cleve and Yarie 1986). In general, coniferous litter has a lower pH value than deciduous litter, and this is partly a result of lower Ca^{++} concentrations in coniferous leaf litter (Alban 1982, Flanagan and Van Cleve 1983, Millar 1974, Rodin and Bazilevich 1969). Moreover, coniferous leaf litter is higher in lignin content and lower in macronutrients. This may lead to the lower decomposition rate, larger accumulation and, in turn, lower soil pH values (Flanagan and Cleve 1983, Jenny et al. 1949).

2.4. Organic dynamics of the forest floor

As litter undergoes periods of weight loss and nutrient mineralization through the process of decomposition, it is likely that neither process will proceed to a completion (Aber and Melillo 1991, Tiessen et al. 1984). When litter reaches the stage of a very slow weight loss, a biochemical synthesis (anabolism) begins to replace the process of decomposition (catabolism). This process involves polymerization or even repolymerization of lignoprotein complexes (Minderman 1968). This process may result in a continuing organic accumulation on the forest floor (Anderson 1979, Brady 1990). Such organic complexes are normally resistant to microbial attack in spite of their high content of N in the form of amino ($-NH_2$) groups (Flaig et al. 1975).

This accumulation of organic matter is the function of the annual amount of litter fall minus the annual rate of decomposition. It was stated that as the production of litter was uniform among tree species growing under similar soil and climatic conditions, the amount deposited onto the forest floor was differentiated by spacing and species (Rodin and Bazilevich 1969). The rate of litter decomposition, on the other hand, is determined not only by the chemical composition and physical structure of the litter but also by the microenvironment.

These two factors, species and microenvironment, will therefore determine the amount and quality of the organic horizon formed along with actual soil development (Heal et al. 1981, Minderman 1968, Moore 1981).

The accumulation of organic matter occurs as a byproduct of decomposition. Present initially as monomers, organic matter is enzymatically united into polymers. The formation of polymers is encouraged by the presence of colloidal clays (Brady 1990). In peatlands, the accumulation may continue for thousands of years; however, in most terrestrial ecosystems this will eventually achieve an apparent steady-state level which is characteristic of the climatic conditions (Jenny et al. 1949, Olson 1963, Waring and Schlesinger 1985). In this case, organic storage represents a stable pool of organic carbons and nutrient elements. This pool not only acts as a buffer to the effects of natural and human disturbance on the forest ecosystem, but also as a major resource of cation-exchange sites for ions in the soil solution (Pritchett and Fisher 1987, Waring and Schlesinger 1985). This phenomenon is particularly important in the northern environment where the decomposition process is slow, and also where the loss of some elements to the surface or ground water is made possible by snow conversion (Spurr and Barnes 1980). On the other hand, losses of organic carbon to surface or ground water are lowest since the carbon input from litter approaches a balance with the carbon output through microbial respiration or mineralization (Edwards and Harris 1977).

Often the rate of decomposition is measured by the amount of CO_2 evolution from soil. However, measuring CO_2 evolution to indicate decomposition rate on the forest floor would be erroneous, since microbial respiration may be intermixed with the respiration of plant roots (Sing and Gupta 1977). Alternatively, a mass-balance approach is often selected to predict the rate of annual decomposition. Under the organic matter equilibrium, this rate should equal the annual input of fresh litter (Minderman 1968, Olson 1963, Lang and Forman 1978). In this case, if the annual decomposition is a fraction, **k**, of forest floor mass, then at the steady state:

$$\textbf{litter mass} = \textbf{k (forest floor mass)}$$

$$\text{or} \qquad \mathbf{k} = \frac{\mathbf{lf}}{\mathbf{ff}} \qquad (1)$$

(Where lf represents the annual litter fall, and ff represents the forest floor mass).

There are again some limitations in the use of the mass-balance approach. For instance, the possible nonuniform distribution of forest floor mass following the litter fall, and also the changing proportion of litter fraction with time relative to decomposition rate (Welbourn et al. 1981). With the mass-balance approach, an over- or underestimation can occur. The litterbag approach becomes the remaining alternative to calculate k (Berg and Agren 1984, Singh and Gupta 1977). Under this method, fresh litter is confined in mesh bags, placed on the forest floor, and collected at periodic intervals for measurements. The decomposition constant (k) for litter confined in mesh bags is formulated by Jenny et al. (1949) and Olson (1963) as follows:

$$e^{-kt} = \frac{x_t}{x_0} \qquad (2)$$

where:

x_t = weight of litter inside the bag after t time
x_0 = initial weight of litter inside the bag
e = exponential function
k = decomposition constant
t = time span from x_0 to x_t (yr)

In this equation, the process of decomposition is assumed to be constant; and the assumption may not be completely valid, since the rate of decomposition might change with time (Wieder and Lang 1982). However, the exponential nature of decomposition factor provides a statistically useful method both during the early stages of litter decomposition and in comparing different litter materials (Aber and Melillo 1991, Berg and Agren 1984, Waring and Schlesinger 1985). Therefore, it has been the method most frequently used in decomposition research.

In comparison, the k values of forest litter are reported as **0.001** for boreal peatlands, **0.03** for boreal tundra, **0.13** for boreal coniferous forest, **0.50** for temperate deciduous forest, **1.50** for temperate grassland, **3.00** for tropical savannah, and **5.00** for tropical rainforest (Olson 1963, Swift et al. 1979). For wood decomposition, the values range from **-0.006** to **-0.506** between northern coniferous and tropical forests respectively (Foster and Lang 1982). And for tree decomposition, the values are **0.063** for pine forests in Minnesota pine forests

(Olson 1963); and **0.009** for lodgepole pine (Pinus contorta) at 3,000 m altitude in California (Jenny et al. 1949).

Because such a small fraction of annual litter production is being decomposed annually, the steady state of organic accumulation (i.e. the asymptotic level of accumulation rate) can be reached within a certain time (Minderman 1968). Particularly for coniferous forests, this equilibrium, signified by maximum net primary production, is reached between 30-80 years (Rodin and Bazilevich 1969). Ovington and Pearsall (1956) found that this stage is reached approximately at an age of 30 years for pines and 40 years for spruces. With decreasing site quality, these ages can be more advanced (Barbour et al. 1980). As the decomposition rate proceeds exponentially (eq. 2), the time parameter 3/k (i.e., -ln 0.05/k) is used to calculate values for 95 % of the steady state organic accumulation, or 5 % decomposed organic matter.

Considering the previous comparison of k values for various ecosystems in the world, it can be generalized that organic accumulation in the forest floor increases as tropical < temperate < boreal forests. Mor forest floors, performed by a great organic accumulation (Gessel and Balci 1965), often develop in cold-temperate coniferous forests where the decomposition is typically slow (Larsen 1980). Here high concentrations of phenolic substances and lignin complexes in the litter generate numerous acid residues in the surrounding soil (Waring and Schlesinger 1985). Under such acidic conditions, fungi predominate over bacteria and soil mesofauna (Gessel and Balci 1965, Seastedt and Tate 1981, Steubing

1973). Fragmentation and mixing becomes limited, and the organic soil is easily distinguished from the underlying mineral soil which usually consists of podzols or spodosols (Pritchett and Fisher 1987).

Mulls, on the other hand, are typically found under warm temperate deciduous forests. With chacteristics opposite to those of mors, organic decomposition is found to be more rapid in this type of soil. Under the generally more favorable pH condition, bacteria play a significant role in nutrient-releasing processes such as nitrification as well as elemental oxidation and reduction. Moreover, the abundant population of mesofauna in mulls allows a substantial amount of litter fragmentation and mixing to take place, resulting in obscure boundaries between soil horizons (Brady 1990, Pritchett and Fisher 1987). In addition, litter fragmentation and mixing produce an increased surface area for microbial attack. This also facilitates the moving of fragmented litter to the relatively more constant environment of a lower profile (Murphy 1955). Compared to mor soils, mull soils are reported to contain six times as much soil organism biomass (Witkamp and Ausmus 1976).

3. THE STUDY SITE

This study was conducted in the Thunder Bay Spacing Trial, near the Thunder Bay Forest Nursery. The exact location of this 82 ha study site is in Lot 1 of Concession II Paipoonge township, 20 km west of Thunder Bay. The climate of the area is characterized by a mean annual precipitation of 71 cm including an average rainfall of 53 cm. The mean annual temperature is 2.3 ^{0}C, with a generally mild summer season of 15 ^{0}C and a cold winter season of -8 ^{0}C (Anon. 1991b). The relative humidity is moderate to high (i.e., 52 to 95 %). The mean annual length of growing season in the area is approximately 170 days lasting from April 30 to October 18 (Chapman and Thomas, 1968). Under this Climatic Zone, this area is considered to be a boreal region (Bonan & Shugart 1989). Average climatological data from the previous ten growing seasons (1982-1991) as well as the daily temperature, rainfall, and relative humidity readings during two growing seasons (1991 and 1992) are presented in Figures 2, 3, 4, and 5.

The soil was formed on a glaciolacustrine plain (glacial lake bottom) with a relatively flat landscape and uniform physical characteristics (Towill and Siczkar 1988). The soil profile of the plantation (based on a preliminary study) indicated that the organic horizon ranged from 5 to 10 cm in depth (Table 1). At depths greater than 1.6 m, intermittent lenses of very fine sandy loam frequently occur. Soil structure was moderate to weak according to the standard soil manual (Anon. 1985). Soil texture was loamy sand, with higher amounts of sand at deeper layers.

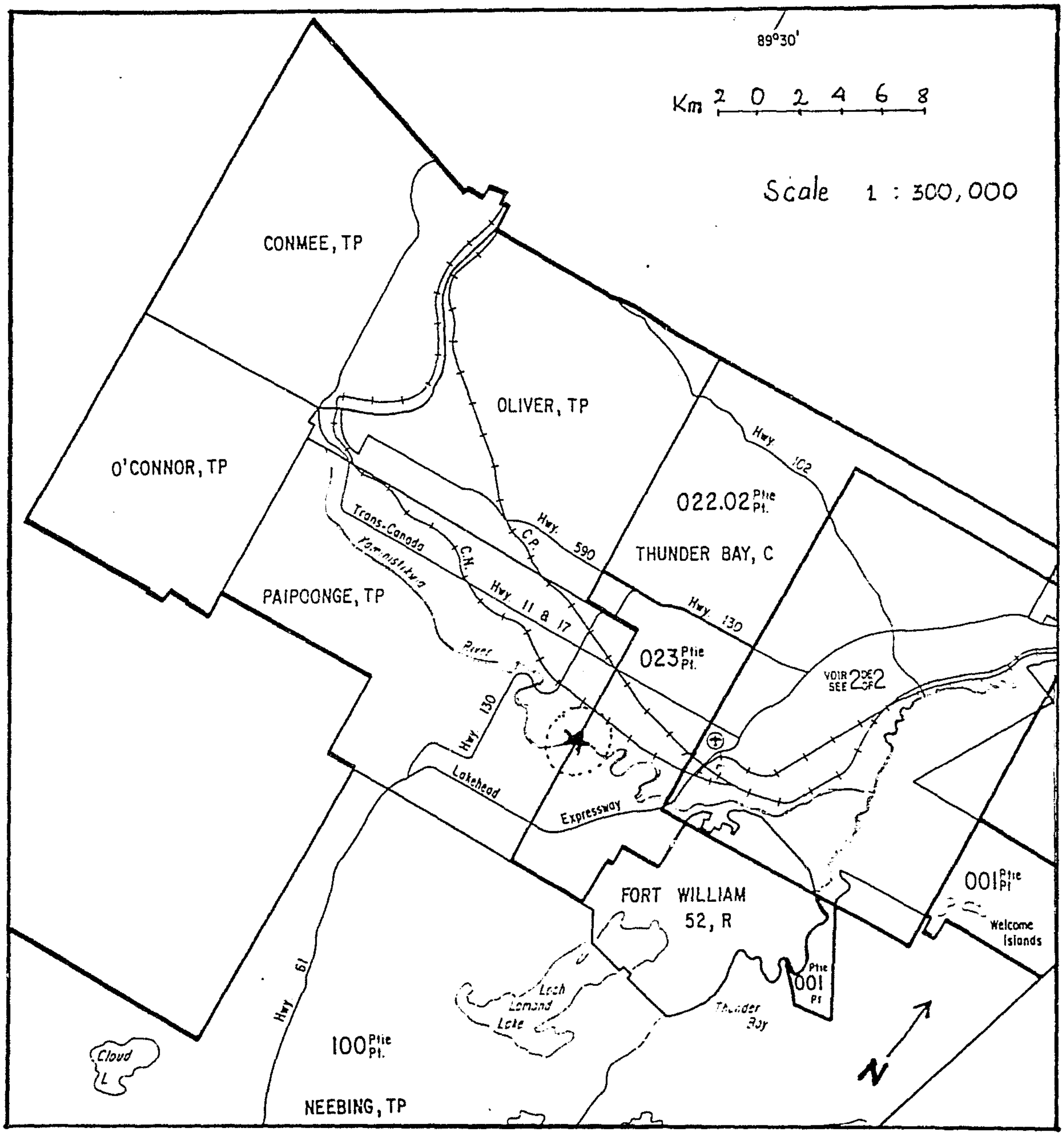

Fig 1. The location of the Thunder Bay Spacing Trial

The soil consistency was relatively loose, resulting in moderate to rapid drainage and fresh soil moisture regime. The forest floor was considered to be raw moder in which litter (L) and fermentation (F) layers were fairly distinctive from the very thin humus (H) layer. The site quality ranged from site class 1 and site index 21 for red pine to site class 2 and site index 18 for white spruce (Anon. 1991a).

The surface mineral soil was formed by a plowed, accumulated organic soil horizon, or **Ap**. This is underlain by an amorphous and hydrolyzed soil horizon, or **Bf** and a hydrolyzed, oxidated, and soluted soil horizon, or **Bm**. Next is a transition zone of B and C soil horizons, or **BC**, and finally the **C** soil horizon unaffected by the pedogenic processes operative in the A and B horizons. The characteristics of each horizon is described in Table 1 (preliminary study).

Table 1. Soil profile description of the study site (based on the standard soil mannual, Anon. 1985).

Horizon	Depth (cm)	Texture	Structure	Consistency	Root abundance
L, Moss	>0 to 10				abundant
Ap	<0 to -9	loamy sand	medium	friable	plentiful
Bf	-9 to -30	loamy sand	medium	loose	plentiful
Bm	-30 to -42	sand	medium	loose	few
BC	-42 to -70	sand	medium	loose	very few
C	< -70	sand	medium	loose	none

Four conifers, black spruce (Picea mariana (Mill.) B.S.P.), white spruce (P. glauca (Moench) Voss), red pine (Pinus resinosa Ait.), and white pine (P. strobus L.) were planted separately in three different spacing regimes in permanent rectangular plots each with three replications (Fig. 6). The spacings established in the plantation were:

- close spacing (1.8x1.8 m: 2,900 trees/ha);
- medium spacing (2.7x2.7 m: 1,300 trees/ha);
- wide spacing (3.6x3.6 m: 730 trees/ha).

The plantations were established in 1951 on previously briefly cultivated land, and have been maintained under the Provincial Forest Management guidelines. As a spacing trial of four major conifers in Northwestern Ontario, the site was planted to obtain information on how various spacings can affect the aboveground biomass. Silvicultural treatments such as fertilization, thinning, weeding, and pruning have never been applied to this plantation. This relatively undisturbed condition of the plantation has provided a good opportunity to study the dynamics of the soil organic matter; in particular, the addition, accumulation, and turnover of organic matter developed by different species and spacings.

The trees were measured in 1967, 1976, 1983, and 1988 to determine their growth responses to different spacings over time (Anon. 1991a). In 1988 a self-guiding trail was established to allow public access. From the trail, one can view the individual species performance for different spacings. At wider spacings, trees have more foliage and support larger crowns in terms of length and width. However, for all species, the canopy overlap from trees planted at closer spacings is generally larger than that of trees planted at wider spacings (Anon. 1991a). Therefore, despite the larger canopy at wide spacing sites, light penetration was greater at wider spacings.

The present study will focus on the red pine and white spruce plantations. These parts of the plantation were selected because both species have statistically equal replications per treatment (i.e., species and spacing combinations). In 1965 all white pines were removed following the attacks from white pine weevil (Pissodes strobi Peck) and white pine blister rust (Cronartium ribicola Fisch. ex Rabh.). In addition, black spruce from two replication plots in the close spacing treatment have failed to grow (Fig. 6).

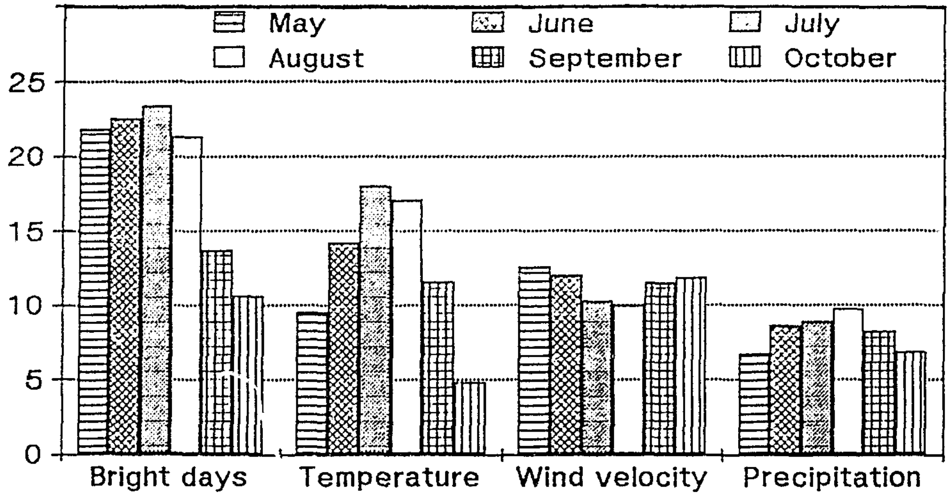

Fig 2. Monthly values on mean bright sunshine days (day), mean temperature (^{0}C), mean wind velocity (km/h), and total precipitation (cm) in Thunder Bay area for the previous ten growing seasons (after: Environment Canada, Thunder Bay).

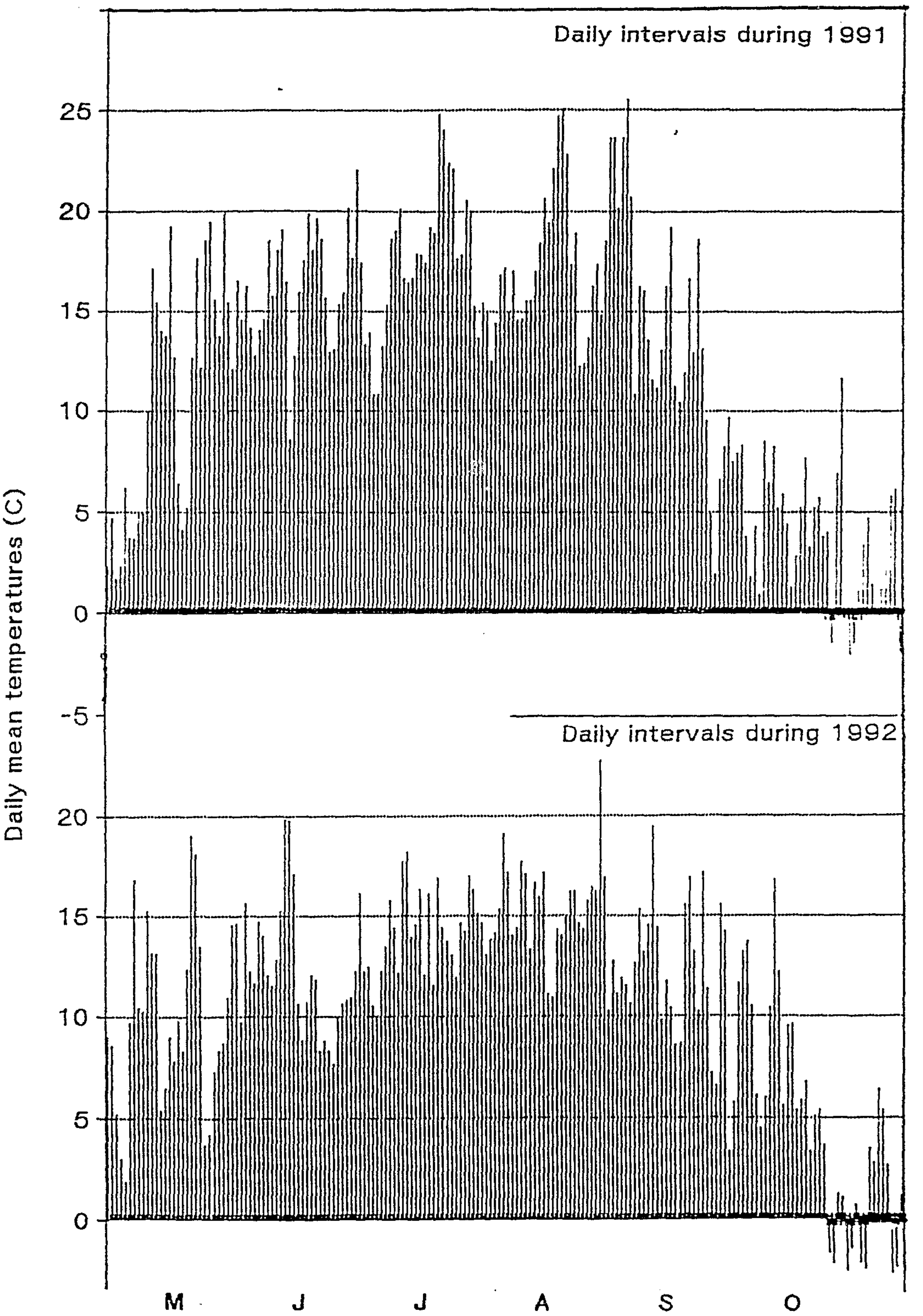

Fig 3. Daily mean temperatures in Thunder Bay area during 1991 and 1992 (after: Environment Canada, Thunder Bay).

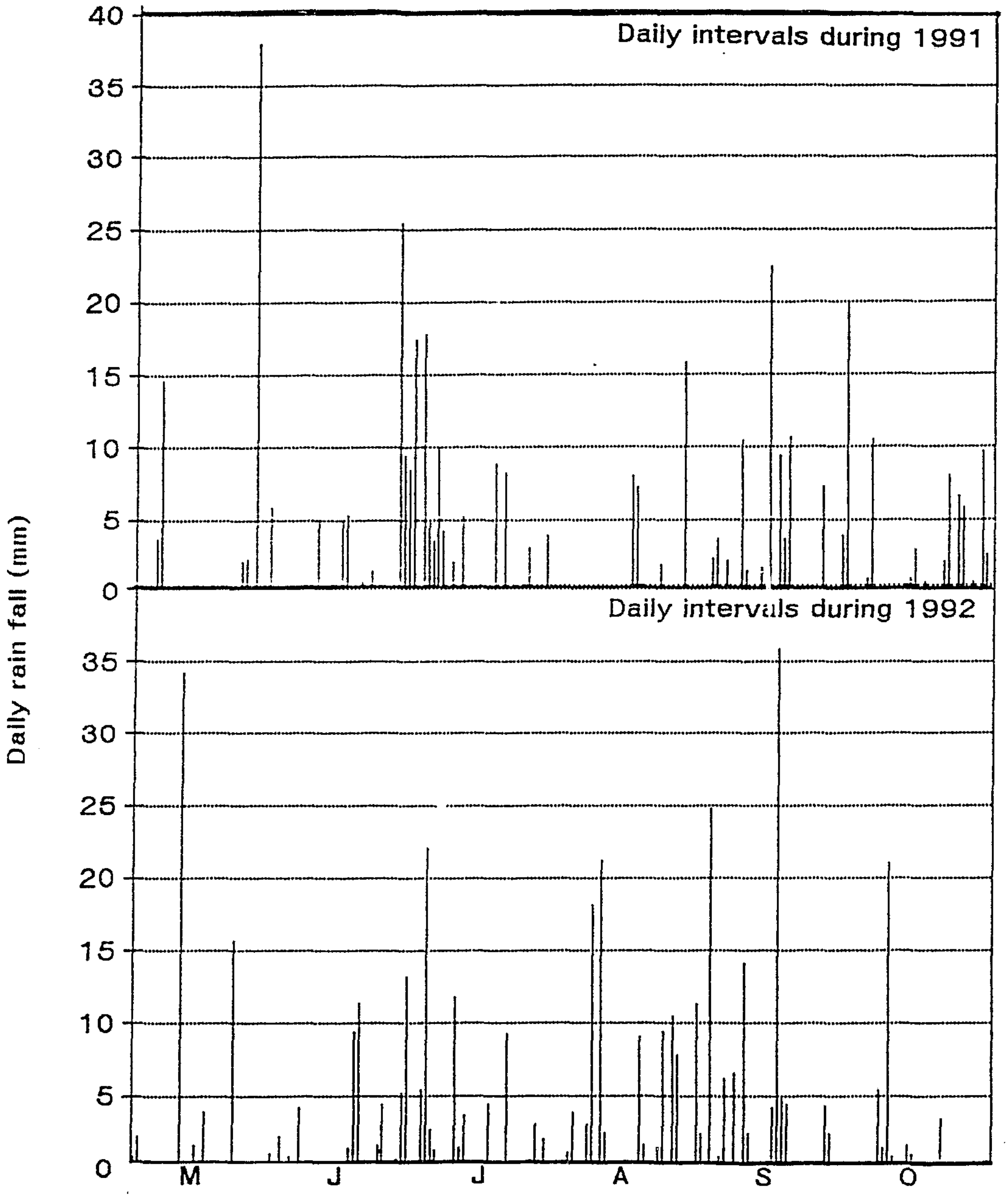

Fig 4. Daily rainfall in Thunder Bay area during growing seasons 1991 and 1992 (after: Environment Canada, Thunder Bay)

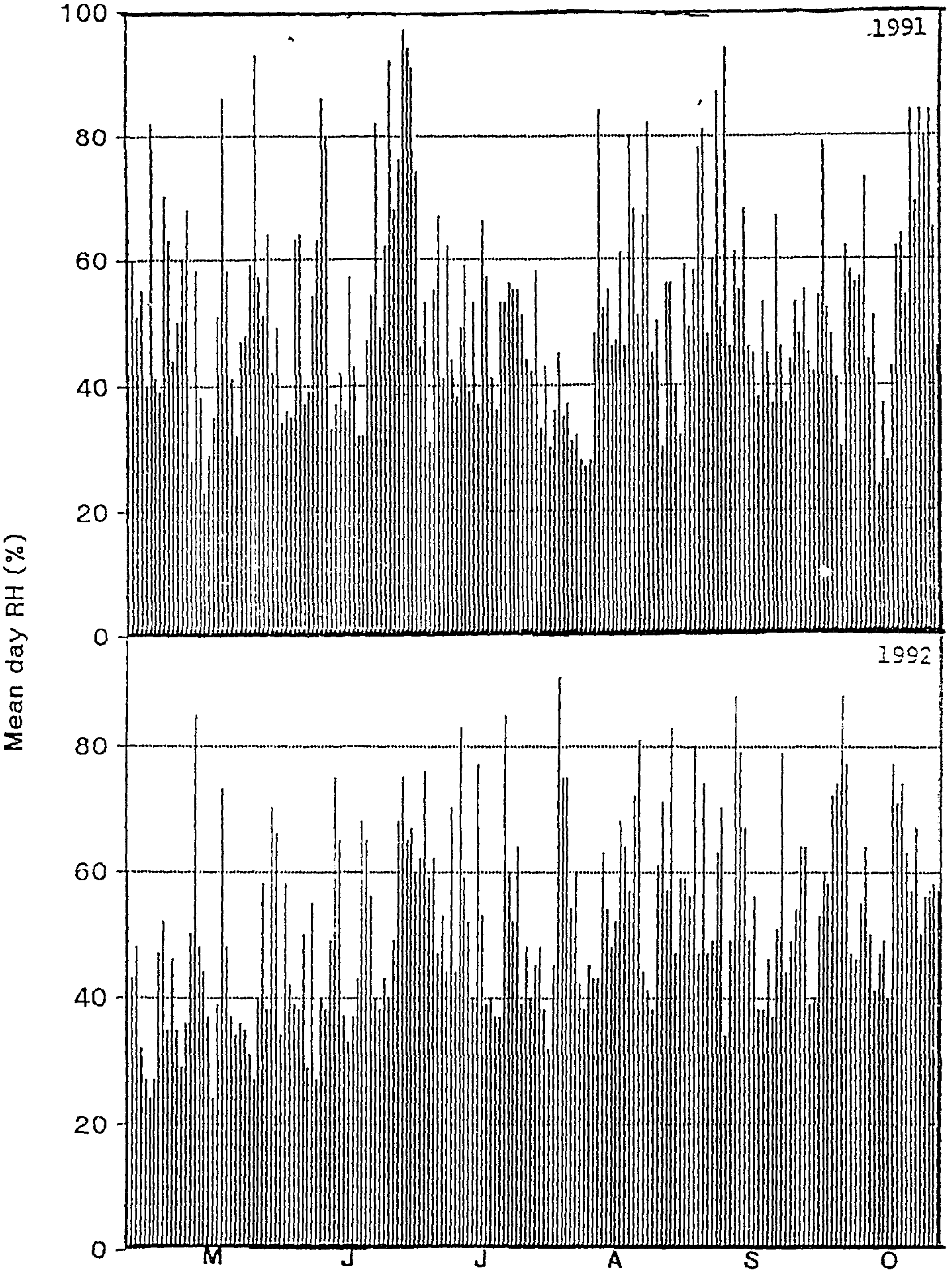

Fig 5. Daily relative humidities in Thunder Bay area during growing seasons 1991 and 1992 (after: Environment Canada, Thunder Bay).

Tree spacings

Medium (2.7m)			Wide (3.6m)			Close (1.8m)	
Px	Sw		Sw	Px		Sx	Sb
Px	Px		Px	Sb		Sw	Sw
Sw	Pr		Sw	Sb		Pr	Sx
Pr	Sb		Px	Pr		Px	Px
Sb	Sw		Sb	Sw		Px	Pr
Sb	Pr		Pr	Pr		Pr	Sw

Fig 6. Layout of the Thunder Bay Spacing Trial where **Pr**, **Sw**, **Sb**, **Px**, and **Sx** indicate red pine, white spruce, black spruce, failed white pine, and failed black spruce respectively.

4. METHODS

The study was made from May 1991 to October 1992 and thus covered two growing seasons and one winter season. The field study included measurements of microenvironmental parameters (temperature, relative humidity, soil moisture, and pH), litter fall, litter weight loss, and organic accumulation. Litter organic constituents and the effect of various temperatures on litter weight loss were studied in laboratory. For litter weight loss measurements and organic component analysis, plant litter was represented by the needle fraction which is reported to be the highest component (60-90 %) of coniferous litter in northern environments (Bray and Gorham 1964, Rodin and Bazilevich 1969, Stohlgren 1988).

4.1. Microenvironmental measurements

4.1.1. Near ground temperature

During the two growing seasons, weekly readings of temperatures were taken at heights of 100 cm, 10 cm, 0 cm, -2 cm (in the litter layer), and -10 (in the soil layer) at each species and spacing regime (referred to hereafter as a species-spacing treatment). All the readings were taken between 11 a.m. and 2 p.m. so the temperature fluctuations would be relatively minimal. Surface, litter layer, and soil layer temperatures were measured using copper-constantan thermocouples connected to a multi-input thermometer model 08500-40 completed with a probe switch box (Cole-Parmer Inst. Co.). A wooden template with three holes to hold the thermocouples at desired depths was fixed into the ground on each measurement site. Readings at 100 cm and 10 cm were taken using the Tri-sense meter model 37000-00 (Cole-Parmer Instr. Co.) by holding the probe at the stated heights above ground. Since the temperature fluctuation was higher above the ground, 10 readings were taken per species-spacing treatment plot whereas 3 readings were taken per treatment plot for below ground temperatures.

4.1.2. Relative humidity

Weekly readings of relative humidity were conducted during the two growing seasons. Three different readings, i.e. 100 cm, 10 cm, and 0 cm above the surface, were taken for each species-spacing treatment with 9 replications. All readings were again taken between 11 a.m. and 2 p.m. The relative humidity was measured using the Tri-sense meter model 37000-00 (Cole-Parmer Instr. Co.) connected with a relative humidity probe which during the measurement was held at appropriate heights.

4.1.3. Soil moisture

During the two growing seasons, monthly measurements of moisture content of the surface soil were conducted gravimetrically following the method described by Wilde (1972). Nine soil cores were collected at random from each species-spacing treatment plot, weighed, labelled, placed in paper bags, and brought back to the laboratory. In the laboratory the samples were oven-dried at 110 ^{0}C for 24-48 h to a constant mass. The samples were then placed directly into a dessicator to cool before taking the dry weights. The moisture content was calculated as follows (Carmean and Vanson 1982):

$$\text{Percent soil moisture} = \frac{\text{moist soil weight - dry soil weight}}{\text{dry soil weight}} \times 100$$

4.1.4. Soil pH

Soil acidity was measured as the active pH value indicating the concentration of H^+ within the soil solution (Brady 1990). Using the same samples collected for soil moisture analysis, soil pH was determined monthly during the two growing seasons. Following the method described by Carmean & Vanson (1982), active acidity of each dried soil sample was determined in distilled water with the ratio of soil to water at 1:2.5. The solution pH was measured with a Fisher Accument Model 805 pH Meter, using a combination glass electrode.

4.2. Litter fall

Thirty-six litter traps (2 species x 3 spacings x 3 replicates x 2 traps/replicate) were placed throughout the plantation. Within each plot of a given species and spacing treatment, two 1x1 m litter traps were placed on the forest floor to capture litter (needles, fruits, and twigs <2.5 cm in diameter) of red pine and white spruce. During 18 months of the field study, litter trap contents were emptied monthly during the two growing seasons (May to October), and once for winter litter accumulation (i.e. November 1991 to April 1992).

Once collected, the litter samples were sorted by tissue type (needle, twig, and reproductive components) and then labelled for each species-spacing treatment. All samples, separated by components, were oven-dried at 65 ^{0}C to a constant mass (Bockheim and Leide 1986, Flanagan and Van Cleve 1983, Weber 1987), and weighed to the nearest 0.01 g. Thus monthly and seasonal amounts of litterfall were obtained for each species-spacing treatment.

4.3. Litter decomposition

The weight loss rate of red pine and white spruce needle litter in each spacing regime was determined using the (1-mm mesh) decomposition bags (Fogel and Cromack 1977). This technique underestimates the true value of decomposition, since it prevents the access of larger soil fauna (Wieder and Lang 1982). However, it has been useful in minimizing the loss of litter particles into the soil environemnt (Crossley and Hoglund 1962) and it has been the method most frequently cited in the literature. Furthermore, the mesofauna community present in boreal conifers does not seem to have a significant effect on the process of decomposition (Persson, 1980).

A total of 468 (2 species x 3 spacings x 3 replicates x 2 bags/replicate x 13 collection times) decomposition bags were randomly placed underneath the fresh litter layer throughout the plantation. Fresh fallen needles from each species-spacing treatment were collected, air-dried for 24 h and labelled. A subsample of 15 g from each species-spacing treatment, each with five replications, was oven-dried at 50 ^{0}C for 48 hours (to a constant mass) in order to obtain the initial weight of litter. The results provided the initial values for litter subsequently collected from the decomposition bags.

Other subsamples of similar quantities, 15 g each, were enclosed in 25x25 cm nylon mesh bags and then securely placed in the site from which they had been collected. Monthly collections were done during the two growing seasons and one collection for the winter period. All samples were oven-dried at 50 ^{0}C for 24 to 48 h in a ventilation oven to a constant mass. This temperature was selected to minimize errors associated with heat induced organic decomposition (Stohlgren 1988). The weight losses obtained were compared to the initial values to determine the percentage loss for all the species-spacing treatments. The decomposition constant, k, and the time for litter confined in mesh decomposition bags to decay 95% (i.e. 3.0/k) were calculated following the equation developed by Jenny et al. (1949) and Olson (1963):

$$e^{-kt} = \frac{x_t}{x_0}$$

where :

x_t = weight of litter inside the bag after t time
x_0 = initial weight of litter inside the bag
e = exponential function
k = decomposition constant
t = time span from x_0 to x_t (yr)

4.4. Forest floor mass

Forest floor mass at the study sites was measured in October 1992 by excavating 20x20 m organic soil samples with nine replicates per each treatment plot. The dry weight values were determined after oven-drying the samples at 100 ^{0}C to a constant mass. A mass balance approach was used to estimate decomposition constants, k, and the time to 95% decay (i.e. 3.0/k) for each species-spacing treatment after Olson (1969) and Stohlgren (1988). The estimated k values resulting from the mass balance approach were compared with the measured k values from the standard litterbag experiment (see Section 4.3). A 95 % decay parameter was calculated to assess the time needed for the litter to approach a steady state accumulation described by Olson (1969). The following equation was employed to estimate the decomposition constant of the forest floor mass (Olson 1969, Reiners and Reiners 1970, Stohlgren 1988):

$$k = \frac{Lf}{Ff}$$

where:

k = decomposition constant
Lf = annual litter fall (g/m^2)
Ff = forest floor mass including Lf part (g/m^2)

4.5. Laboratory studies

4.5.1. Proximate analysis of litter organic constituents

The major organic constituents of coniferous needle litter, i.e. lipid (fats, waxes, oils, and resins), cellulose, and lignin (Bray and Gorham 1964, Millar 1974, Swift et al. 1979) were determined for both red pine and white spruce. Seasonal needle litter samples from medium spacing treatments previously collected every month from the decomposition bags that had already been oven dried were ground to pass through a 1 mm mesh. The samples were then analyzed for lipid, cellulose, and lignin. The wet chemical proximate analyses described in Klinka and Lowe (1975) and Schlesinger and Hasey (1981) were followed.

4.5.2. Temperature effects on litter decomposition

Under field conditions the effects of temperature are difficult to separate from those of other environmental variables, and yet this is the principal factor influencing the microbial activity in boreal forests (Bonan and Van Cleve 1992, Edwards 1975, Fox and Van Cleve 1983). Therefore, it was decided to perform an experiment on the effect of temperature using controlled environmental conditions.

Litter samples of fresh and partly decomposed needles of red pine and white spruce were collected from the field and brought immediately to the laboratory. There were ten replications each for both fresh and partly decomposed litter of the two study species. All samples were kept at room temperature for 1 h before they were cut into pieces measuring no more than 1 cm in length. From each sample, a sub sample was retained to determine the initial dry weight. These initial weight values would be used to determine the total initial dry weights of the litter (a). Litter samples were brought to 100% moisture content (dry weight basis) with distilled water and then left sealed in the controlled environment chambers for 24 h before measurements began. This was to allow the moisture to become evenly distributed (Moore 1986).

Four controlled environment chambers each set at -5 ^{0}C, 15 ^{0}C, 25 ^{0}C, and 35 ^{0}C were used. This range of temperatures is assumed to produce the doubling of microbial activity (Q_{10}) characteristic of the exponential decomposition curve (Hendrickson 1985, Singh and Gupta 1977, Swift et al. 1979). Measured amounts (approximately 5 g) of litter material were placed in 32.5 x 21.0 x 7.0 cm sealable plastic boxes (Tupperware) as suggested by Moore (1986). Each box contained fresh and partly decomposed litter in 10 replications. Prior to the experiment, plastic containers containing water (Nagy and Macauley 1982) differing in surface areas were each placed inside the box in each chamber to monitor the relative humidity (RH) inside the box. This was done because RH influences the amount of water in the substrate available to microorganisms during decomposition. Every six hours, the RH inside the box was checked, and after a two week period, the amount of water needed in each box per chamber was determined. The relative humidity was monitored using the Tri-sense meter model

37000-00 (Cole-Parmer Instr. Co.). During the incubation period, the correct amount of water in the container inside each box, which varied considerably, was consistently maintained. After 100 days, all samples were removed, dried at 80 ^{0}C for 2 days (Nagy and Macauley 1982), and weighed for dry weights (**b**). Based on **a** and **b**, rates of weight loss in percentage were calculated.

4.6. Statistical analysis

Data on (1) microenvironment, (2) litter fall, expressed in g/m^2 oven dry mass, (3) decomposition, expressed as percentage of mass loss, (4) forest floor mass, expressed in g/m^2 oven dry mass were all subjected to two-way ANOVA to test for differences between species and spacing treatments. When ANOVA indicated significant differences, further tests among the means were performed using the Tukey-HSD procedure at 0.05 level (Snedecor & Cochran 1980). ANOVA tables with selected dates would be presented in the result section.

5. RESULTS AND DISCUSSION

5.1. Near ground microenvironment

5.1.1. Temperature

Weekly average temperature readings at 100 cm, 10 cm, 0 cm (surface layer), -2 cm (litter layer), and -10 cm (soil layer) of each species-spacing treatment during two growing seasons are presented in Figures 7 to 11. Contrasting temperature readings were obtained between above and below ground measurements with respect to species and spacings. The above ground temperatures were generally ranked among wide pine (meaning wide spacing plot of red pine) > wide spruce > medium pine > medium spruce > close pine > close spruce (Figs. 7-9). This trend became reversed for the below ground temperatures (Figs. 10-11). Above the ground (i.e. at 100 cm, 10 cm, and 0 cm levels), wider spacing treatments showed 1 - 2 ^{0}C higher temperatures than the readings obtained from closer spacings for both tree species. In October the soil temperature was warmer than the surface and above ground temperatures.

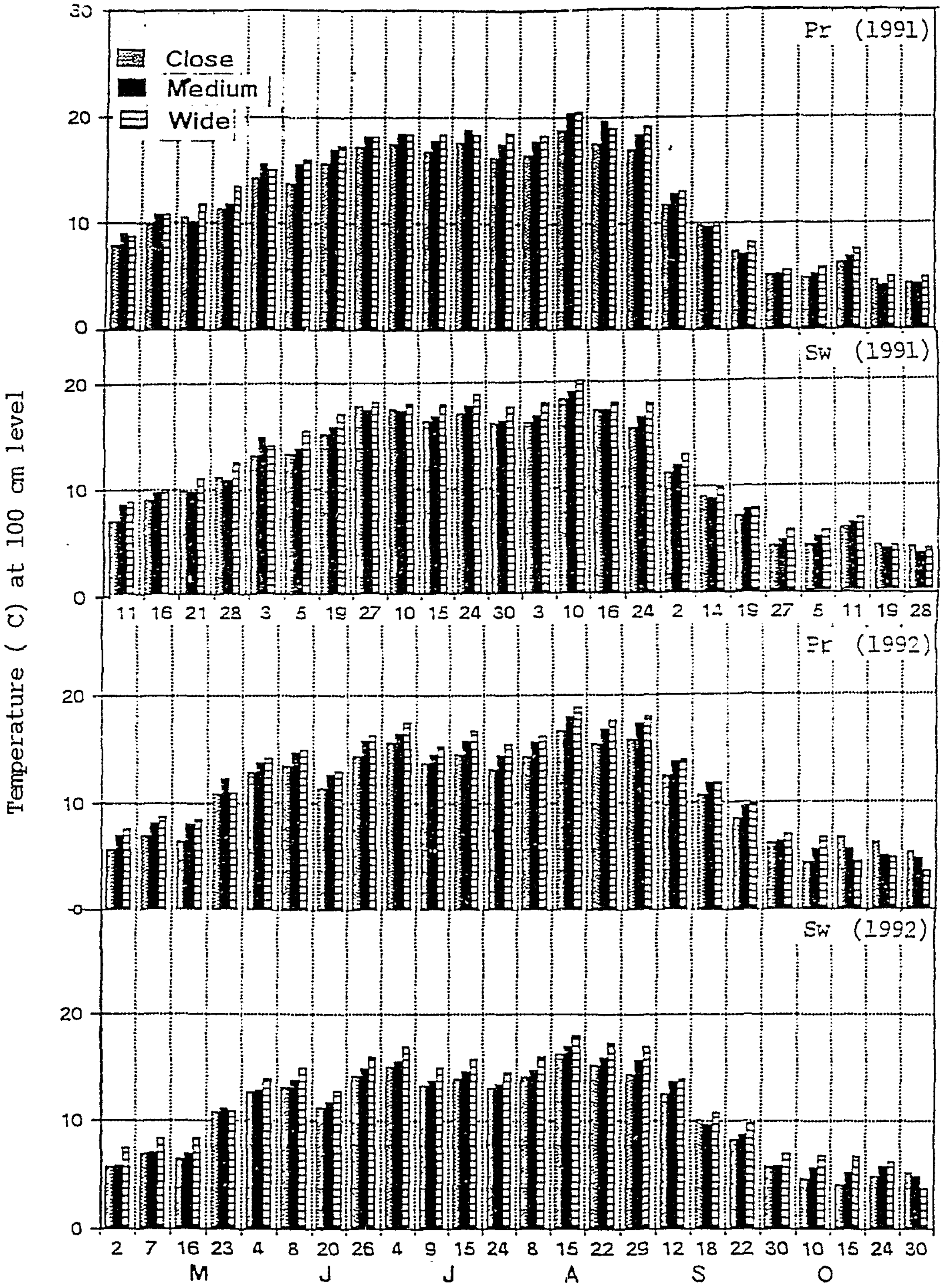

Fig 7. Temperatures at 100 cm in red pine (Pr) and white spruce (Sw) plantations measured weekly during two growing seasons under three different spacings (close, medium, and wide).

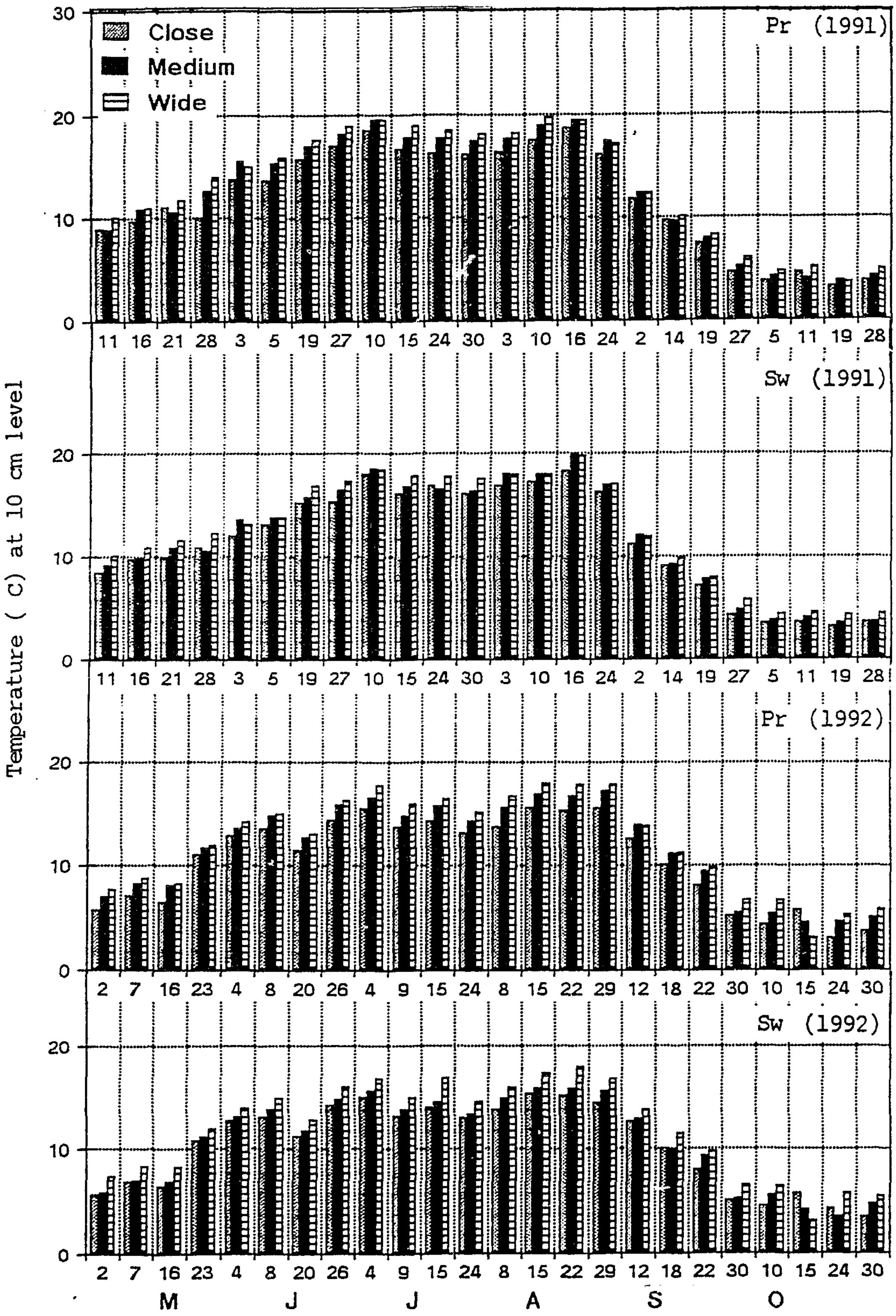

Fig 8. Temperatures at 10 cm in red pine (Pr) and white spruce (Sw) plantations measured weekly during two growing seasons under three different spacings (close, medium, and wide).

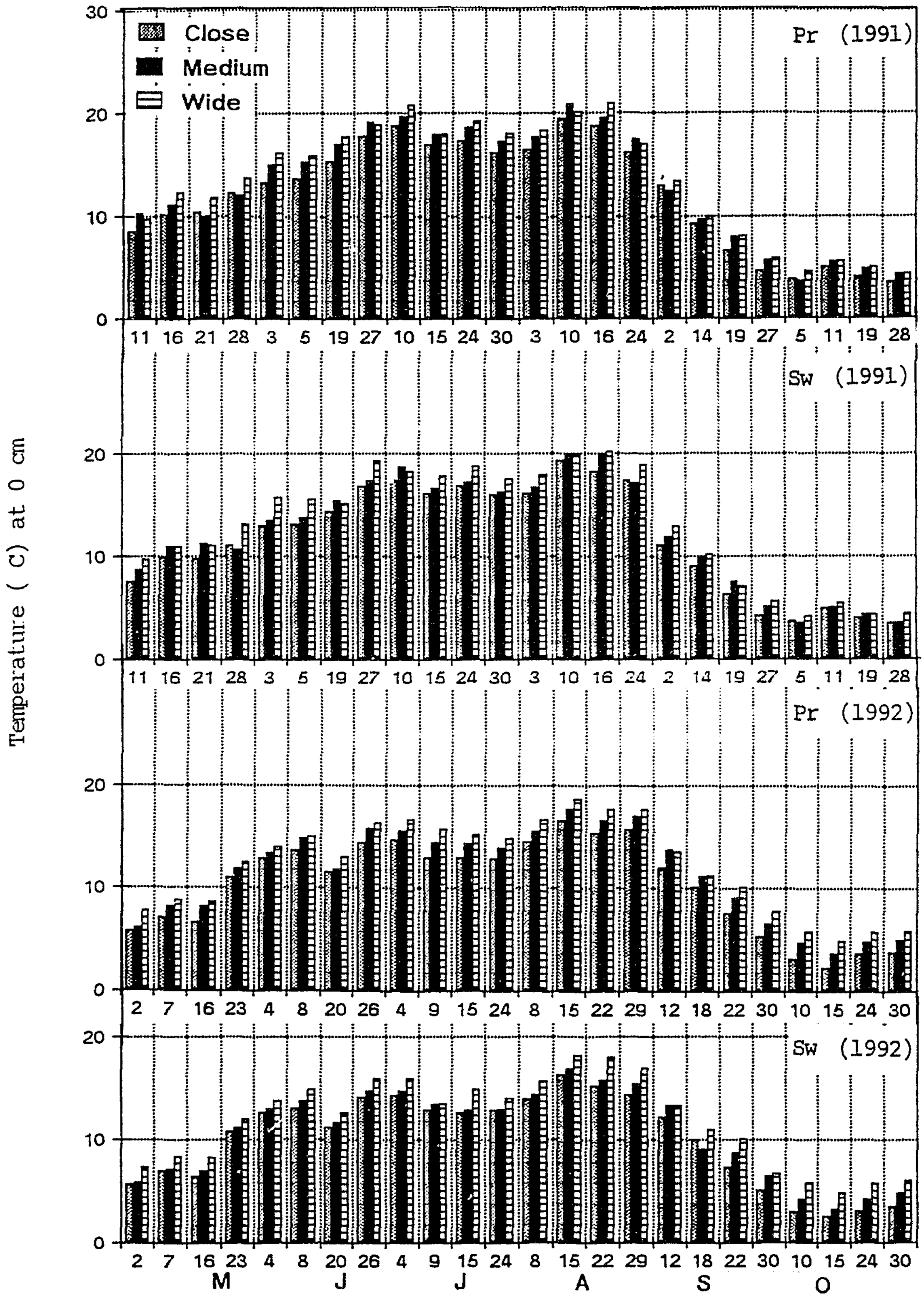

Fig 9. Temperatures at 0 cm in red pine (Pr) and white spruce (Sw) plantations measured weekly during two growing seasons under three different spacings (close, medium, and wide).

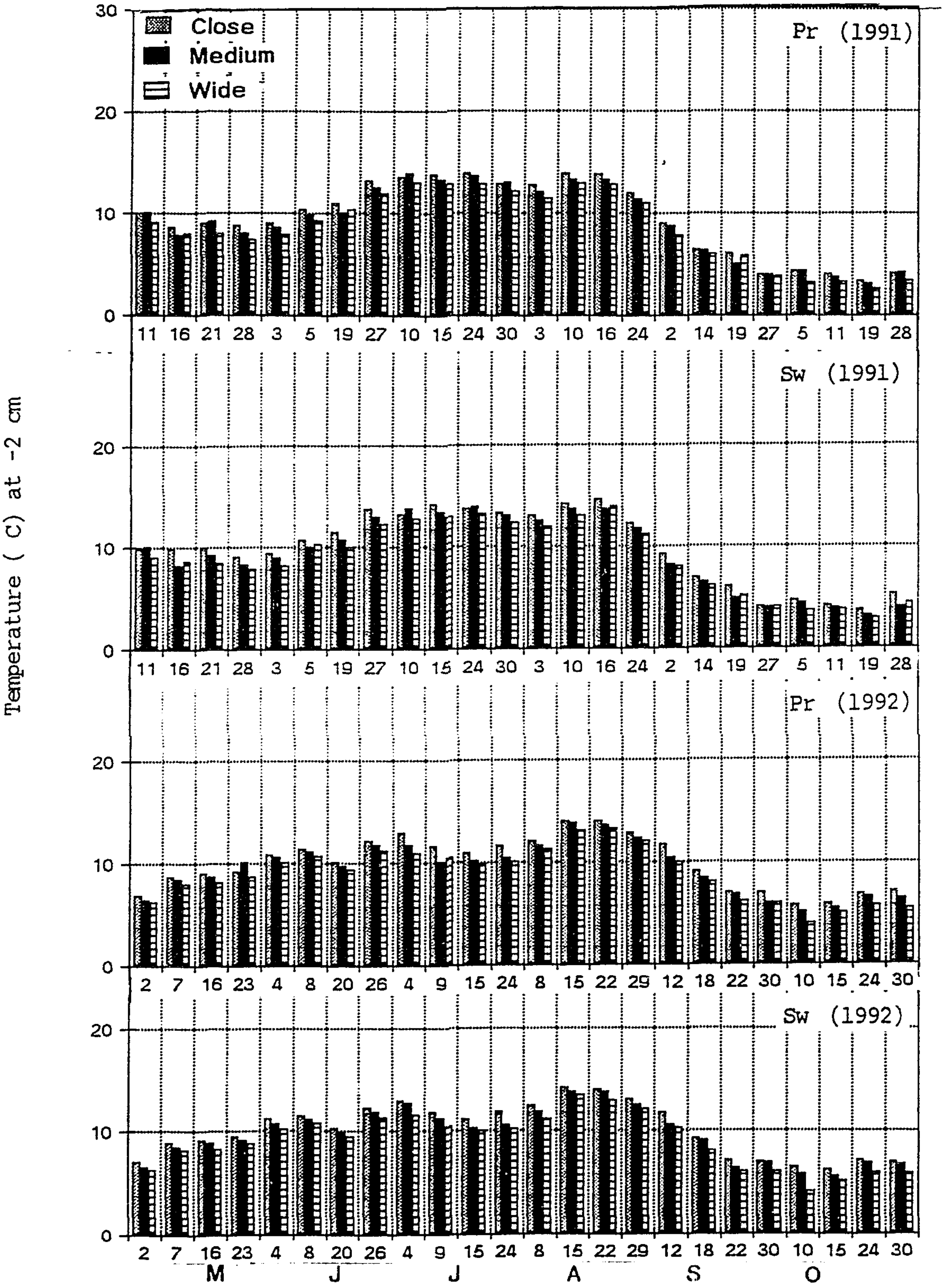

Fig 10. Temperatures at -2 cm in red pine (Pr) and white spruce (Sw) plantations measured weekly during two growing seasons under three different spacings (close, medium, and wide).

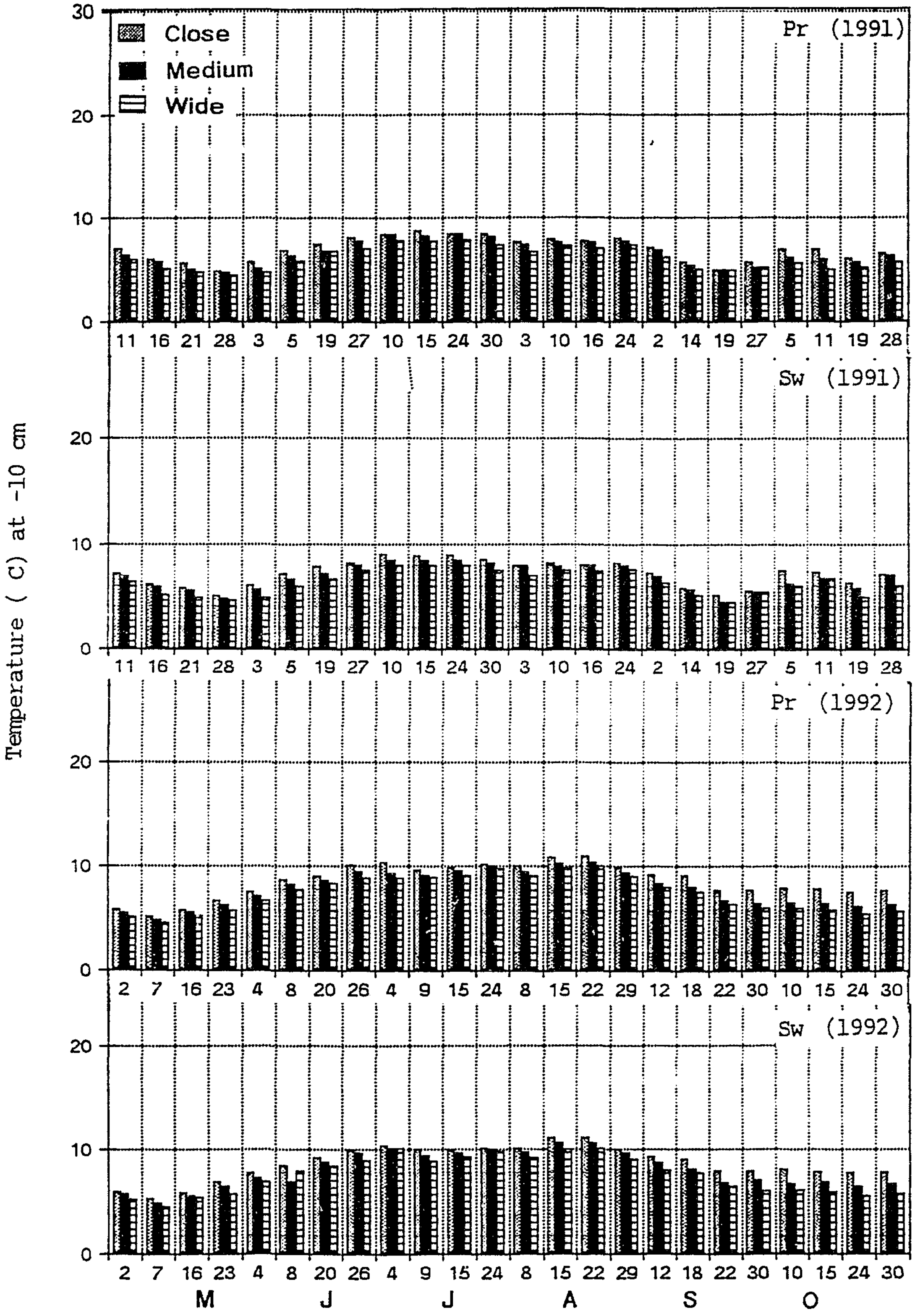

Fig 11. Temperatures at -10 cm in red pine (Pr) and white spruce (Sw) plantations measured weekly during two growing seasons under three different spacings (close, medium, and wide).

Table 2. Temperatures at litter layer in red pine (Pr) and white spruce (Sw) plantations established under three different spacing regimes: close (1.8m), medium (2.7 m), and wide (3.6 m) observed during growing season 1991.

Plots	28 May	27 June	30 July	24 Aug.	27 Sep.	28 Oct.
Pr 1.8	6.77 ac	13.18 ad	12.79 ad	12.00 ad	4.06 a	4.94 ac
Pr 2.7	6.02 ab	12.47 b	12.68 ad	11.34 bc	4.00 a	4.21 cd
Pr 3.6	5.34 b	11.91 c	12.16 b	11.03 c	3.89 a	3.34 b
Sw 1.8	7.01 c	13.67 d	13.23 c	12.22 d	4.06 a	5.20 a
Sw 2.7	6.26 ad	12.89 ab	12.96 ac	11.69 ab	3.97 a	3.93 d
Sw 3.6	5.85 bd	12.23 bc	12.34 bd	11.17 c	4.00 a	3.67 bd

Note: Unlike letters in a column indicate values significantly different at 0.05 level.

Table 3. The summary tables of ANOVA representing each stated date during growing season 1991.

Source of variation	df	MS					
		May 28	June 27	July 30	Aug. 24	Sept. 27	Oct. 28
Species	1	0.49	0.76	0.41	0.25	4.60	0.05
Spacing	2	2.54	2.76	0.94	1.55	13.2	3.77
Interaction	2	0.04	0.01	0.03	0.02	0.81	0.17
Error	12	0.69	0.34	0.18	0.21	0.48	0.59
Total	17	0.82	0.61	0.27	0.35	2.25	0.88

Table 4. Temperatures at litter layer in red pine (Pr) and white spruce (Sw) plantations established under three different spacing regimes: close (1.8 m), medium (2.7 m), and wide (3.6 m) observed during growing season 1992.

Plots	May 23	June 26	July 24	Aug. 29	Sep.30	Oct.30
Pr 1.8	7.14 ac	12.13 ad	11.62 a	12.81	7.04 a	7.09 a
Pr 2.7	7.07 c	11.77 b	10.41 b	12.37 a	6.05 b	6.44 abc
Pr 3.6	6.70 b	11.19 c	10.09 b	12.11 a	6.00 b	5.42 d
Sw 1.8	7.39 a	12.25 a	11.87 a	13.00	6.91 a	6.94 a
Sw 2.7	7.08 ac	11.86 bd	10.50 b	12.52	6.88 a	6.71 ab
Sw 3.6	6.79 bc	11.25 c	10.21 b	12.11 a	6.00 b	5.83 cd

Note: Unlike letters in a column indicate values significantly different at 0.05 level determined by the Tukey-HSD test.

Table 5. The ANOVA summary for the litter temperature on selected dates during the 1992 growing season.

Source of variation	F values					
	May 23	June 26	July 24	Aug.29	Sep.30	Oct.30
Species	2.384	0.223	2.751	0.910	1.983	3.071
Spacing	9.603*	8.777*	11.05*	15.05*	12.25*	16.21**
Interaction	0.140	0.080	0.312	0.237	0.565	1.001

Note: * and ** indicate values which differ significantly at 0.05 and 0.01 level, respectively, determined by the Tukey-HSD test.

Larger tree crowns were produced by wider spacing, however, the canopy overlap was generally greater in closer spacing plots. Crown coverage affects the physical obstruction performed by the canopy to the air and radiation movements (Barry and Chorley 1987); and, in turn, alters the heat and water balance within the stand (Geiger 1965). As the forest canopy becomes completely closed, the heat flux to the ground is normally reduced (Ford 1984). In closer spacings, canopy closure occurs earlier due to the decreased time period needed for the stand to reach the complete stage of site utilization (Bufford 1991, Ford 1984). Hence, the above ground temperatures in closer spacings were lower compared to the those in wider spacing plots.

Below the ground, closer spacings of both conifers showed higher (0.5-2 ^{0}C) temperatures than those shown at the wider spacings. From the litter fall study, it was shown that, in most cases, the rate and thus the accumulation of litter fall was higher in closer spacings (Table 6). The resulting decomposition process may affect the soil microenvironment (Facelli and Pickett 1991). As an oxidation process, this microbial activity of decomposition releases energy which will mostly be lost as heat (Brady 1990). Therefore, the elevated below ground temperatures within the closer spacings could be the result of the dissipated heat released as the byproduct of microbial decomposition.

Near ground temperature were different in the two conifer species. Under similar spacings, pine plots showed higher readings of above ground temperatures than did white spruce. Even though this difference was not statistically significant (Tables 2,4), such a trend remained evident for most cases throughout the two growing seasons. The different structure of pine and spruce canopies may result in a different nature of light obstruction. The spruce canopy is denser and darker compared to the sparse and light colour of the pine canopy. The later characteristic allows more light penetration to reach the forest floor resulting in higher temperature readings in the pine stand.

Contrary to the above trend, spruce plots showed higher readings of below ground temperatures than did the pine plots. No obvious mechanism can be proposed here. It may be related to the root system or the different nature of microbial activity in the decomposition processes generated from the different litter accumulation between the two species. From the forest floor study (Section 5.4), it was observed that mosses were more abundant in spruce sites than pine sites notably those of Pleurozium schreberi, Rhytidiadelphus triquetrus, and Ptilium crista-castrensis. As mosses absorb water, their presence in the forest floor can influence the microclimate within the soil (Larsen 1980). During the absence of rain, however, soil under the mosses can become very dry. Under such conditions the forest floor of spruce may conduct heat more readily than that of pine (Bonan and Shugart 1989). In addition, the dry conditions and the low light intensity resulting from the dense canopy of spruce may depress other herbaceous understory species, and thus permit a greater opportunity for mosses to dominate the forest floor.

When the temperatures inside the plantation were compared with the daily temperature record in Thunder Bay area (Fig. 3 in Chapter 3), a similar parabolic trend was observed reaching a maximum in late summer and a minimum in early winter. It was also observed that in all cases, the differences between the two readings were more marked in spruce than in pine stand. For both species, however, the differences are minimal in early winter, and maximal during summer. This can be related to the evapotranspiration normally being highest during the warm summer days (Etherington 1975). In the early winter, when the open area temperature had dropped, the above ground temperatures also decreased accordingly. The soil temperatures, however, remained relatively unfluctuated giving the highest readings during this time compared to readings from other levels. As a consequence, soil temperatures of both pine and spruce sites exhibited relatively small fluctuations compared to the readings at other levels (Figs. 7-11).

Temperature measurements were related in this study to the process of decomposition. From the decomposition study (Section 5.3), it was found that the rate of litter mass loss was proportional to the trend shown by below ground temperatures. In this case, the highest reading observed in close spruce was in concert with the highest mass loss values resulting from the same treatment combination. In both parameters (i.e., below ground temperatures and decomposition) the same trend was also noted in which the highest values shown in close spruce was followed by close pine, medium spruce, medium pine, wide spruce, and wide pine (see the discussion in Section 5.3).

Between the below ground temperatures (i.e., those of litter and soil layers), soil temperatures remained more or less uniform regardless of the temperature fluctuations occurring in the open area throughout the two growing seasons. Litter temperatures, on the other hand, were more responsive to the open area temperatures even though such responses were apparently less marked than that obtained at above ground levels.

All temperature readings were statistically analyzed, but only the litter layer selected from one date per month during the two growing seasons will be presented (Table 2,4), because this was considered to be the most relevant to the process of decomposition. Litter decomposition bags also were incubated within the litter layer (F horizon) during the eighteen months of study period.

In most cases, based on 0.05 alpha level (or 95 % confidence level), only the spacing factor had a significant effect on temperature readings. Neither the species nor the interaction factors contributed to the temperature changes in the plantation. Between the species, temperature readings in spruce plots were generally higher than those of the pine plots. However, this trend was only true under similar spacing regimes (Table 2, 4) suggesting a stronger effect of the spacing factor than the species factor in affecting the near ground temperatures.

5.1.2. Relative humidity

The relative humidity readings over the two growing seasons are presented in Figures 12-14 and Tables 6-7. In general, relative humidity values increased following the order of wide pine, wide spruce, medium pine, medium spruce, close pine, and close spruce. Among the reading levels, the values increased following the order of 100 cm, 10 cm, and 0 cm. Under a similar spacing, the values were higher in white spruce than in red pine plots. Geiger (1965) found that, in general, spruces intercept almost twice as much solar radiation as do pines under the same density. This leads to a decreased amount of diffuse radiation reaching the forest floor of spruces. As high as 20 to 40 % of the incident radiation may penetrate on the floor of pine forests whereas only 10 to 25 % reached the forest floor of spruce and fir (Barry and Chorley 1987).

A separate field study also demonstrated a comparable result where at each spacing, the pine forest floor generally received 20-35 % more short-wave radiation than did the forest floor of spruce. Reduced temperatures due to decreased light penetration in the spruce plots resulted in higher relative humidity readings in the spruce plots than in the pine plots.

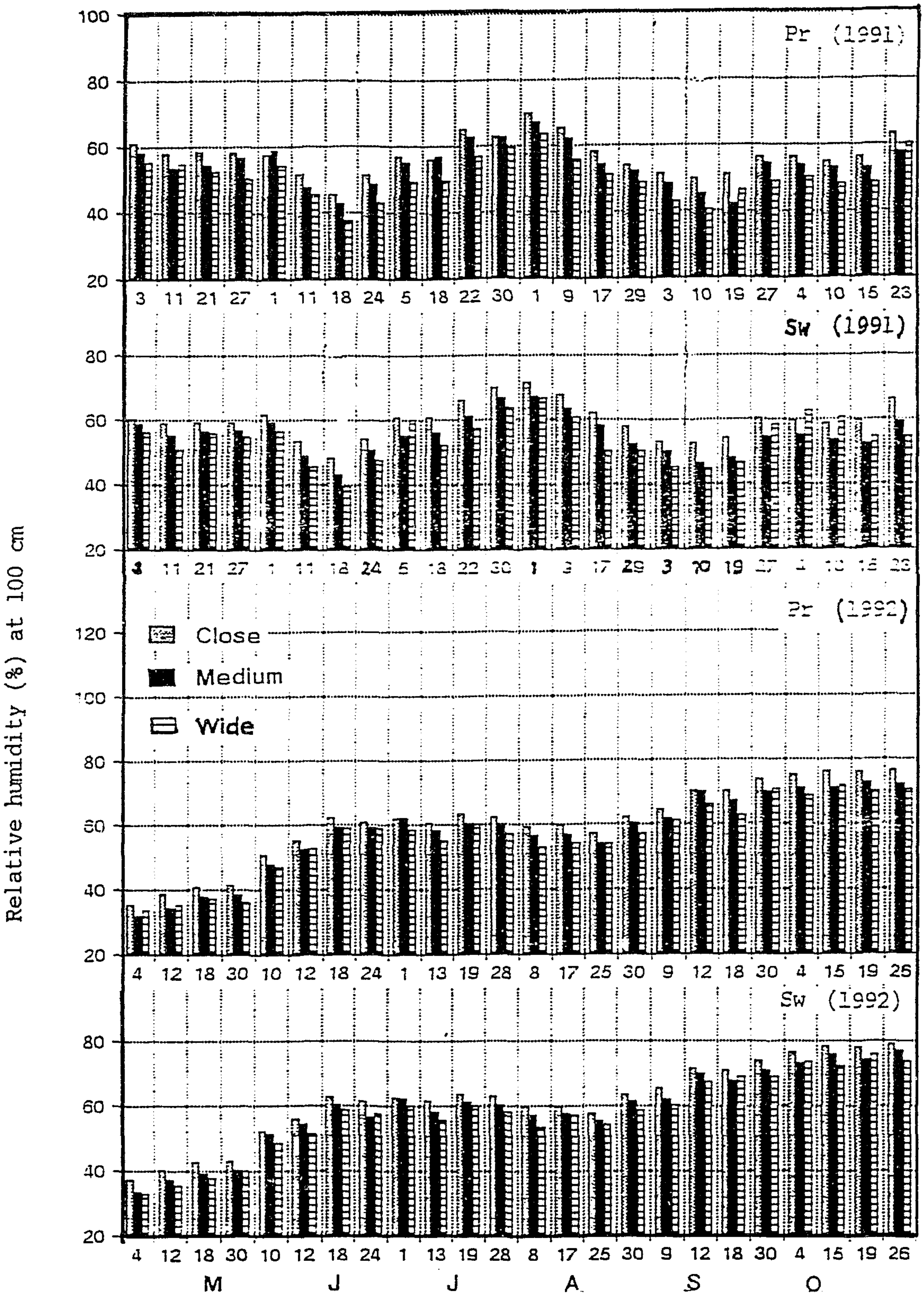

Fig 12. Relative humidity at 100 cm in red pine (Pr) and white spruce (Sw) plantations measured weekly during two growing seasons under three different spacing regimes (close, medium, and wide).

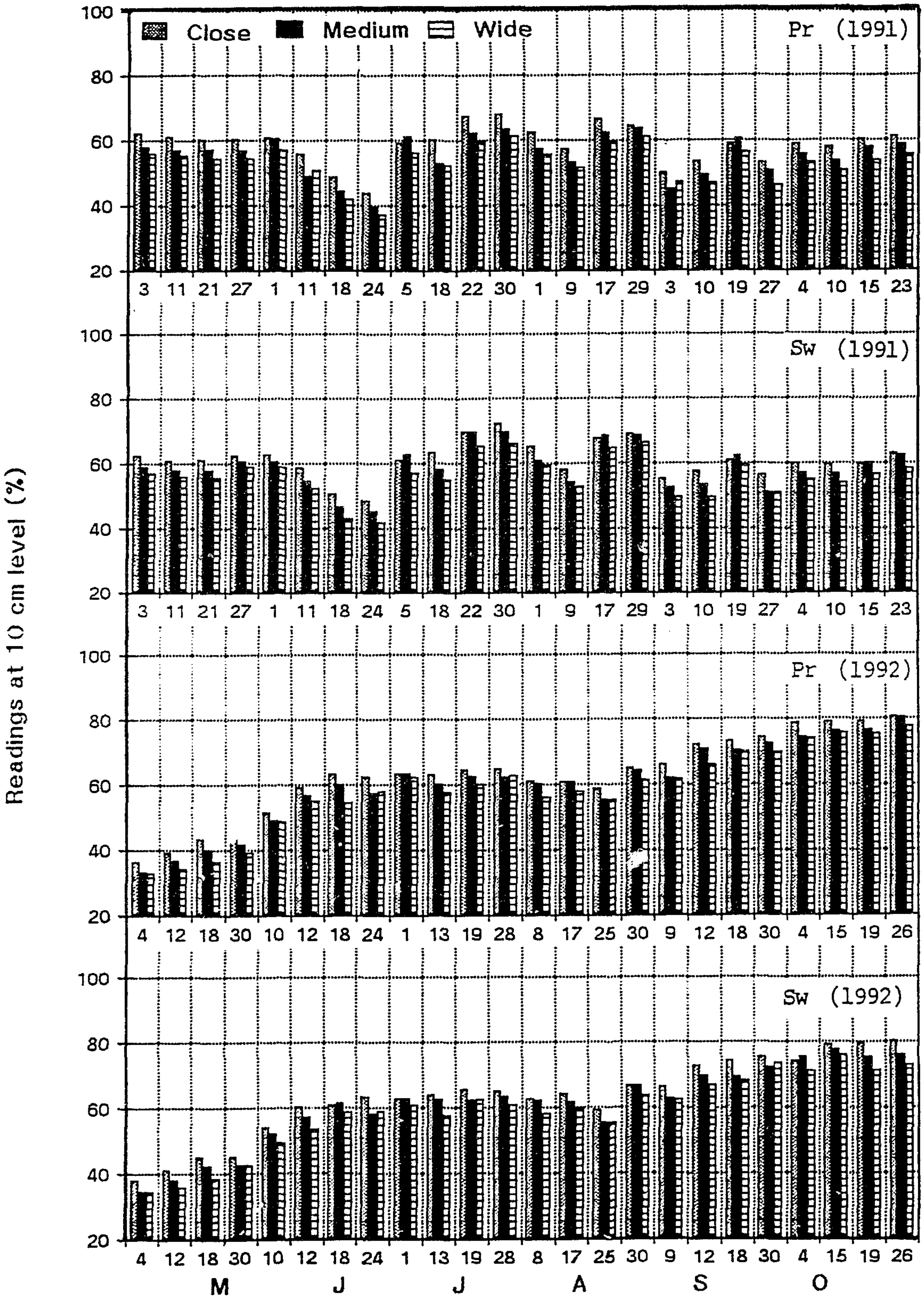

Fig 13. Relative humidity at 10 cm in red pine (Pr) and white spruce (Sw) plantations measured weekly during two growing seasons under three different spacing regimes (close, medium, and wide).

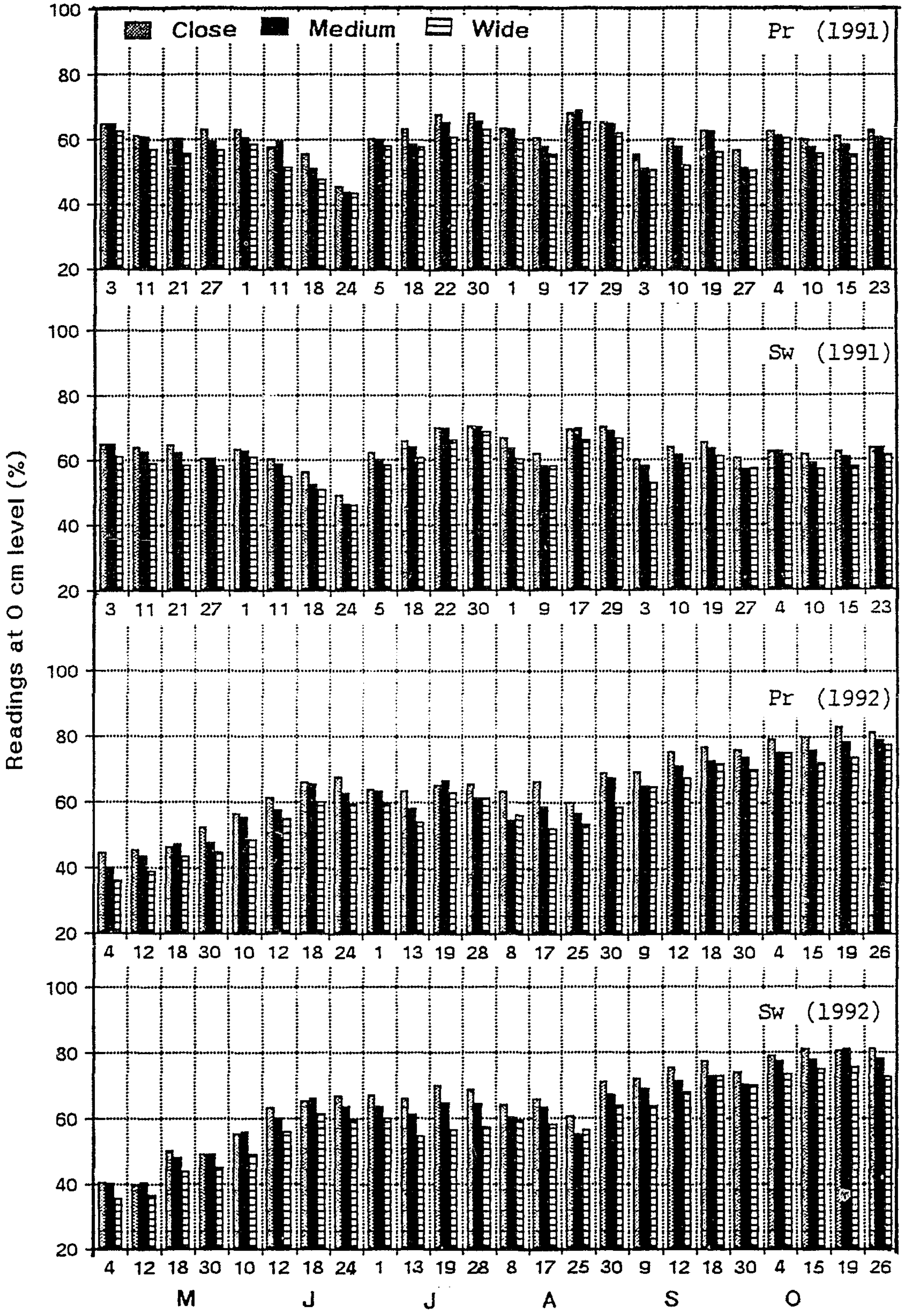

Fig 14. Relative humidity at 0 cm in red pine (Pr) and white spruce (Sw) plantations measured weekly during two growing seasons under three different spacing regimes (close, medium, and wide).

Table 6. Relative humidity at 0 cm in red pine (Pr) and white spruce (Sw) plantations established under three different spacing regimes: close (1.8 m), medium (2.7 m), and wide (3.6m) on selected dates during the 1992 growing season.

Plots	May 27	June 24	July 30	Aug.29	Sep.27	Oct.23
Pr 1.8	66.99 a	60.53 ad	75.62 a	84.64 a	56.96 a	71.97 a
Pr 2.7	62.68 b	55.94 b	67.57 d	75.09 b	51.63 b	65.54 b
Pr 3.6	59.71 c	45.67 c	68.27 c	71.32 c	50.82 b	62.27 c
Sw 1.8	70.65 a	63.59 a	77.86 a	87.27 d	64.71 c	75.83 d
Sw 2.7	77.58 b	58.42 bd	72.71 e	82.50 e	60.12 a	73.72 a
Sw 3.6	75.46 c	49.95 c	69.97 cd	78.72 b	53.59 b	67.90 b

Note: Unlike letters in a column indicate values significantly different at 0.05 level determined by the Tukey-HSD test.

Table 7. The ANOVA summary for the relative humidity at 0 cm on selected dates during the 1992 growing season.

Source of variation	F values					
	May 27	June 24	July 30	Aug.29	Sep.27	Oct.23
Species	2.312	6.251*	5.220*	5.686*	11.69**	4.436
Spacing	7.302*	7.812*	22.23*	24.40**	34.03*	10.25*
Interaction	1.530	1.041	0.913	0.114	0.940	0.704

Note: * and ** indicate values which differ significantly at 0.05 and 0.01 level, respectively, determined by the Tukey-HSD test.

Relative humidity values varied with species, but the effect of spacing was found to have the more pronounced effect in relative humidity (Tables 6-7). In many cases, the highest readings were in close spruce followed by the subsequent rankings of close pine, medium spruce, medium pine, wide spruce, and wide pine (Figs. 12-14). More pronounced effects of spacing over species on the ground level relative humidity was evident from the ANOVA tables (Table 7). However, significant effects of species may be detected when the confidence level was decreased from 95 % to 90 %. In this case a higher risk (i.e., from 5 % to 10 %) of not including all the measured parameters under data analysis may occur due to the sample size. The precision, on the other hand, may be more reliable since the standard error becomes smaller as the 95 % level of confidence is reduced to 90 %. Within similar spacing the effect of species on relative humidity readings was, in many cases, found to be significant (Table 6).

Relative humidity at the forest floor increases with the density of the trees as it does in a vertical gradient toward the forest floor. The process of evapotranspiration can be one of the factors responsible for this trend (Battan 1979). It is particularly true during the summer months when the rate of evapotranspiration reaches its peak with the maximum seasonal temperatures. The presence of understory vegetation during this time of the year may also contribute to the higher rate of evapotranspiration.

5.1.3. Soil moisture

In general soil moisture content increased in the following order: close spruce, close pine, medium spruce, medium pine, wide spruce, and wide pine (Fig. 15). Early in the season, however, soil moisture was higher in the close spacing than in the wide spacing plots for both red pine and white spruce (Fig. 15). Dense tree canopies at close spacings may intercept more falling snow than the wider spacings (Barry and Chorley 1987). However, field observations indicated that despite the decreased amount of snow in the close spacings plots, snow cover stayed longer with close spacing than with wider spacings. Snow retention in the closer spacing plots supports the sub-surface moisture recharge through this period of gradual snow conversion to water. For the relatively sandy soils of the present study site, when the snow supply ceased the moisture charge of the site also decreased.

In the wide spacing plots, earlier conversion of snow to melt water resulted in an apparently substantial increase in soil moisture content for the succeeding months, leaving a higher percentage of soil moisture in this spacing for the rest of the season. The rising temperatures toward the peak of the growing season may stimulate greater evapotranspiration losses from the soil (Etherington 1975). This loss, however, is more evident in closer spacing sites due to the presence of greater number of trees (Fig. 15).

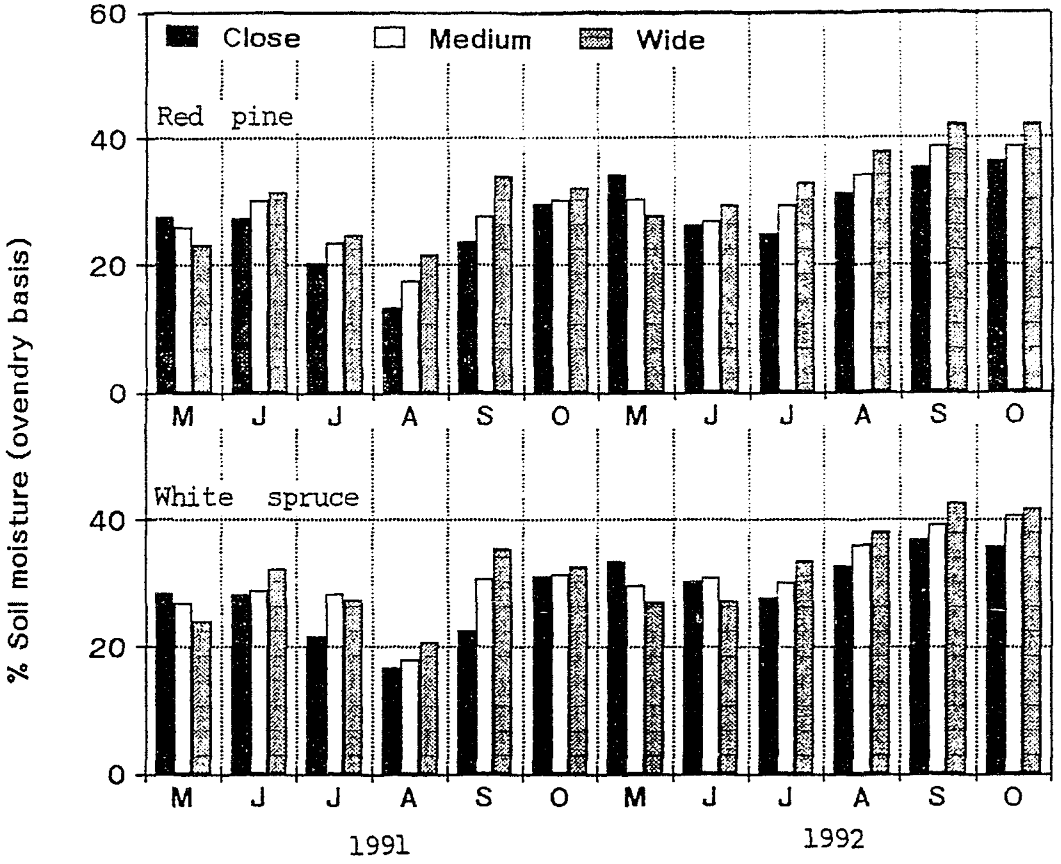

Fig 15. Soil moisture content of red pine and white spruce plantations under three different spacing regimes (close, medium, and wide) observed monthly during growing seasons 1991 and 1992.

Table 8. Soil moisture content in red pine (Pr) and white spruce (Sw) plantations measured in three different spacing regimes: close (1.8 m), medium (2.7 m), and wide (3.6m) in 1992.

Plots	May 30	June 27	July 25	Aug.29	Sep.26	Oct.24
Pr 1.8	27.48 ac	27.36 a	20.16 a	13.22 a	23.52 a	29.43a
Pr 2.7	25.65 d	30.01 b	23.38 b	17.37 b	27.56 b	30.02 ab
Pr 3.6	23.04 b	31.40 b	24.47 c	21.42 c	33.78 c	31.94 b
Sw 1.8	28.23 c	28.13 a	21.43 a	16.68 b	22.38 a	30.98 ab
Sw 2.7	26.89 a	31.72 b	28.49 d	17.96 b	30.74 d	31.37 b
Sw 3.6	23.89 b	34.08 c	27.24 e	20.67 c	35.46 e	32.44 b

Note: Unlike letters in a column indicate values significantly different at 0.05 level determined by the Tukey-HSD test.

Table 9. The ANOVA summary for monthly soil moisture during the 1992 growing season.

Source of variation	F values					
	May 30	June 27	July 25	Aug.29	Sep.26	Oct.24
Species	2.426	7.947	20.40*	1.457	1.555	1.939
Spacing	36.70**	22.80**	39.10**	14.97**	45.98**	2.152
Interaction	0.074	0.817	3.848*	1.856	1.622	0.156

Note: * and ** indicate values which differ significantly at 0.05 and 0.01 level, respectively, determined by the Tukey-HSD test.

There seems to be an inverse relationship between soil moisture content and stand density, i.e. the soil moisture content increases with the decreasing stand density (Fig. 15). In addition, soil moisture was generally higher in spruce stands than in pine stands at all spacings even though it was statistically insignificant (Table 8). In relation to the decomposition study (Section 5.3.), the trend shown by this moisture study was not in parallel. Apparently the soil moisture content within the plantation has little effect on the decomposition process (see Section 5.3.).

The amount of precipitation reaching the ground is a product of total rainfall minus the amount intercepted by the tree canopy (Geiger 1965). Trees planted at wide spacings normally produce larger crowns. However, canopy closure occurs earlier at close spacings. Canopy overlap was also greater at close spacings (Anon. 1991b). This greater canopy interception within the close spacing may thus explain the decreased amount of moisture storage for close spacing. For both species, it was observed that wide spacing plots received higher amount of throughfall than did closer spacing plots, although the differences were not statistically significant (data not presented here).

The difference in crown geometry between pine and spruce trees may also contribute to the differences in rainfall interception between the two species. The large, oval crowns of pine intercepts greater amounts of precipitation than the symmetrical, conical crowns of spruce. Mahendrappa (1990) calculated the amount of rain water under several different stands. Compared to red pine, white spruce received a higher amount of throughfall (73%, compared to 69%), and stemflow (6.4%, compared to 0.7%), but less water interception (20.6%, compared to 28.3%). Moisture storage can therefore be higher under spruce stands. Despite the apparent differences in moisture content between the two stands in the present study, these values were not significant at 0.05 level (Table 8).

Unlike the species influence on soil moisture content, the effect of spacing was found to be significant with higher values of soil moisture with wider spacings (Table 9). This suggests that the effect of spacing surpasses the effect of species in regulating the overall soil moisture content. In addition, root system architecture can also contribute to the variation in soil moisture regime among the plots. Unfortunately, no data are available to show how spacing influences the formation and distribution of roots. Nonetheless, greater number of trees in closer spacing plots might produce greater number of roots competing to remove moisture from the soil.

5.1.4. Soil pH

Monthly soil pH values during the 1991 and 1992 growing seasons are presented in Figure 16. Few differences were observed among the spacings throughout the whole seasons as also indicated in Table 10. The analysis of variance (Table 11) shows a relatively weak effect of spacing on the soil pH values (p averages 75 %). On the other hand, generally strong effects were observed due to the species factor controlling the values of soil pH. A trend reaching a maximum level of pH around October was observed during the two growing seasons. This highest value of soil pH likely related with the release of certain minerals during this time of the year. Rodin and Bazilevich (1969) concluded from a number of studies on boreal coniferous and mixed forests that an increase in the total mineral content of the soil was mainly the result of increases in Ca, P, and Mg, released by decomposing litter deposited from the preceding year.

The pH values were significantly higher for white spruce than for red pine plots. Perala and Alban (1982) compared the plant nutrient content of several tree species including those of red pine and white spruce in north central Minnesota. They compared red pine and white spruce needles and found that white spruce had higher concentrations of all essential nutrient elements such as N (with the ratio of 1.2 to 1 between white spruce and red pine), P (1.5:1), K (1.1:1), Ca (4.2:1), except for Mg (1:1.1). The difference in Ca is very striking, a factor which is believed to be responsible for the higher pH values for spruce compared to the pine plots.

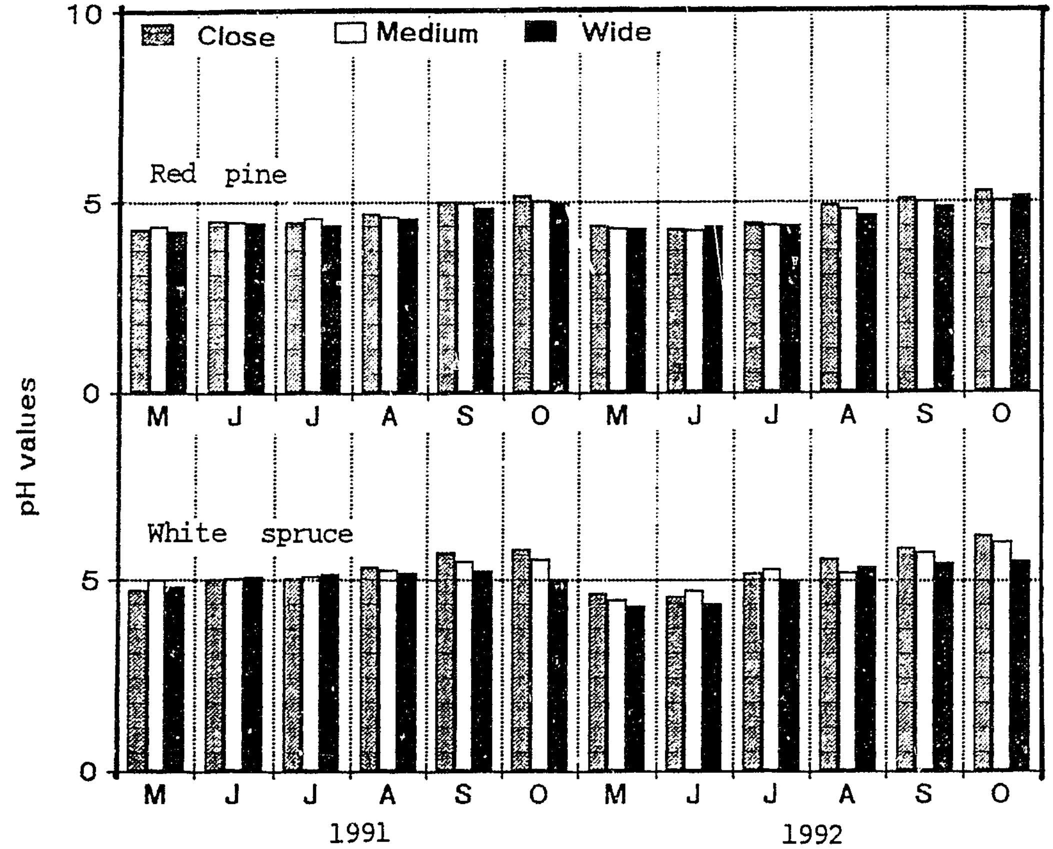

Fig 16. Monthly changes of pH values on the forest floor of red pine (Pr) and white spruce (Sw) stands established in three spacing regimes (close, medium, wide) during the 1991 and 1992 growing seasons.

Table 10. pH values in red pine (Pr) and white spruce (Sw) plantations established under three spacing regimes: close (1.8 m), medium (2.7 m), and wide (3.6 m) during the 1992 growing season.

Plots	May 30	June 27	July 25	Aug.29	Sep.26	Oct.24
Pr 1.8	4.39 a	4.27 a	4.46 a	4.93 a	5.10 a	5.03 a
Pr 2.7	4.30 a	4.25 a	4.41 a	4.82 a	5.00 a	5.06 a
Pr 3.6	4.28 a	4.34 a	4.39 a	4.64 a	4.86 a	5.17 a
Sw 1.8	4.65 b	4.58 b	5.18 b	5.57 b	5.87 b	6.20 b
Sw 2.7	4.49 ab	4.72 b	5.30 b	5.23 b	5.75 b	6.03 b
Sw 3.6	4.31 a	4.36 ab	4.98 b	5.36 b	5.47 ab	5.51 a

Note: Unlike letters in a column indicate values significantly different at 0.05 level determined by the Tukey-HSD test.

Table 11. The ANOVA summary for monthly soil pH during the 1992 growing season.

Source of variation	F values					
	May 30	June 27	July 25	Aug.29	Sep.26	Oct.24
Species	12.07*	10.12*	18.69**	15.43**	19.38**	10.51*
Spacing	0.102	0.003	0.321	0.271	2.282	1.117
Interaction	0.652	0.047	0.025	0.000	0.587	1.818

Note: * and ** indicate values which differ significantly at 0.05 and 0.01 level, respectively, based on the Tukey-HSD test.

5.2. The pattern of litter fall

The monthly (during the growing seasons) and seasonal (during winter season) patterns of litter fall during the study period are presented in Figures 16-19. The total litter biomass increased following the general order of wide spruce, medium spruce, close spruce, wide pine, medium pine, and close pine. The amount of total litter fall is in accordance with the amount of needle litter fall which comprises about 80 % of pine litter and 77 % of spruce litter. The twig fraction is 14 % and 19 % for pine and spruce litter, respectively, and the reproductive fraction is 6 % and 4 % for pine and spruce litter, respectively. Monthly and seasonal litter fall of red pine and white spruce are shown in Table 10. Seasonal variations are statistically evident between any of the two growing seasons and the winter season. However, the differences are not significant at the 0.05 level between the two growing seasons. The first growing season (1991) shows a higher amount of total litter fall compared with the second growing season (1992) which, in turn, shows a higher amount of litter fall than the winter season.

Total litter fall of red pine is found to be significantly greater than that of white spruce. The table of ANOVA (Table 11) shows a statistically stronger effect of the species factor on the litter biomass than the spacing factor which also is significant at the 0.05 level. From Table 10, it is shown that a closer spacing generally produced a significantly greater amount of litter fall for both red pine and white spruce. This trend was also shown by the pattern of needle and twig fraction. Reproductive fractions, on the other hand, increased with wider spacing (i.e., decreasing tree density). In most cases, however, the differences are more significant between species rather than between spacings (Table 10) in which reproductive fraction of pine was mostly greater than that of spruce.

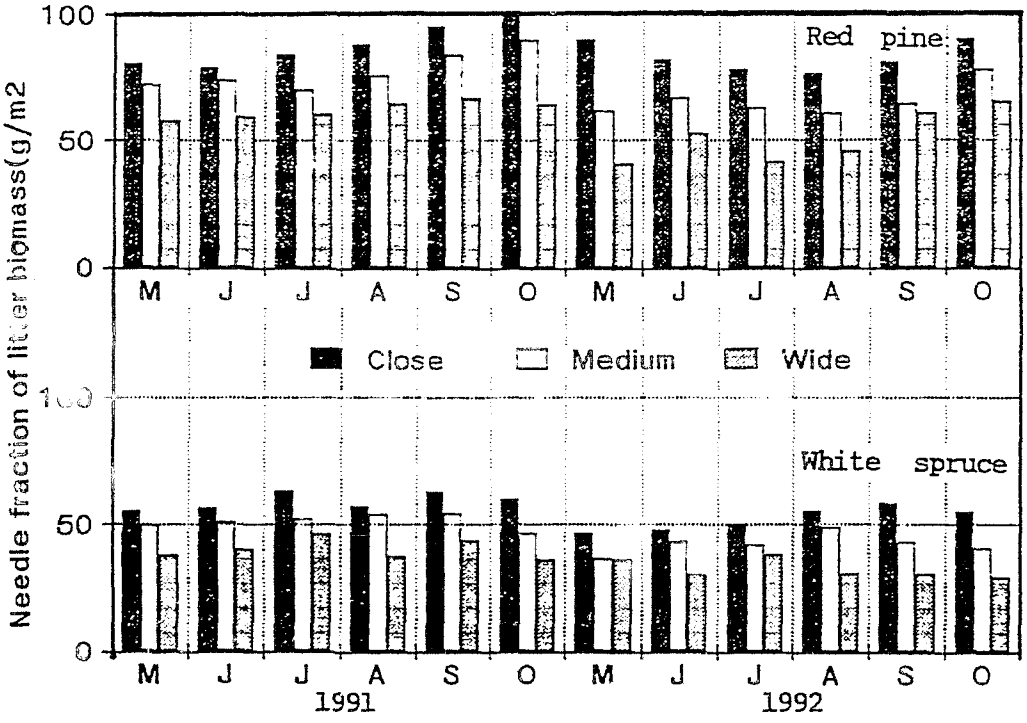

Fig 17. Monthly biomass of needle fraction of red pine and white spruce litter under three different spacing regimes (close, medium, and wide) during the 1991 and 1992 growing seasons.

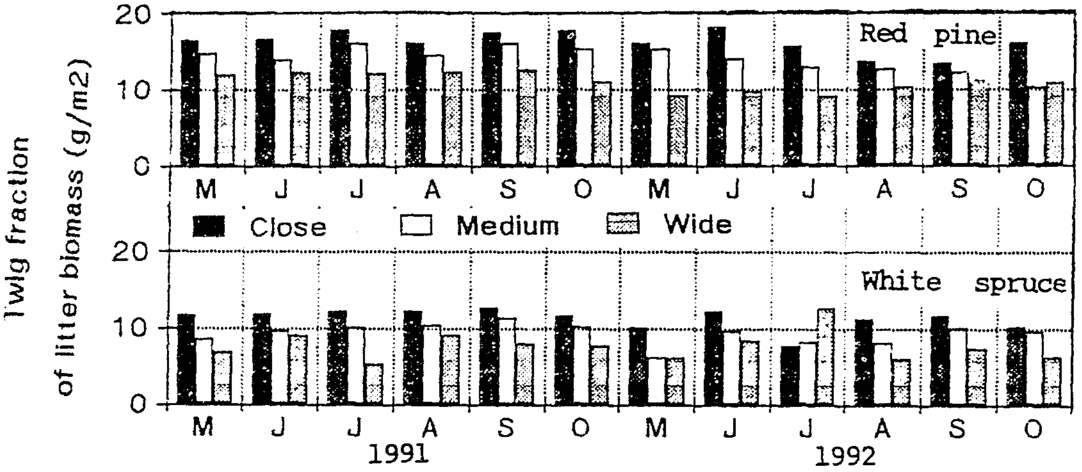

Fig 18. Monthly biomass of twig fraction of red pine and white spruce litter under three different spacing regimes (close, medium, and wide) during the 1991 and 1992 growing seasons.

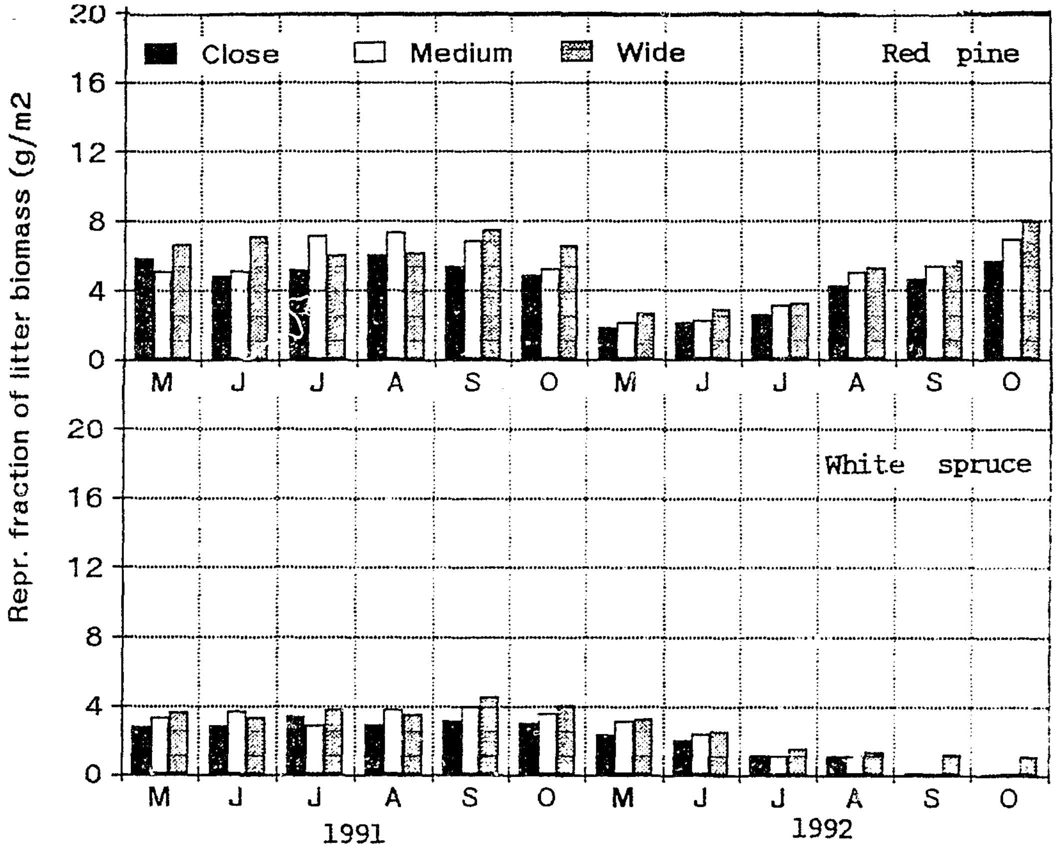

Fig 19. Monthly biomass of reproductive fraction of red pine and white spruce litter under three different spacing regimes (close, medium, and wide) during the 1991 and 1992 growing seasons.

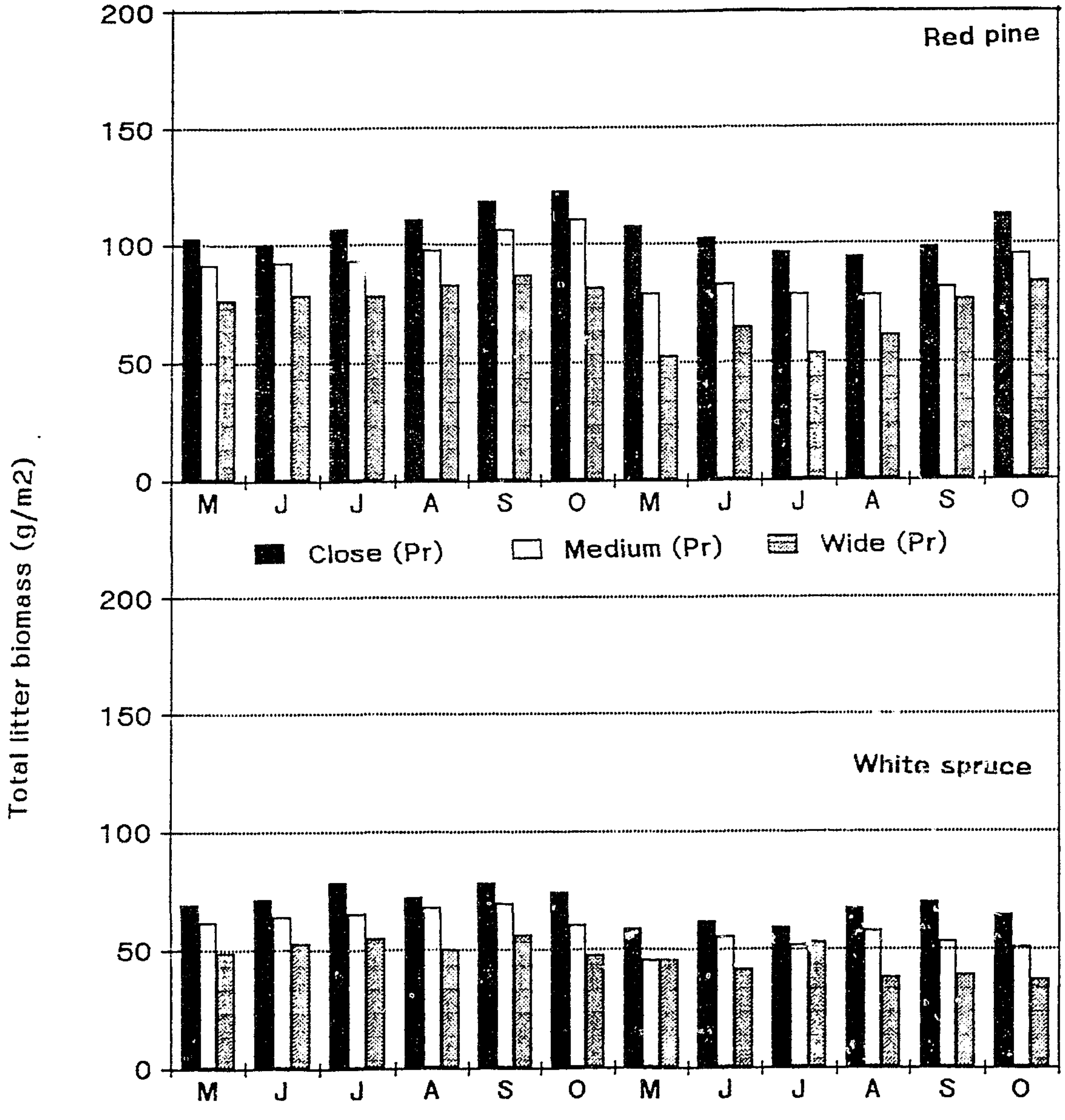

Fig 20. Total litter biomass of red pine (Pr) and white spruce (Sw) under three different spacing regimes (close, medium, and wide) during the 1991 and 1992 growing seasons.

Table 12. Seasonal pattern and amount of litter fall (g dry wt. m^{-1}) under three different spacing regimes (close: 1.8 m^2, medium: 2.7 m^2, wide: 3.6 m^2) of red pine and white spruce plantations in the Thunder Bay Spacing Trial.

	Needle fraction	Twig fraction	Repr. fraction	Total litterfall
A. Season 1 (May - October 1991)				
Red pine				
close	526.1 a	101.8 a	31.9 a	659.8 a
medium	463.8 b	90.1 a	36.7 a	590.5 b
wide	372.2 c	71.5 b	39.9 a	483.6 c
White spruce				
close	353.8 c	71.61 b	17.9 b	443.3 c
medium	306.7 d	60.22 b	21.1 b	388.0 d
wide	241.0 e	45.95 b	22.7 b	309.7 e
B. Season 2 (November 1991 - April 1992)				
Red pine				
close	266.6 a	52.0 a	2.6 a	321.2 a
medium	236.3 b	34.2 b	4.6 be	275.1 b
wide	206.3 c	27.7 c	6.3 c	240.3 c
White spruce				
close	165.8 d	27.1 c	3.2 ad	196.0 d
medium	120.6 e	15.0 d	3.9 bd	139.4 e
wide	63.5 f	8.9 e	4.6 e	77.0 f
C. Season 3 (May - October 1992)				
Red pine				
close	496.7 a	92.5 a	21.0 a	610.2 a
medium	393.3 b	77.1 a	24.8 ab	495.1 b
wide	305.9 c	58.9 b	27.8 b	392.6 c
White spruce				
close	311.8 c	62.7 b	6.6 c	381.2 c
medium	254.4 c	51.8 b	7.8 c	314.0 cd
wide	195.8 d	46.9 b	11.0 c	253.6 d

Note: Unlike letters in a column indicate values significantly different at 0.05 level determined by the Tukey-HSD test.

Table 13. The ANOVA summary for the seasonal litter biomass of red pine and white spruce established at three spacing regimes.

Source of variation	F values		
	Season 1	Season 2	Season 3
Species	145.326***	144.569***	59.108**
Spacing	29.010**	24.286**	18.184**
Interaction	0.516	0.910	1.238

Note: ** and *** indicate values which differ significantly at 0.01 and 0.001 level, respectively, based on the Tukey-HSD test.

Fyles et al. (1986) recognized three categories of controlling factors that determine various rates of litter fall within stands. First are the chronic factors such as insect and disease activities; second are the random factors such as seasonal weather; and third are the predictable physiological events such as needle abscission. There did not appear to be a chronic factor operating in these red pine and white spruce plots. But there were a number of white spruce trees attacked by certain fungi including Polyporus circinatus and Fomes pini. Both are common fungi infecting white spruce trees in the boreal region of Ontario (Sutton 1970).

The random controlling factors are associated with seasonal weather relative to growing season duration and rainfall distribution. The total amount of rain fall (Fig. 4 in Chapter 2) was higher for the growing season 1992 (435.8 mm) compared to the amount of rain fall for the growing season 1991 (400.7 mm). However, there were more rain and wind storms during the 1991 growing season, and this might partly explain the higher seasonal amount of total litter fall. This finding is in line with litter fluctuations for jack pine in eastern Ontario (Weber 1987) and northern Alberta (Fyles et al. 1986). It also is consistent with litter measurements in a mixed forest in New Hampshire (Gosz et al. 1972), khasi pine (P. kesiya) in northeastern India (Das & Ramakrishnan 1985), and eucalyptus in northern Australia (Lamb 1985).

Storms may cause the premature fall of many types of plant organs. In this study, storms generally influenced the fall of needles and twigs. Most of the premature needle fall occured with the autumn storms, whereas twig fall occurred mainly with early spring storms (Figs. 16,17) when twigs were brittle due to the previous dormant conditions.

The amount of the reproductive fraction was also higher in the 1991 growing season for both red pine and white spruce (Fig. 18). Furthermore, the presence of the rain and wind storms during this time likely had resulted in an obscure pattern for the reproductive fraction of litter fall. The pattern is instead more marked during the 1992 growing season in which the amount of reproductive litter of pine and spruce was increasing and decreasing, respectively, toward the end of the growing season. In addition to the differing distribution of rain fall, the monthly average of day temperatures was higher during the 1991 growing season (12.75 ^{0}C) than during the 1992 growing season (12.03 ^{0}C) (Anon. 1992). The favourable temperature might have promoted a greater production in the 1991 growing season (Barbour et al. 1980, Facelli and Pickett 1991).

The third group of controlling factors is the physiological factors of trees, particularly the process of organ abscission. This factor is species specific (Millar

1974). Red pine and white spruce did not show a distinctively seasonal pattern of litter fall throughout the year. There tends to be a higher rate of litter deposition in late autumn for both species, especially for red pine (Figs. 19). However, the values were not significantly different suggesting a relatively constant monthly pattern of total litter fall throughout the whole season. This finding is in agreement with other investigators working on similar species in the boreal forest of Russia (Rodin and Bazilevich 1969) as well as in Minnesota (Perala and Alban 1982). Litter fall patterns of other conifers such as Scots pine (P. sylvestris) are distinctivly seasonal (Berg and Agren 1984), as are those of red spruce (P. rubens) (Gosz et al. 1972).

The rate of litter fall is also affected by stand density (Barbour et al. 1982, Rodin and Bazilevich 1969). Especially under a managed plantation, effects of density is important, since it not only determines the success of natural regeneration through seedling germination, but also affects the nature of the decomposition process (Bray and Gorham 1964). Differences in litter accumulation resulted from different tree spacings can either stimulate or restrict biological processes through the microenvironment it creates. Furthermore, the organic composition of plant litter influences the forest floor condition relative to the nature of the decomposition process (Facelli and Pickett 1991).

5.3. Litter decomposition

5.3.1. Litterbag study

Figure 21 illustrates the loss percentage of litter mass during the whole study period. In general, a greater mass loss occured with closer spacings. After 18 months (Table 14), the order ranked from wide pine (24.92 %), wide spruce (25.94 %), medium pine (26.89 %), medium spruce (27.09 %), close pine (27.92 %), to close spruce (29.54 %). Consequently, the decomposition rate constant was lowest in wide pine where the decomposition was slowest, and it was highest in close spruce where the decomposition was the most rapid. For both species at all spacings, litter decomposition was highest in the first growing season (May-October 1991), followed by the winter season (November 1991-April 1992), and the second growing season (May-October 1992). Analysis of variance showed significant effects of species and spacings on litter decomposition (Table 15).

There were no significant differences in mass loss (p=0.84) between: close pine and medium pine, medium pine and medium spruce, wide pine and wide spruce, and medium pine and wide spruce. Obviously, the process of decomposition was affected by either(/both) species or(/and) spacing. However, between the two factors spacing shows the stronger effect on decomposition (Table 15).

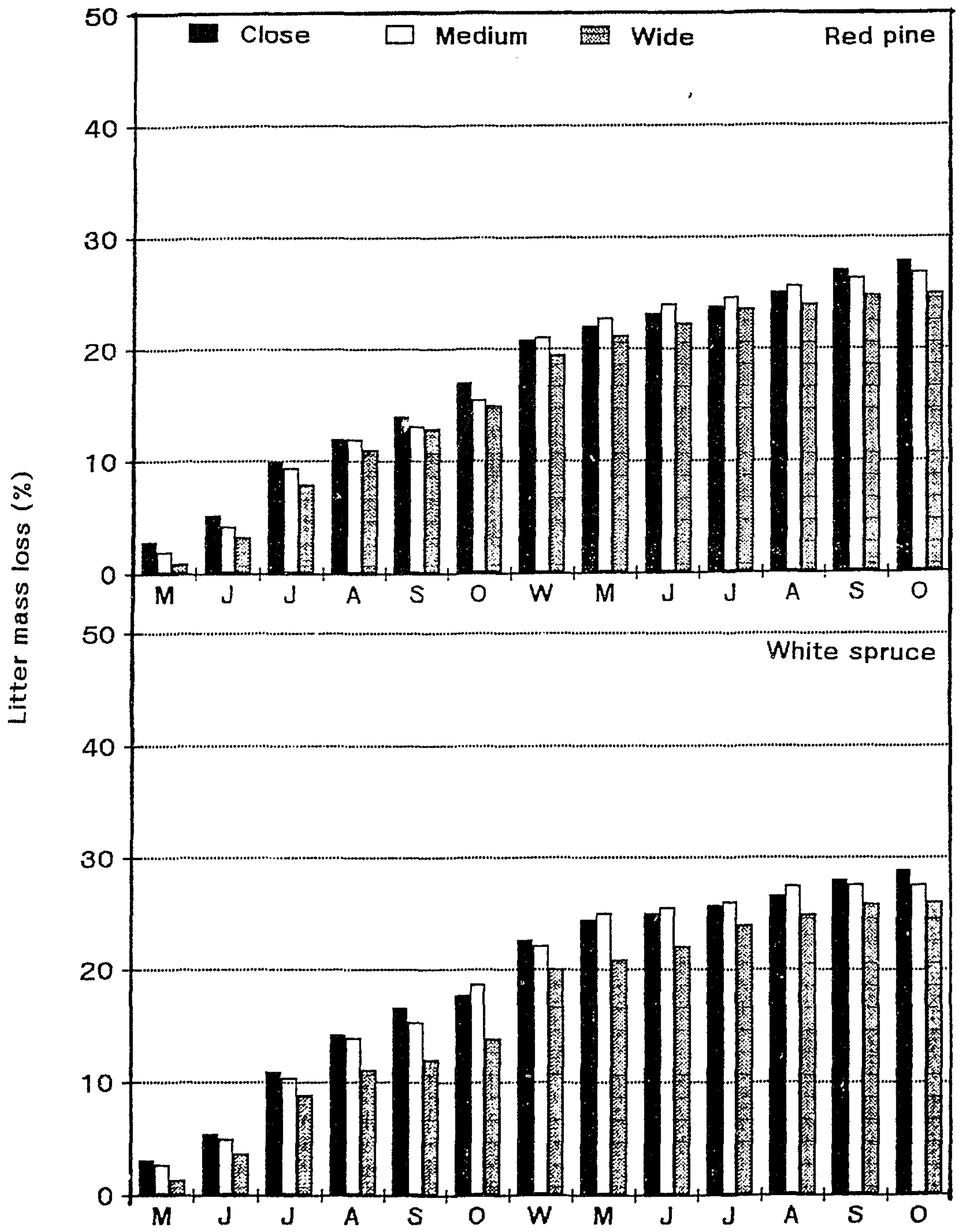

Fig 21. Mass loss of red pine (Pr) and white spruce (Sw) litter measured by decomposition bags, placed in three spacing regimes (close, medium, wide), and collected monthly during growing seasons and once during winter season (W).

Table 14. Percentage of mass losses in red pine (Pr) and white spruce (Sw) litter at three spacing regimes (close: 1.8 m^2, medium: 2.7 m^2, and wide: 3.6 m^2).

Plot	Mass loss (%) after		
	6 months	12 months	18 months
Pr 1.8	16.99 ab	23.16 a	27.92 a
Pr 2.7	15.36 ac	21.08 b	26.89 ab
Pr 3.6	14.86 cd	19.44 c	24.72 c
Sw 1.8	17.72 b	22.58 ab	29.54 d
Sw 2.7	18.68 b	22.13 ab	27.09 a
Sw 3.6	13.82 d	20.06 bc	25.94 bc

Note: Unlike letters in a column indicate values significantly different at 0.05 level determined by the Tukey-HSD test.

Table 15. The ANOVA summary for the litter mass loss after 6, 12, and 18 months.

Source of variation	F values		
	After 6 months	After 12 months	After 18 months
Species	6.143*	2.165	6.577*
Spacing	48.367***	24.724***	19.843***
Interaction	10.443***	3.678*	0.773

Note: *, **, and *** indicate values which differ significantly at 0.05, 0.01, and 0.001 level, respectively, determined by the Tukey-HSD test.

Table 16. The decomposition factor and times to 95% decay based on the decomposition bag study.

Plot	Decomposition factor (k) after			Time to 95 % decay (yr)
	6 months	12 months	18 months	
Pr 1.8	0.37 a	0.26 a	0.22 ab	13.6 a
Pr 2.7	0.33 b	0.24 b	0.21 a	14.3 ab
Pr 3.6	0.32 b	0.22 c	0.19 c	15.8 b
Sw 1.8	0.39 c	0.26 a	0.23 b	13.0 a
Sw 2.7	0.41 d	0.25 ab	0.21 a	14.3 ab
Sw 3.6	0.30 e	0.22 c	0.20 ac	15.0 b

Note: Unlike letters in a column indicate values significantly different at 0.05 level determined by the Tukey-HSD test.

Table 17. The ANOVA summary for the k values and the time to 95 % decay.

Source of variation	F values			
	k after			time to 95% decay
	6 months	12 months	18 months	
Species	135***	2.62	1.53	0.26
Spacing	203***	85.7***	10.3**	13.2**
Interaction	108***	1.15	0.38	0.10

Note: ** and *** indicate values which differ significantly at 0.01 and 0.001 level, respectively, determined by the Tukey-HSD test.

The decomposition factor (i.e., k values) and the times to approach a steady state accumulation (i.e., 95 % decay) based on the standard decomposition bag are presented in Table 14. The times to 95% decay suggest that a 13 to 16 year period without disturbance of the litter layer (such as fire or severe flooding) would be necessary for red pine and white spruce litter to reach a steady accumulation state. It is shown that such a state will first be approached by close spruce and pine sites, succeeded by medium spruce and pine sites, and finally by wide spruce and pine sites.

5.3.2. Temperature and Decomposition

Results of this laboratory study are presented in Figure 21 and Table 16. It was found that the rate of mass loss generally increased from 5, 15, to 25 ^{0}C but dropped at temperature 35^{0}C. The Q_{10} values ranged between 1.71-1.78 for red pine needles, and 1.88-1.84 for white spruce needles. Such trends are consistent for fresh litter of red pine and white spruce. Conversely, the decomposing litter showed a different trend toward the increasing temperature. The rate of mass loss of decomposing litter consistently increased over the whole ranges (the Q_{10} values never became < 1.00), indicating a continual process of decreasing mass. As litter accumulates on the forest floor, the decomposition rate may grow slower with time. However, decomposition never ceases, but instead approaches an asymptotic level indicated by a steady-state condition (Minderman 1968, Odum 1983). Moreover, species influence was relatively negligible in the decomposing litter (Table 17) as indicated by the non significant differences for their Q_{10} values. Witkamp (1976) reported, after studying decomposition of various leaf litters, that freshly fallen litter was more responsive to environmental changes. This may partly be due to the higher concentration of nutrient elements and soluble carbohydrates in fresh litter which cause it to be chemically and physically susceptible to microbial attack (Waring & Schlesinger 1985).

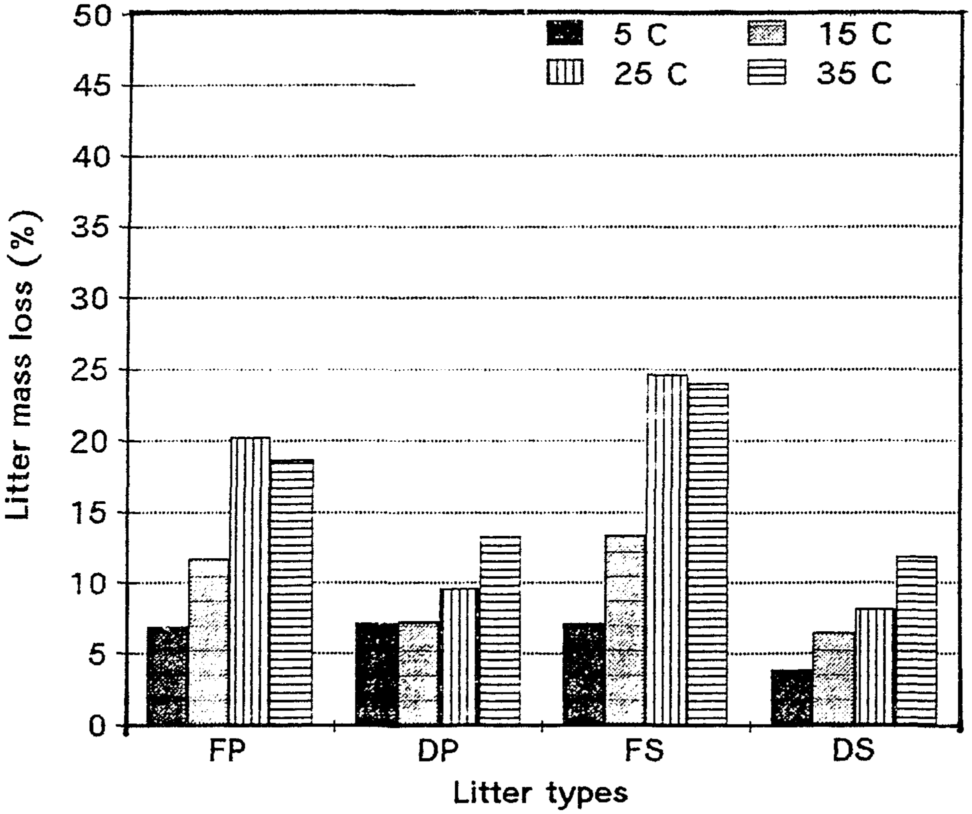

Fig 22. Mass losses of red pine fresh (FP) and decomposing (DP) litter, white spruce fresh (FS) and decomposing (DS) litter in response to the temperature increase (5, 15, 25, and 35 °C) observed after a 100 day-incubation period.

Table 18. Mass losses (%) on litter of fresh pine (FP), partially decomposed pine (DP), fresh spruce (FS), and partially decomposed spruce (DS) in response to temperature increases.

Tempe-ratures (^{0}C)	Litter types			
	FP	DP	FS	DS
5	6.8 a	7.1 a	7.1 a	3.9 a
15	11.7 b	7.3 ab	13.2 b	6.5 ab
25	20.2 c	9.6 b	24.6 c	8.1 bc
35	18.7 d	20.8 c	24.0 c	11.8 c

Note: Unlike letters in a column indicate values significantly different at 0.05 level determined by the Tukey-HSD test.

Table 19. The ANOVA summary for the effect of temperature on litter mass loss.

Source of variation	F values
Temperature	287.151 ***
Litter types	251.066 ***
Interaction	36.522 ***

Note: *** indicates values which differ significantly at 0.001 level determined by the Tukey-HSD test.

Table 20. The Q_{10} values on litter of fresh pine (FP), partially decomposed pine (DP), fresh spruce (FS), and partially decomposed spruce (DS) in response to temperature increases.

Litter types	Q_{10} values at:		
	5-15 (^{0}C)	15-25 (^{0}C)	25-35 (^{0}C)
FP	1.71 a	1.78 a	0.89 a
DP	1.03 c	1.31 c	1.49 b
FS	1.88 b	1.84 b	0.98 a
DS	0.37 c	1.23 c	1.46 b

Note: Unlike letters in a column indicate values significantly different at 0.05 level determined by the Tukey-HSD test.

Table 21. The ANOVA summary for the Q_{10} values in response to the temperature increases.

Source of variation	F values
Temperature	12.923 ***
Litter type	8.465 ***
Interaction	20.906 ***

Note: *** indicates values which differ significantly at 0.001 level determined by the Tukey-HSD test.

As temperature increased from 25 to 35 °C, the decomposition rate decreased (Tables 18, 19). Moore (1986) reported that the increasing decomposition rate of Douglas-fir and oak leaf litter from 0 to 40°C was reduced abruptly as the temperature reached 40°C. High rates of decomposition were maintained longer in fresh litter of white spruce than of red pine (Figure 22).

5.3.3. Decomposition and substrate quality

The results of this 18 month laboratory study are presented in Figure 23. In general, pine litter contained higher percentages of lipid, cellulose, and lignin than spruce litter. After a 12 month period, the differences in lipid content were significant (Table 20). The difference in cellulose content continued for approximately one year. At month 18, the values seemed to approach a similar level as these differences in pine and spruce litter became non significant.

The lignin content of pine and spruce litter did not differ signficantly during the whole study period. Unlike the concentrations of other organic components, lignin content in both species increased as the decomposition proceeded to month 6. From this point on, it slowly decreased approaching a similar value at month 18 (Fig. 23).

Table 22. Mass remaining of major organic components in red pine and white spruce litter during the study period (mean values of similar organic components are being compared **per** species).

Organic component	Month 6 (%)	Month 12 (%)	Month 18 (%)
Red pine			
Lipid	83.67 a	74.52 a	69.26 a
Cellulosse	67.43 a	26.48 a	19.82 a
Lignin	119.27 a	116.45 a	112.44 a
White spruce			
Lipid	80.15 a	62.76 b	58.63 b
Cellulose	57.46 b	20.89 b	18.04 a
Lignin	122.15 a	117.44 a	108.67 a

Note: Unlike letters in a column indicate values significantly different at 0.05 level determined by the Tukey-HSD test.

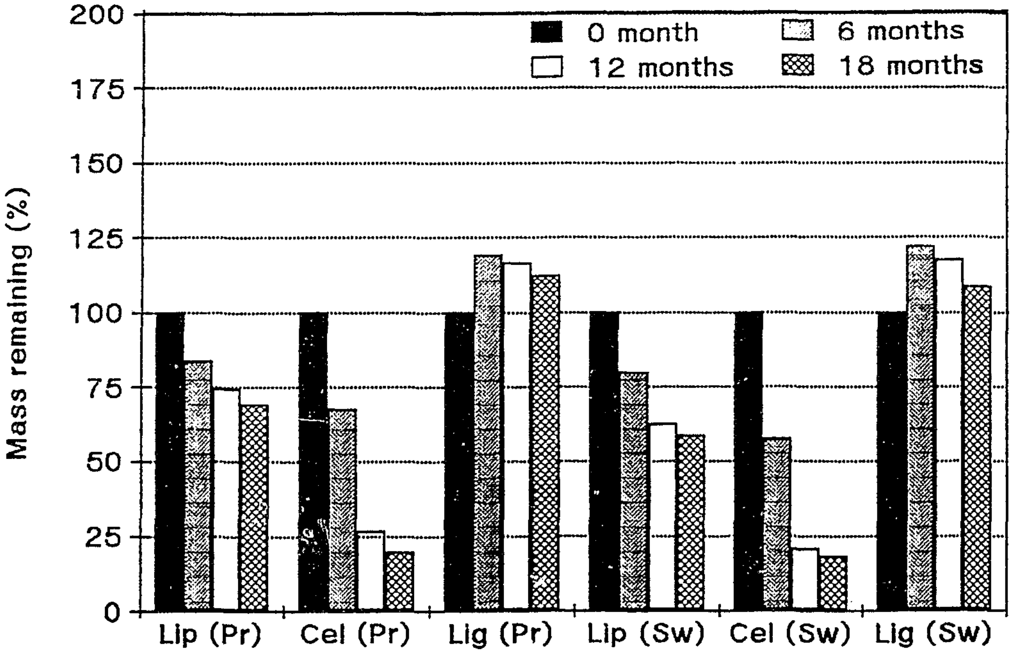

Fig 23. Seasonal mass remaining of red pine (Pr) and white spruce (Sw) litter organic components: lipid (Lip), cellulose (Cel), and lignin (Lig) observed during the study period.

5.3.4. Decomposition: a synthesis

5.3.4.1. The species and spacing factors in the decomposition process

The effects of tree spacing on decomposition processes are likely produced by changes in the microenvironment created within the stands. It was found that the rates of decomposition were enhanced by the improved microenvironmental conditions surrounding the litter. The trend of decomposition rates within the plantation follows that of below ground temperature readings (Figs. 10-11). The process of decomposition mainly occurs in a soil environment involving soil microorganisms. The rates were higher in closer spacing plots due to the warmer below ground temperatures. Bonan and Van Cleve (1992) calculated the increase of carbon loss during 25 years of decomposition of white spruce litter. The increase of mass loss was between 4-19 $g.m^{-2}.yr^{-1}$ with the 5^0C soil warming. Among the vegetation types in interior Alaska, a 10^0C increase in heat was associated with a 0.2 cm decline in forest floor thickness (Van Cleve and Yarie 1986). Soil warming is reported to increase foliage N concentration in black spruce (Van Cleve et al. 1990), and consequently a better litter quality for decomposition.

The higher rate of decomposition due to the increased temperature is also related to the increased activity of microorganisms (Witkamp 1976). The effect of temperature alone was studied by Daubenmire and Prusso (1973) using the litter of coniferous and deciduous forest trees incubated in the laboratory. They found that among the 13 species, 9 species showed an increase in mass loss (i.e., 1.5 to 6 %) by increasing the temperatute from 10 to 15 ^{0}C. In their experiment they counted the microbial population and concluded that temperature affected decomposition rate through its controls on microbial populations in the litter. A close correlation between temperature and CO_2 evolution has been found in many field studies (e.g. Edwards 1975; Kowalenko et al. 1978). Witkamp (1966) indicated that leaf litter decomposition is controlled, in order of importance, by temperature, bacterial density, moisture, and time since litter fall.

Heat stimulates microbial activity because enzymatic metabolism is temperature dependent (Bunnell et al. 1977). Thermal kinetic energy breaks the chemical bond of molecules formed during plant development, and the rate of destruction of these substances increases exponentially with temperature in the form suggested by the Arrhenius equation (Odum 1983):

$$dS/dt = A \exp(-E_a/RT)$$

where:

dS/dt = the reaction rate (change of quantity of substrate per unit time)
A = a constant
E_a = the activation energy
R = the gas constant (0.008314 $kJK^{-1}mol^{-1}$)
T = absolute temperature (K)

This negative exponential model of decomposition rate implies an optimum level of temperature for bacterial processes. In the present study this optimum level was observed at 35 ^{0}C (Fig. 21, Tables 18, 19). Above the optimum temperature, enzymes will be denaturated (Quinlan 1981), and once denatured they cannot be replaced. This condition is reported to occur sooner on litter with low quality substrates. Daubenmire and Prusso (1963) reported that at 30^{0}C the rate of decomposition was sustained for a 16-week period, but it lasted for only a 5-week period when a poorer quality substrate was used. Thus, the higher the quality of the litter, the longer a rapid rate of decomposition is sustained.

Soil moisture seemed to have little influence on decomposition process in this study as was also the case with other studies conducted in northern boreal climates (Flanagan and Bunnell 1980, Fox and Van Cleve 1983). Soil moisture was generally high in wide spruce and lowest in close pine (Fig. 15). Soil moisture content therefore was not a limiting factor in the process of decomposition in the study site, since the higher rates generally occured in the closer spacing site. It was reported (Towill and Siczkar 1988) that the relatively uniform sandy soil characteristics of the plantation have resulted in a moderate to rapid drainage throughout the area. And even though species and spacing affected the soil moisture content within the site, the resultant differences did not influence the process of decomposition. In other words, the range of soil moisture throughout the plantation seem to provide a sufficient moisture supply for the process of decomposition.

Relative humidity is another microenvironmental factor that influences the process of decomposition. It was shown (Figs. 12-14) that the process of decomposition in the plantation was also affected by relative humidity. A similar trend was found in which the highest decomposition rate in close spruce sites was supported by the highest reading of relative humidity. The importance of relative humidity in decomposition processes has received little attention. Most decomposition studies concentrated on either the organisms responsible for litter breakdown or the chemical composition of the substrate during the process. On the other hand, studies investigating the effects of physical factors have mainly focussed on the influence of temperature. Relative humidity influences the amount of water in the substrate which is available to microorganisms, and in turn influences the activity of the decomposers. Nagy and Macauley (1982) found the relationship between mass loss rate and relative humidity to be roughly linear. Since relative humidity is related to the moisture content of the litter, it can be concluded that white spruce litter contains more moisture than red pine litter, a finding that is also consistent with the data for the fresh litter of both species (1.82:1 for white spruce).

Among the two conifers, white spruce litter produces a higher quality substrate than red pine litter with respect to decomposition. Such quality can be viewed from several standpoints including the enhanced microenvironment (below ground temperature, soil moisture, relative humidity, and soil pH) as well as the organic chemicals found in these species (Fig. 23). In terms of needle physical characteristics, the needle-like leaves of both species display different features in size and toughness. White spruce needles are smaller than red pine needles, and thus provide more surface area (per volume) for microbial attack. Furthermore, pine needles are found to be harder than spruce needles due possibly to the higher content of refractory fractions in pine needles (i.e. lignin, cellulose, and lipid) (Fig. 23).

5.3.4.2. The time factor in the decomposition process

Both red pine and white spruce exhibited a short period of rapid leaf litter decay followed by a longer period of slower decomposition (Fig. 21). The decomposition rate constant was highest during the first 6 months, afterwards decomposition was reduced with time. Table 16 shows that the rate constant (k) of close pine, for example, was 0.37 during the first 6 months, then it decreased to 0.26 after 12 months, and to 0.22 after 18 months of decomposition.

The chemical composition of leaf litter can be conventionally divided into labile compounds (such as simple carbohydrates) versus refractory compounds (lipids, polysaccharides, and lignin) (Kogel et al. 1988). The reduction in the decomposition rates may be due in part to the rapid loss of the labile components. Simple carbohydrates such as sugar and starch are water soluble and are easily leached with the presence of water in the soil (Seastedt et al. 1983, Yavitt and Fahey 1986). Subsequent breakdown of the refractory compounds in leaf litter is slower and may account for the asymptotic shape of the negative exponential curves of mass loss over time (Minderman 1968, Olson 1963, Stohlgren 1988).

Berg and Ekbohm (1991) reported the changes in chemical composition during leaf decomposition of seven species of pines, birch, and alder in Sweden. It was indicated that concentrations of water-soluble substances decreased quickly (within one year of litter fall) before reaching relatively similar and stable levels in all litter types. The ethanol-soluble fractions (including lipids) of the litter remained relatively constant, and the lignin fraction, in fact, increased as decomposition proceeded. Figure 23 shows the similar trend for lignin fraction in which it increased as the process progressed. For both red pine and white spruce, the increase was almost parallel with the accumulated mass loss.

Hart et al. (1992) reported that water soluble compounds of ponderosa pines decreased rapidly during the first 3 months of decomposition which accounted for about half of the total mass loss from litter over 2-year period. Lignin increased rapidly during the first 3 months, and cellulose declined in concert with the litter mass loss. The loss of cellulose was reported to account for about half of the total mass loss in the litter during the first 2-year period.

5.4. Organic accumulation

The oven-dried mass of the soil organic layer, its decomposition rate based on mass-balance approach, and the steady accumulation time are presented in Table 23. The greatest biomass of the organic layer was found in close pine followed by medium pine, wide pine, close spruce, medium spruce, and wide spruce (Fig. 24). Significant differences were found between close and wide spacings of each species as well as between species at each spacing. The value of k was highest in close spruce, and lowest in wide pine. Compared to the steady accumulation time results from the litterbag study (Table 14), the length of time resulting from the mass-balance approach was higher by approximately 3 years (Table 23). Such an accumulation time would be reached earliest in close spruce, and latest in wide pine, following the trend of k values. However, almost no significant differences were found among all the plots, except between the close spruce and wide pine.

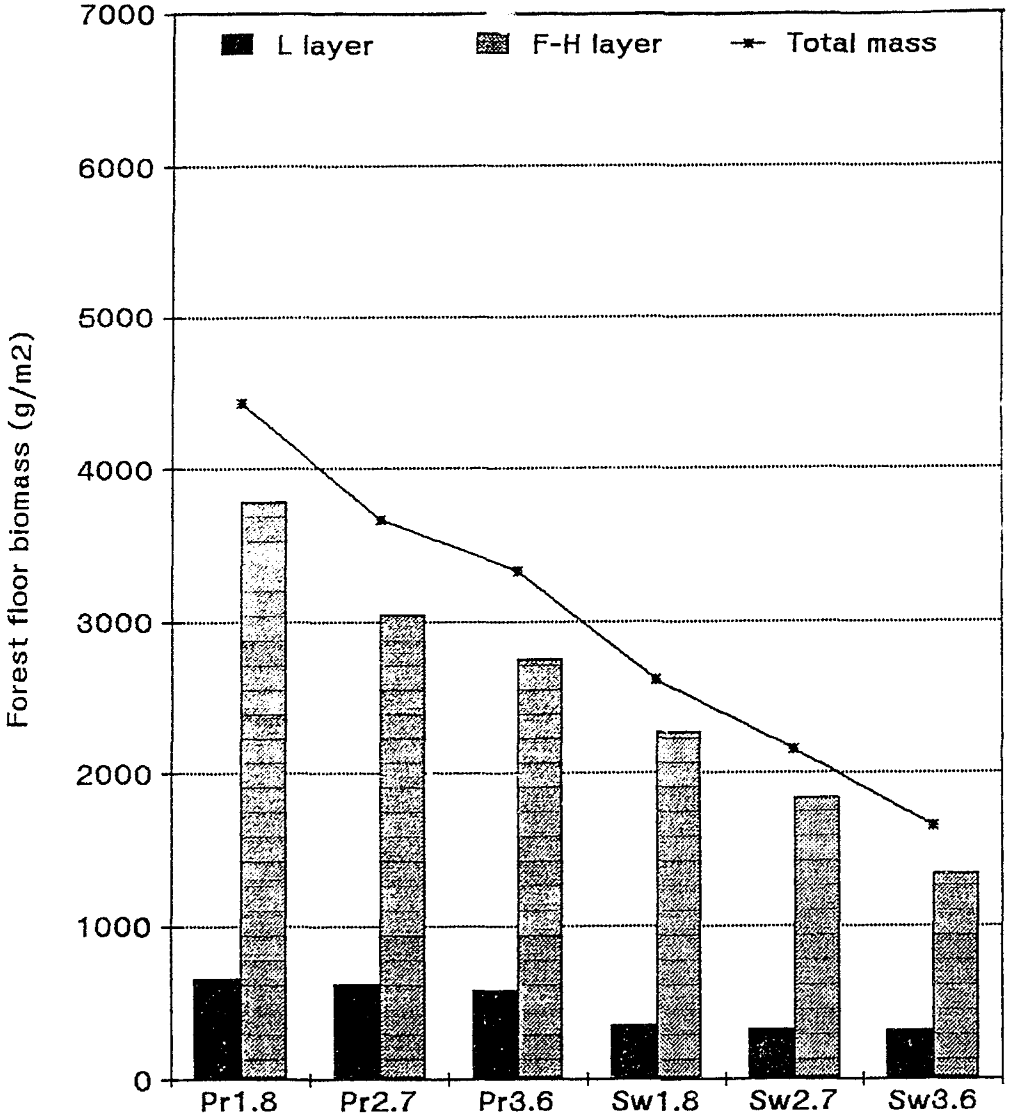

Fig 24. The organic accumulation in the forest floor of 40-year-old plantations of red pine (Pr) and white spruce (Sw) under three spacing regimes (1.8 m^2, 2.7 m^2, and 3.6 m^2) represented by fresh (L) and decomposing (F-H) litter layers.

Table 23. Forest floor biomass (g/m^2), decomposition rate (k) and steady accumulation time (95% decay) under three spacing regimes of 40-year-old red pine and white spruce plantations in Thunder Bay.

Plot	Oven-dried mass			k values	Time to 95% decay (yr)
	L	F-H	T		
Pr 1.8	653.17a	3782.07a	4435.24a	0.17ab	17.7 ab
Pr 2.7	619.22a	3048.40b	3667.62b	0.17ab	17.7 ab
Pr 3.6	576.43a	2754.62c	3331.05b	0.16a	18.8 a
Sw 1.8	353.59b	2270.05c	2623.64c	0.18b	16.7 b
Sw 2.7	328.13b	1830.92d	2159.05c	0.17ab	17.7 ab
Sw 3.6	316.78b	1336.22d	1653.00d	0.17ab	17.7 ab

Note: Unlike letters in a column indicate values significantly different at 0.05 level determined by the Tukey-HSD test.

Table 24. The ANOVA summary for the forest floor mass (i.e. L, FH, and Total layers), k values, and the time to 95 % decay.

Source of variation	F values				
	L	F-H	T	k	Time
Species	1245***	450**	604***	4.55*	8.81*
Spacing	17.6**	101**	69.1**	3.46*	1.83
Interaction	7.41*	2.68	9.23*	1.27	2.41

Note: *, ** and *** indicate values which differ significantly at 0.05, 0.01 and 0.001 level, respectively, determined by the Tukey-HSD test.

The forest floors under various species-spacing combinations differed in appearance particularly because of the character of the tree needles which represented more than 70 % of the total litter fall mass. Such differences were more apparent between species, and less between the spacings. However, values on decomposition rates based on the mass balance approach showed that in general all species-spacing treatments exhibited a relatively similar rate, except for the close spruce and wide pine (Table 23). The close and random distribution of the sites within this spacing trial (Fig. 2 in Chapter 2) might partly be responsible for the masked environmental effects produced by different species within a plantation. Several different species-spacing treatments are located adjacent to each other which may result in little difference in the forest floor development.

However, the mass balance values are useful for comparisons with those produced by the litterbag studies (Table 14). All k values derived from the litterbag studies are higher than the mass balance values suggested in Table 23, resulting in a shorter time of the former to attain a steady-state condition. Leaf litter decomposition rates obtained from litterbag studies would clearly overestimate long-term decomposition rates in the entire forest floor (Aber and Melillo 1991). The organic material in the lower profiles of the forest floor generally decomposes more slowly than the material in the upper profile (Waring and Schlesinger 1985, Yavitt and Fahey 1986). Moreover, branches and cones often decompose at less than half the rate of foliage (Edmonds 1987, Edmonds et al. 1986, Fogel and Cromack 1977), and large woody litter (>15 cm diameter) decomposes even more slowly (Harmon et al. 1987). The lower decomposition rates estimated by the mass balance approach implies that although the non-leaf litter only comprises a small fraction of the total litter fall (<30%), it may give a significant contribution to the organic accumulation rate for the forest floor.

The times to accomplish 95% decay suggests about 17 and 19 years for spruce and pine, respectively, would be required to reach a steady state accumulation. These results do not necessarily imply static conditions (Odum 1983). It is a dynamic mechanism of an ecosystem to be functioning as a buffer toward the ecological changes caused by natural or human disturbances (Waring and Schlesinger 1985). It is assumed that one aspect of ecosystem development involves the readjustment of all components toward an asymptotic condition. It is a stage in which no net additions of matter or energy occurs (Olson 1963). This condition is controlled by the rates of production as well as decomposition. Since net primary production shows an inverse relationship with the organic accumulation in regard to the environmental effects, such conditions are largely determined by the rate of decomposition (Minderman 1968).

The concept of steady state in the forest floor implies a number of ecological insights. Some biological processes (for instance, seed germination or nutrient mineralization) may be specifically delayed until the accumulated litter has approached its steady-state development (Olson 1963, Rodin and Bazilevich 1969). Such an advanced stage of litter accumulation also has several implications for soil properties that determine a better medium for supporting the biological processes. Potential applications include the improvement of soil physical properties (such as granulation and water holding capacity); soil cation exchange capacity; and, particularly important, soil nutrient supply (Brady 1990).

6. SUMMARY

The rate of litter decomposition was greatest in close spacing of white spruce, followed by close spacing of red pine, medium spacing of white spruce, medium spacing of red pine, wide spacing of white spruce, and wide spacing of red pine. The rate of decomposition increased proportionally to litter and soil temperatures as well as to ground relative humidity. The physical and chemical quality of litter, and also pH values, indicated that white spruce litter decomposed faster than red pine litter. Statistical analysis also indicated that overall the effects of spacing were stronger than the effects of species suggesting that species influences would only be reliable under similar spacing regimes. Moreover, no interaction factors were found to be influential.

Unlike the trend found in decomposition rates, litter biomass was highest in the close spacing of red pine. This was followed by medium spacing of red pine, wide spacing of red pine, close spacing of white spruce, medium spacing of white spruce, and wide spacing of white spruce. Further studies particularly on nutrient dynamics within the plantation would be an important step to determine which treatment combination(s) of species and spacing produce(s) the best nutrient conditions for plant growth. This has direct bearing on site productivity and plantation management.

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