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EFFECTS OF FOREST SITE PREPARATION METHODS ON CARABID BEETLE (COLEOPTERA: CARABIDAE) DIVERSITY.

BY

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SHORT TITLE

Effects of forest site preparation methods on carabid diversity.

ABSTRACT

The objective was to analyze the effects of logging and prescribed burning on carabid beetles (Coleoptera: Carabidae) at a jack pine stand and white spruce plantations in order to assess short-term impacts of these forestry practices on the diversity of this beetle group. In addition, soil scarification was also included at the jack pine stand. Based on previous reports on forest disturbance influences on carabids, it is hypothesized that short-term effects of studied forestry practices do not reduce carabids' diversity. Four carabid assemblage characteristics were compared: a) number of catches; b) dry mass; c) species richness; and, d) diversity index. Species responses and dry mass distributions were also investigated. Treatments either increased or maintained studied variables compared with control sites. Diversity indices were highest in burnt-over areas. Similar response patterns of species or groups of species were observed in both forest types. The presence of regenerating sites among the natural landscape increased carabid diversity.

RÉSUMÉ

L'objectif était l'analyse des effets de coupes forestières et du brûlage dirigé sur les Carabidae dans une forêt de pins gris et des plantations d'épinettes blanches afin d'en évaluer les impacts à court-terme sur la biodiversité de ce groupe de coléoptères. En plus, le scarifiage du sol a aussi été inclus au site de la forêt de pins gris. En se basant sur les études antérieures relatant les effets de perturbations forestières sur les Carabidae, l'hypothèse est que les effets à court-terme des pratiques forestières à l'étude ne diminuent pas la biodiversité des Carabidae. Quatre caractéristiques des assemblages de Carabidae sont comparées: a) nombre de captures; b) masse sèche; c) nombre d'espèces; et, d) indice de diversité. Les réponses des espèces ainsi que les distributions de masse sèche ont aussi été étudiées. Les traitements ont soit augmenté ou maintenu les variables étudiées à comparer avec les sites contrôles. Des réponses similaires d'espèces ou de groupes d'espèces ont été observées dans les deux types de forêts. La présence d'aires en régénération parmi des sites naturels de forêt semble permettre une biodiversité plus élevée de Carabidae.

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GENERAL INTRODUCTION

For the past twenty years or so, several world conferences and commissions have emphasized our concern towards sustainable management of natural resources: 1) the 1972 United Nations Conference on the Human Environment held in Stockholm; 2) a World Commission on Environment and Development (WCED) in 1983 which produced the Brundtland Report (WCED, 1987); and, more recently, 3) the 1992 United Nations Conference on Environment and Development (UNCED) held in Brazil and referred to as the "Earth Summit". The Brundtland Report defined "sustainable development" as a resource development that would meet present needs without compromising the ability of future generations to meet theirs (WCED, 1987). Following trends promoting implementation of sustainable forestry practices, Canada signed, in March 1992, its first Canada Forest Accord and released a new national forest strategy entitled "Sustainable Forests: a canadian commitment" (Forestry Canada, 1992). The goal of the Forest Strategy includes the protection of forest ecosystem integrity, sustainability, and biodiversity.

It is now widely accepted that biological diversity is essential for providing sustainable forest ecosystems (Forestry Canada, 1993). The earth's biological diversity (commonly shortened to "biodiversity") received international attention in 1992 at the Earth Summit by the creation of a Biodiversity Convention which was signed first by Canada and considered as a key element to a global strategy (Prescott, 1994). Furthermore, efforts are now under way, in Canada, to promote and conserve biological diversity at all levels. For example, a National Strategy for the Conservation of Biodiversity is due in November 1994. Biodiversity enables organisms to adapt to a changing environment (McNeely *et al.* 1990) but is susceptible to variations in environmental conditions (Kim, 1992). From these facts it appears important to: 1) manage ecosystems on a sustainable basis to maintain essential ecological processes (U.S. Congress, 1987); 2) preserve landscape diversity (Suffling *et al.* 1988; Primack, 1993); 3) protect habitats; 4) preserve wild biological genetic resources; and, 5) monitor biodiversity as it is affected by habitat disturbances (McNeely *et al.* 1990). Thus, monitoring and understanding the effects of management practices are essential in order to utilize ecosystems and natural resources on a sustainable basis (McNeely *et al.* 1990).

Although a rapid depletion of global biodiversity justifies our present concern, it is not the first time for biodiversity to diminish. Through fossil records, scientists have been able to identify five major extinction periods in the earth's history. However, past mass extinctions were the result of natural processes whereas the present rate of species loss is mainly the result of human disturbances such as habitat alterations, over-harvesting, pollution, and demographic pressures (McNeely *et al.* 1990). With the rapid destruction of the world's most diverse ecosystems, especially in the tropics, most experts conclude that perhaps up to a quarter of the earth's total biological diversity will be at serious risk of extinction in the next 20-30 years (Raven, 1988). By many indications, the world is already experiencing extinction rates of greater scale and impact than at any previous time in the earth's history (Wilson, 1988; Primack, 1993). More species than ever before are threatened with extinctions, with thousands - mostly insects - disappearing each year, many before they are even described (McNeely *et al.* 1990). Species extinctions were balanced or exceeded by new species evolution in past geological times, whereas contemporary extinction rates exceed known rates of species evolution (Primack, 1993).

Many attempts have been made to define the broad concept of *biodiversity*. The most widely accepted definition was proposed in 1987 by the U.S. Government's Office of Technology Assessment (U.S. Congress, 1987):

> "Biological diversity refers to the variety and variability among living organisms and the ecological complexes in which they occur. Diversity can be defined as the number of different items and their relative frequency. For biological diversity, these items are organized at many levels, ranging from complete ecosystems to the chemical structures that are the molecular basis of heredity. Thus, the term

> encompasses different ecosystems, species, genes, and their relative abundance."

There are three levels of biodiversity: 1) genetic diversity is the sum of genetic information contained in the genes of organisms; 2) species diversity is the variety of living organisms on earth estimated to be between 5 and 50 million or more, of which only about 1.4 million are described; and, 3) ecosystem diversity relates to the variety of habitats, biotic communities, and ecological processes in the biosphere (McNeely *et al.* 1990). The loss of biological diversity is occurring at all these levels (Primack, 1993).

Ecologists are interested in biological diversity and its measurement because: 1) diversity has always been an important concept in ecology; 2) diversity measurements are often perceived as indications of ecosystems' condition; and, 3) considerable debate surrounds diversity and its measurement (Magurran, 1988). The diversity concept remains hard to grasp mainly because several models and indices exist to describe and measure it, and also because it consists of two components, namely species variety and relative abundance (Magurran, 1988).

Microorganisms and invertebrates are increasingly becoming subjects of studies related to biodiversity. However, in Canada, the impacts of human-caused forest disturbances such as logging and harvesting, prescribed burning, and soil scarification on the diversity of carabid beetles, an important group of soil predators, have been little documented. The objective of the present investigation is twofold: 1) analyze carabid beetle assemblages after disturbance in two different forest types, namely a jack pine (*Pinus banksiana* Lamb.) stand in Ontario and white spruce (*Picea glauca* (Moench) Voss) plantations in Québec; and, 2) assess the short-term effects of these forestry practices on the diversity of carabids. On the basis of previous reports on the effects of forest site management practices on soil properties and on carabids, it is hypothesized that short-term effects of studied forest site preparation methods do not reduce carabid diversity.

CHAPTER 1

LITERATURE REVIEW

I. MEASUREMENT OF BIODIVERSITY

Species richness

Species richness is the oldest concept of species diversity (Krebs, 1989). It is assessed in two basic forms: 1) species density i.e. the number of species per unit area; and, 2) a simple species count. A number of simple indices have been derived using S (species richness) and N (the total number of individuals sampled). These simple indices include Margalef's diversity index and Menhinick's index (Magurran, 1988). However, species richness indices do not take into account relative abundances of species within a particular community (Magurran, 1988).

Diversity indices

In contrast with species richness indices, diversity indices all take into account the number of species (species richness) and evenness (relative abundance of each species). High diversity measures are associated with high evenness which occurs when species approach equal relative abundance. Evenness and species richness are given different weights according to the diversity index used (Magurran, 1988). One of the most widely adopted diversity index was borrowed from *information theory* and was independently derived by Shannon and Wiener (Magurran, 1988). Information specialists wish to predict the next letter in a coded message. Applied to ecological studies, the question could be "*How difficult would it be to predict the species of the next sampled individual?*". The Shannon-Wiener index (H) is a measure of this uncertainty: the higher it is, the greater the uncertainty, thus diversity. This diversity index increases with an increasing number of species as well as when species are more equally distributed. Furthermore, if the Shannon-Wiener index is obtained for a number of samples, the indices will be normally distributed (Taylor, 1978) and it is then possible to use the analysis of variance for statistical comparisons of diversity estimates. In addition, the ratio of the observed diversity to maximum diversity (i.e. when all species are equally abundant) is a measure of evenness, also referred to as "equitability". The Brillouin index (HB) is another "information index" but is less utilized because it involves rather long and complicated calculations.

A second group of diversity indices are the dominance measures which put more weight on the abundance of the commonest species rather than on species richness. Examples of dominance measures are the Simpson's index, McIntosh's measure of diversity, and Berger-Parker index (Magurran, 1988). Indices biased towards species richness, like the Shannon-Wiener index, are more effective to detect differences between sites than indices which emphasize the dominance/evenness component of diversity (Magurran, 1988).

Species abundance models

Species abundance models were developed to describe species abundance distributions within data sets. Based on the observation that most species are represented by one or few individuals while only a few species are very abundant, there are four main species abundance models: 1) the geometric series; 2) the log series; 3) the log normal; and, 4) MacArthur's broken stick model (May, 1974). Most community studies show a log normal distribution of species abundance, characteristic to large and species rich communities with species of intermediate abundance becoming more common (Sugihara, 1980). The best description of species diversity is provided by species abundance models (Magurran, 1988).

As sample size increases so does the species richness (Magurran, 1988). To overcome this problem, a rarefaction index was developed to calculate the expected number of species for samples of equal size (Krebs, 1989). The limitation of this method is that information on the number of species and their relative abundance is lost and the index leaves only an expected number of species per sample (Magurran, 1988). The Jack-knife and Bootstrap procedures are two alternative methods employed when quadrats are used for community sampling (Southwood, 1978).

No consensus exists on the best diversity measure to use and no index has received universal approval. Their selection remains a question of fashion or habit. It would be more practical if scientists could agree on the use of one or a few diversity measures. Data sets would then be more comparable (Magurran, 1988).

II. SAMPLING FOR BIODIVERSITY

Census of every individual in a community is rarely feasible nor desirable (Magurran, 1988). Sampling methods are used to provide an estimate of community composition. As diversity measurements rely on data obtained from sampling, diversity results will be affected by the sampling method.

Random sampling is often necessary but is not always easy to obtain. For instance, when organisms show aggregated distributions, it is almost impossible to ensure random sampling (Pielou, 1975). Another possible source of sampling bias happens when the organisms under study respond differently to the sampling device according to species or groups of individuals (ex. groups of insects differ in their susceptibility to light traps) (Southwood, 1978; Magurran, 1988).

There are many sampling methods to choose from: 1) the spacing or nearest neighbour methods for measuring population size or departure from random distribution are generally used for rather stationary organisms such as trees, snails, barnacles, and tube-building animals (Southwood, 1978); 2) the capture-recapture method which involves marking individuals (Southwood, 1978); 3) methods to sample a unit of habitat like the air, plants, soil, and freshwater (Southwood, 1978); and, 4) by removal trapping either by catching animals randomly or attracting them. Various apparatus are used for trapping aerial (e.g. flight, sticky, and light traps), aquatic (e.g. water traps), and land (e.g. pitfall traps) organisms.

More particularly, pitfall traps have been used extensively for studies on surface-active invertebrates such as spiders (McIver *et al.* 1992), ants (Jennings *et al.* 1986b), and beetles, especially *Carabidae* (Greenslade, 1964; Thiele, 1977). In short, a pitfall trap consists of a glass, plastic, or metal container which is sunk into the soil so that its rim is level with the soil surface (Southwood, 1978). Pitfall traps are often arranged in transect lines (e.g. Niemelä *et al.* 1985; Baguette and Gérard, 1993; Day *et al.* 1993; Holmes *et al.* 1993a,b; Niemelä *et al.* 1993). Baits and preservatives seem to affect groups and species of invertebrates differentially (Greenslade and Greenslade, 1971), including carabids (Luff, 1968; Holopainen, 1990, 1992). Pitfall traps are not expensive, relatively easy to operate, and can yield great amount of data (Southwood, 1978). However, many factors affect pitfall trap catches. For example, catches of carabid beetles can be affected by: 1) population density and activity level of individuals (Greenslade, 1964); 2) ground vegetation obstructing carabid movements and differential species responses to the traps (Greenslade, 1964; Halsall and Wratten, 1988); 3) environmental factors such as temperature, moisture, and other weather conditions (Briggs, 1961; Mitchell, 1963); 4) the nature, size, and shape of the traps (Luff, 1975); and, 5) the position of the rim (Greenslade, 1964). Despite all the factors affecting the catches obtained from pitfall traps, they often remain the only suitable method available for carabid population studies (Greenslade, 1964). In addition, pitfall trapping still represents the most commonly used method for determining carabid beetle activity density (Martel *et al.* 1991).

Usually, for quantitative analyses, 10 to 20 traps are sufficient to provide a valid population sample at a study site (Obrtel, 1971). Continuous pitfall trapping has been shown to provide reliable comparative estimates of population sizes (Baars, 1979). Furthermore, when the size and number of traps and the sampling period are about the same, catches reflect the relative abundance of each species and thus yield comparable data (Bombosch, 1962 cited by Refseth, 1980). Pitfall data have previously been used to compare relative abundances of species between habitats and to assess habitat effects on carabid diversity (e.g. Niemelä *et al.* 1993). Since the number of carabids trapped not only depends on their abundance but also on their activity level, Heydemann (1956 cited by Thiele, 1977) and Tretzel (1955 cited by Refseth, 1980) introduced the notions of "activity density" and "activity abundance" respectively to refer to pitfall trap catches. These notions are generally accepted and used to provide good estimates of a species' role in its habitat (Thiele, 1977; Lenski, 1982a).

III. ENVIRONMENTAL MONITORING

Environmental monitoring has become an essential step towards sustainability by providing feed-back information on the response of ecological systems to disturbances such as environmental management practices (Spellerberg, 1991). Today, diversity assessment finds two major areas of application, namely nature conservation and environmental monitoring (Magurran, 1988). Nature conservationists make extensive use of species richness measurements. On the other hand, environmental monitoring makes ample use of diversity indices as well as species abundance distributions and assumes that disturbances detrimentally affect diversity or modifies distribution patterns of species abundance (Magurran, 1988). May (1981) observed that mature communities often display log normal patterns of species abundance. After disturbance, this pattern changes to log or geometric series, which are less species equitable and demonstrate increased species dominance (Patrick, 1973 cited by Magurran, 1988). There are some authors, however, who question the universally accepted pattern of log normal distributions for mature communities and other distributions for disturbed ones (Shaw *et al.* 1983; Lambshead and Platt, 1985). Diversity measures are then used as environmental indicators of disturbance influences. Care must, however, be brought into the interpretation of diversity measures because increases in species diversity does not necessarily mean higher environmental quality (Magurran, 1988).

Indicator species

Cairns (1979) defined the concept of biological monitoring as the regular and systematic use of organisms to determine the quality of the environment. Taken in this context, biological monitoring is biased towards studies on the effects of pollution (Spellerberg, 1991). But more and more, biological monitoring takes a broader sense and also encompasses studies of changes in biological communities, ecosystems and species brought upon by other disturbances, including natural and human made. Environmental quality can be monitored using indicator species (Spellerberg, 1991). Living organisms integrate a great amount of information concerning the impact of human influences (Spellerberg, 1991). For example, lichens have long been known for their high sensitivity to air pollution.

As a major forest country, Canada accounts for 10% of the earth's forest area and is one of the world's largest supplier of forest products and services (Forestry Canada, 1992). The main forest disturbances in Canada are caused by insects, disease, fire, and harvesting (Forestry Canada, 1993). Forest harvesting has increased over the past 70 years; highest levels were recorded between 1980 and 1990 (Forestry Canada, 1993). Recent studies indicate that there are about 300,000 described species of animals, plants and microorganisms in Canada; at least two thirds of them reside in forests (Forestry Canada, 1993). By their presence, activity, and diversity, forest-inhabiting microorganisms and invertebrates participate in many essential ecological processes such as organic matter decomposition, mineralization, nutrient cycling, and biological pest control (Waring and Schlesinger, 1985; Olembo, 1991; Ditchfield, 1993). Soil organisms are generally classified on the basis of their size. The microbiota refers to bacteria, fungi, and algae. The meso- and macrobiota refers to the soil fauna and consists of a great variety of groups. Examples include protozoa, round worms, snails, slugs, pot worms, earth worms, leaches, flat worms, insects, centipedes, millipedes, spiders, and mites (Waring and Schlesinger, 1985).

Given the great diversity of soil flora and fauna and the procedures required to study them, indicator organisms are needed for a full assessment of ecosystem perturbations on such organisms. Invertebrates, in particular insects, make up the majority of life-forms on earth (Holloway and Stork, 1991). It is not surprising to notice their increasing usage as biological indicators (moths, algae, mayflies, mites, ants). Following this trend, the usefulness of carabid beetles as an indicator group is increasing in popularity (Thiele, 1977; Refseth, 1980; Dufrêne *et al.* 1990; Niemelä, 1990; Holloway and Stork, 1991). Indeed, carabids possess all the required characteristics necessary to be used as such: 1) their ecological requirements are well documented; 2) they are widely distributed in all terrestrial ecosystems; 3) they are taxonomically stable and well known, and adult species identification is relatively easy; 4) they can be sampled by a standardized technique (pitfall trapping); and, 5) they are highly influenced by changes in environmental conditions (Thiele, 1977; Refseth, 1980). Furthermore, being mainly predators (Thiele, 1977) and assuming that their species number is maintained in constant proportions with that of lower trophic levels, a phenomenon known as scale invariance (Briand and Cohen, 1984), carabids can provide great amount of information concerning soil communities at lower trophic levels (Day and Carthy, 1988).

Forest harvesting through cutting and site preparation methods such as prescribed burning and soil scarification, are commonly used forestry practices (Smith, 1986). The main goal of forest site preparation after cutting is to eliminate slash and competitive vegetation in order to create a more favourable environment for the establishment and growth of seedlings (Orlander *et al.* 1990 cited by Prévost, 1992). Conflicting reports in the literature suggest that their effects on soil properties are probably due to variations in topography, site history, soil and vegetation type, climate, intensity, frequency, severity, and type of treatment applied (Wells *et al.* 1979; Vitousek *et al.* 1982; Johnson *et al.* 1991a; Prévost, 1992). Nevertheless, an overview of their influence on forest soil properties may provide insights on how carabid assemblages and species react to such ecosystem perturbations.

IV. EFFECTS OF LOGGING OPERATIONS

Physical and chemical soil properties

Logging is generally used to prepare a stand before prescribed burning, seeding or plantation (Huhta *et al.* 1967). One of the major concern about forest harvesting through cutting is short- and long-term effects on site fertility and productivity (Jordan, 1986; Johnson *et al.* 1991a,b). It is often reported that biomass removal not only deprives the site from vast amounts of nutrients contained in used forest products (Hunter, 1990) but also increases the potential for: 1) accelerated organic matter decomposition and mineralization because of increased substrate availability, soil temperature, and moisture content (Huhta *et al.* 1967; Bormann *et al.* 1968; Huhta, 1971; Bormann *et al.* 1974; Covington, 1981; Edmonds and McColl, 1989); 2) nutrient loss through leaching (Tamm *et al.* 1974; Bormann and Likens, 1979; Hornbeck *et al.* 1986; Jordan, 1986; Dahlgren and Driscoll, 1994) favoured by a reduction in plant uptake (Snyder and Harter, 1985) and larger quantities of drainage water passing through the system (Bormann *et al.* 1968); 3) soil loss through increased erosion (Jordan, 1986); and, 4) soil and drainage water acidification (Dahlgren and Driscoll, 1994). Several authors report increased nitrification after clear-cut logging (Bormann *et al.* 1968; Krause and Ramlal, 1986; Johnson *et al.* 1991a) leading to excess supplies of nitrate and its loss through leaching (Bormann *et al.* 1968). It is not known if nutrient depletion caused by logging can be balanced by inputs from bedrock weathering and/or atmospheric deposition (Sollins *et al.* 1980). Despite these general trends, there is high variability of forest response to logging that may indicate the importance of factors such as the nutrient status of the site prior to logging (Vitousek *et al.* 1982) and hydrological, climatical, geological, and pedological conditions (Johnson *et al.* 1991a).

Soil microorganisms

Several studies show that bacterial counts and/or biomass increase in clear-cut areas compared to undisturbed forests (Grunda, 1964 cited by Lundgren, 1982; Niemelä and Sundman, 1977; Laudelout *et al.* 1978; Sundman *et al.* 1978; Lundgren, 1982). However, the length of this effect is highly variable.

In contrast, Bååth (1980) found that fungal biomass decreased after clear-cutting of a coniferous forest in Sweden. He suggested that changes in root dynamics played an important role in this reduction, since there was no grass growth following clear-cutting. The areas studied by Sundman *et al.* (1978) in Finland showed increased bacterial counts for up to 7 years after clear-cutting as well as an important growth of grass which is known to have a large root production (Bowen 1979) and would provide soil microflora with an additional energy input (Bååth, 1980).

Higher moisture conditions in some clear-cut sites seem to favour algal growth (Aaltonen, 1940 cited by Huhta *et al.* 1967).

Soil fauna

In a review of the effects of silvicultural practices on soil mesofauna (ex. mites and springtails), Hill *et al.* (1975) reported that clear-cutting changes population densities mainly by affecting environmental conditions such as sunlight, temperature, and moisture regimes, as well as food supply, at the forest floor level. Despite varying results, the mesofauna decreased after logging and slowly returned to normal levels after a few years. Huhta and coworkers, among others, (Huhta *et al.* 1967, 1969; Huhta, 1971, 1976) studied the soil fauna and found, as a result of clear-cutting, changes both in abundance and biomass, as well as in community structure. Sundman *et al.* (1978) found that the forest soil invertebrate biomass and activity increased for 7 years after clear-cutting in a spruce forest in northern Finland. They returned to control levels only 13 years after clear-cutting. The effects of clear-cutting on spiders were reported by Coyle (1981) and McIver *et al.* (1992) in a southern Appalachian forest and in a coniferous forest in western Oregon, respectively. Both studies found an increase in hunting spider species in clear-cut areas. Changes in forest canopy and litter depth are pointed out as major factors contributing to the decrease in abundance and diversity of web builders in favour of hunting species in clear-cut areas. Huhta *et al.* (1967) reported four types of reactions in the densities of soil fauna after clear-cutting of coniferous forests: 1) sudden increase (fly larvae and adult beetles); 2) slow increase (round worms, spring tails, pot worms); 3) initial increase, followed by a decrease (mites, beetle larvae); and, 4) decrease (earthworms, spiders). They related these different responses to subsequent changes in food availability and habitat. For example, the increase in the density of adult beetles seems to be almost exclusively due to increases in small Staphylinidae which in turn feed on algae. The densities of the various soil animal populations differed from the control sites during the first four years after clear-cutting but started to return to normal after this period (Huhta *et al.* 1969). After studying the effects of clear-cut age, Huhta (1976) concluded that the amount of decomposable organic matter largely determines the successional patterns in terms of number, biomass, and community respiration of soil invertebrates. Impacts of clear-cutting on carabid beetles are documented for forests in Czechoslovakia (Sustek, 1981, 1984) and pine forest in Poland (Szyszko, 1983 cited by Niemelä *et al.* 1993), oak forests in North Carolina (Lenski, 1982a,b), spruce-fir forest in Maine (Jennings *et al.* 1986a), boreal forest in Finland (Niemelä *et al.* 1988) and in Russia (Arnoldi and Matveev, 1973 cited by Niemelä *et al.* 1993), and a jack pine stand in eastern Ontario (Duchesne and McAlpine, 1993).

Higher plants

Following plant succession for three years after clear-cutting of a *Myrtillus* type spruce stand mixed with pine, birch, and aspen and planted with pine seedlings, Huhta *et al.* (1967) found several grass species and aspen shoots. Natural regeneration from seed can also be significant after harvesting in northern hardwood stands (Bormann and Likens, 1979; Roberts *et al.* 1989; White, 1991). Indications concerning initial survival of pre-established regeneration of balsam-fir (*Abies balsamea* (L.) Mill.) and black spruce (*Picea mariana* Mill. BSP) left on cut boreal forest sites in the province of Québec are reported by Ruel *et al.* (1991). They found mortality rates of 24% for balsam-fir and 20% for black spruce during the first year after cutting. Mortality was mostly related to stem height and logging damages. The survival of balsam-fir was dependent on stem inclination, live crown ratio, and height growth before logging. Small and low quality stems encountered losses of over 50%, as opposed to tall and high quality stems which mortality was below the 10% level. According to Jordan (1986), clear-cutting rarely results in nutrient depletion important enough to inhibit tree growth. However, on very steep slopes in regions of heavy rainfall such as some areas of western British Columbia, soil erosion is significant enough on clear-cut sites to expose bedrock and impede reforestation efforts (Jordan, 1986). Two years after clear-cutting of a jack pine stand planted with white pine (*Pinus strobus* L.) and red pine (*Pinus resinosa* Ait.) seedlings in eastern Ontario, Tellier (1994) found several species of trees and shrubs (*Amelanchier sp.*, *Comptonia peregrina* (L.) Coulter, *Kalmia angustifolia* L., *Prunus pumila* L., *Vaccinium angustifolium* Ait.), high herbaceous (*Pteridium aquilinum* (L.) Kuhn. var. *latiusculum* (Desv.) Underw.), low herbaceous (e.g. *Gaultheria procumbens* L.), sedge and grass (e.g. *Carex houghtonii* Torr.), and moss and lichen (e.g. *Pleurosium shreberi* (BSG.) Mitt., *Polytrichum sp.*).

V. EFFECTS OF PRESCRIBED BURNING AND FIRE

Physical and chemical soil properties

Following logging, prescribed burning can be used as a site preparation technique for either artificial or natural forest regeneration (Weber and Taylor, 1992). Prescribed burning is usually used only when slash and undesirable vegetation are abundant (Prévost, 1992). In Canada, prescribed burning is mostly used in Ontario and British Columbia (Prévost, 1992). The moisture content of the upper soil layers is generally reduced following fire (Ahlgren and Ahlgren, 1960) and can be attributed, for example, to increased evaporation caused by lack of surface vegetation (Rice, 1932). These moisture reductions can last for at least 50 years (Kivekäs, 1939 cited by Ahlgren and Ahlgren, 1960) or can be temporary (Blaisdell, 1953 cited by Wells *et al.* 1979). On the other hand, no differences in moisture content between burned and unburned sites are reported for various vegetation types (Wells *et al.* 1979).

Due to the vegetation removal and increased light absorption by the darkened surface, soils commonly have greater temperature extremes for some time after fire (Ahlgren and Ahlgren, 1960; Scotter, 1963; Cimon and Maisonneuve, 1990).

Burning often increases available concentrations of certain soil mineral elements such as N, P, Ca, K, and Mg for at least 5 years (Pritchett, 1979) and a long period is generally needed for balanced conditions to re-establish (Viro, 1974). Nutrient losses through leaching then becomes a major concern as uptake is reduced by the lack of vegetation (Viro, 1974). Severe fires usually increase soil losses through erosion and surface run-off by reducing the topsoil's ability to absorb and retain water in the absence of vegetation cover and greatly reduced litter and humus (Ahlgren and Ahlgren, 1960; Wells *et al.* 1979; Wright and Bailey, 1982). Among the main factors influencing soil losses, vegetation cover and slope are the most important under intense rainfalls (Farmer and Haveren, 1971; Meeuwig, 1971).

On severely burned sites, reduced infiltration rates (Kittredge, 1938; Johnson, 1940; Burns, 1952; Tarrant, 1956; Beaton, 1959) and moisture-holding capacity (Austin and Baisinger, 1955) are reported. Severity of burning is probably the best indication of a fire's effect on infiltration as Scotter (1963) found that burning increases infiltration rates in the boreal forest. Another commonly reported effect of burning is the formation of a water-repellent soil layer (Wells *et al.* 1979) which reduces soil water storage capacity (DeBano, 1968; DeBano and Rice, 1971) and is most likely to form in forests (Wells *et al.* 1979). However, even though water-repellent soil layers are generally reported after fire, they do not occur extensively on most burned areas (Wright and Bailey, 1982). The thickness of the water repellent layer depends on fire intensity, soil water content, and soil physical properties (Wells *et al.* 1979). For example, dry and sandy soils are most susceptible to forming water repellent soils under fires of moderate duration, whereas wet, fine-textured soils are the least susceptible to water repellency (DeBano *et al.* 1976). Water repellency may not persists for long periods (Dyrness, 1976 cited by Kraemer and Hermann, 1979).

When mineral soil is exposed, aggregates are dispersed by rainfall blocking soil pores with fine particles, thus reducing soil macropore space, infiltration and aeration (Arend, 1941; Sampson, 1944; Beaton, 1959; Volg and Ryder, 1969). When surface organic horizons are not completely burned, changes in pore space and infiltration may be greatly reduced (Metz *et al.* 1961; Moehring *et al.* 1966 both cited by Wells *et al.* 1979). The extent to which soil physical properties are affected depends mainly on fire severity and intensity, proportion of vegetation destroyed, forest floor consumed, heating of the soil, proportion of the area burned, and frequency of fire occurrence (Ralston and Hatchell, 1971; Raison, 1979; Wells *et al.* 1979; Wright and Bailey, 1982). The variations in reported results depend on soil conditions, forest floor, topography, and climate (Wells *et al.* 1979).

Cation exchange capacity usually decreases after a severe fire (Tarrant, 1956; Scotter, 1963) probably because of a great reduction in humus content (Edwards, 1942).

When organic matter is burned, basic cations are released (Chandler *et al.* 1983) and consequently, most studies report increased soil pH after fire (Isaac and Hopkins, 1937; Austin and Baisinger, 1955; Tarrant, 1956; Raison, 1979; Ruuhijarvi *et al.* 1986; Pietikäinen and Fritze, 1993; Ulery *et al.* 1993) that can persist for up to 50 years (Viro, 1974). The initial fuel loading and soil pH, fire intensity, and postfire rainfalls are factors affecting the extent and duration of pH changes (Chandler *et al.* 1983).

Burning also reduces the amount of organic matter of surface soil layers (Fowells and Stephenson, 1933; Isaac and Hopkins, 1937; Austin and Baisinger, 1955; Beaton, 1959; Sweeney and Biswell, 1961; Wells, 1971; Viro, 1974; Pietikäinen and Fritze, 1993) and accelerate litter decomposition by promoting biological activity through more favourable soil temperatures (Bonan and Shugart, 1989) and pH (Fowells and Stephenson, 1933; Viro, 1974).

Long-term effects of prescribed burning on total soil nitrogen content are complex and vary according to ecosystems (Pritchett, 1979). Nevertheless, great amounts of nitrogen are likely to be lost by volatilization during fire (Kraemer and Hermann, 1979; Wells *et al.* 1979; Chandler *et al.* 1983) and several decades may be needed to reach unburned site levels (Viro, 1974). Nitrogen losses may be compensated by increased nitrogen fixation (Wells, 1971; Pritchett, 1979; Wells *et al.* 1979), nitrification (Fowells and Stephenson, 1933; Ahlgren and Ahlgren, 1960; Viro, 1974), increased organic matter decomposition, and atmospheric N deposition (Kraemer and Hermann, 1979).

Soil fertility either decreases, increases or is not affected by fire depending on the location, soil and vegetation type (Ahlgren and Ahlgren, 1960). Burning may initially benefit plant growth but soil productivity also depends on a gradual organic matter decomposition and mineralization (Fowells and Stephenson, 1933; Ahlgren and Ahlgren, 1960). Therefore, continuous and repeated burning are not expected to promote long-term site fertility unless the initially large amount of released nutrients are quickly incorporated into biological cycles and, therefore, not lost through leaching (Ahlgren and Ahlgren, 1960).

Soil microorganisms

Wells *et al.* (1979) suggested that soil microorganisms are more drastically affected by intense fires (Wright and Bollen, 1961; Ahlgren and Ahlgren, 1965; French and Keirle, 1969) than by low intensity fires, primarily because the latter cause minor changes in soil properties (Berry, 1970 cited by Wells *et al.* 1979; Jorgensen and Hodges, 1970).

Heat causes an initial decrease in the number of bacteria, actinomycetes, and fungi followed by an increase (Warcup, 1981). In the case of bacteria, these increases may persist for months depending on soil moisture (Warcup, 1981). Most studies report that soil actinomycetes and bacteria respond similarly to fire although Ahlgren (1974) noted that actinomycetes appear less affected by heat and drying than bacteria. As for the subsequent increase in fungi, it is slower than that of bacteria (Renbuss *et al.* 1973) and presents considerable variation in composition probably reflecting the different sampling techniques, fire intensities, and diversity of microfungi (Ahlgren, 1974). Burning can also affect the extent and depth of mycorrhizae infection (Tarrant, 1956; Wright and Tarrant, 1958).

Changes in microbial populations following fire are most evident in the upper soil layers (Wright and Tarrant, 1958; Alhgren and Ahlgren, 1965; Neal *et al.* 1965; Jorgensen and Hodges, 1970, 1971). The depth to which fire effects can be detected depends on fire intensity and the moisture content of the soil, for moist cells are more readily killed than dry ones (Warcup, 1981). Moreover, increases in microbial populations in lower soil depths some time after a fire are believed to be due to the gradual leaching of ash minerals (Ahlgren and Ahlgren, 1965).

Soil microorganisms respond differently to the heat produced by fire and to the subsequent chemical and physical changes in the environment. For example, bacteria are known to be more heat-resistant than fungi in either wet or dry soil (Wells *et al.* 1979; Chandler *et al.* 1983). Organisms present as inactive forms such as spores, which are generally more resistant to environmental stress, may survive the heat of fire (Warcup, 1981). Increased soil pH following fire tends to favour bacteria over fungi (Chandler *et al.* 1983). A number of organisms other than bacteria, however, colonize burned areas, such as the discomycetes recognized as pyrophilous fungi (*Pyronema*, *Anthracobia*, *Trichophaea*, and *Peziza*), toad-stools, cup-fungi and the bryophytes *Funaria hygrometrica* Hedw. and *Marchantia polymorpha* L. (Warcup, 1981). The occurrence of pyrophilous fungi fruitbodies is dependent on soil pH and some species seem unable to colonize unburnt soil (El-Abyad and Webster, 1968). It has already been shown that some fungal spores in soil are heat-stimulated (Warcup and Baker, 1963). Postfire pH varies from an alkaline condition soon after fire to more acid conditions later as the ash minerals are gradually leached out. Consequently, the species of fungi found in the area vary with age of burn (Petersen, 1970; Ahlgren, 1974).

Burning can have a beneficial effect on nitrogen-fixing bacteria such as *Azotobacter* and *Clostridium* in several pine stands in the United States (Ahlgren, 1974). On the other hand, both increased and decreased nitrification have been reported following fire (Warcup, 1981). This susceptibility may have important implications concerning N availability for plants and losses through leaching (Wells *et al.* 1979). Increased nitrification rates in burned soils have been reported (Fowells and Stephenson, 1933; Kivekäs, 1939 cited by Ahlgren, 1974) and may persist for up to 12 years after fire (Hesselman, 1917). On the other hand, decreases in N fixation and nitrification were reported after burning (Meiklejohn, 1955).

Soil algae are recognized as colonizers of unfavourable substrate and were found to be first or early colonizers of burned sites (Fritsch and Salisbury, 1915; Veretennikova, 1963; Shields and Durrell, 1964). They are believed to: 1) improve soil conditions for growth of higher plants (Veretennikova, 1963); 2) facilitate infiltration (Booth, 1941); 3) reduce run-off (Elwell *et al.* 1939); 4) provide suitable substrates for seeds of higher plants (Fritsch, 1936); and, 5) fix atmospheric N (Warcup, 1981). Soil algae seem to improve site fertility by forming humus, dissolving certain minerals, maintaining a supply of elements in a semi-available form, and increasing soil N (Shields and Durrell, 1964). The potential use of algae as bioindicators of soil fertility has been documented by Pipe and Shubert (1984).

Environmental changes brought about by fire may alter some host-parasite interactions (Ahlgren and Ahlgren, 1960; Jorgensen and Hodges, 1970; Warcup, 1981). Fire is of value in purging the forest of certain diseases, such as the brown-spot needle blight (*Scirrhia acicola*) of longleaf pine (*Pinus palustris* Mill.) (Lotan *et al.* 1981). In some cases, fire seems to promote the occurrence of certain diseases such as heart rot of aspen and pine (Ahlgren, 1974). Fire may stimulate growth of prolific stands of the host plant or provide entry points on weakened, scared or dead plants, thereby multiplying and spreading the pathogen (Ahlgren and Ahlgren, 1960; Lotan *et al.* 1981).

In conclusion, microbial responses to fire are variable and seem to depend primarily on site, fire intensity, soil type, sampling method, duration of heating, maximum temperatures reached during burning, organisms studied, and soil water content. Changes wrought upon microorganisms by fire may also be reflected in the growth and succession of higher plants (Warcup, 1981).

Soil fauna

Burning does not induce total destruction of the soil fauna (Huhta *et al.* 1967). For moderate fires, the reported reductions in soil faunal populations are primarily governed by subsequent environmental changes in post-burn ecosystems than by the heat itself (Rice, 1932; Coults, 1945; Huhta *et al.* 1967). But wildfires, which are often more intense than prescribed burns and destroy much of the forest floor (Hill *et al.* 1975), greatly reduce the mesofauna either directly by heat or indirectly by destroying their food supply and shelter (Hill *et al.* 1975). Less drastic and lasting effects are reported for prescribed burnings as only the surface of the forest floor is destroyed (Hill *et al.* 1975). Decreased soil fauna after fire can be related, for example, to loss of incorporated and unincorporated organic matter that reduces food supplies for smaller soil organisms and, in turn, for their predators (Buffington, 1967), to drier soil surface conditions (Rice, 1932; Heyward and Tissot, 1936), or to greater soil temperature extremes found on burned sites (Ahlgren, 1974). Reduction in soil fauna also varies with the area, type of fire, organisms and species studied, and trophic levels (Pearse, 1943; Hill *et al.* 1975; Abbott, 1984; McSorley, 1993).

At least initially, earthworms, snails, spiders, mites, spring tails, centipedes, millipedes, and round worms seem to be particularly sensitive to fire (Rice, 1932; Heyward and Tissot, 1936; Pearse, 1943; Buffington, 1967; Huhta *et al.* 1967; French and Keirle, 1969; Huhta, 1971; Metz and Farrier, 1971; Ahlgren, 1974). The reductions of earthworms following fire could be related to post-fire moisture decline (Rice, 1932). Grasshoppers and leafhoppers, however, appear to be less drastically affected by fire (Rice, 1932; Tester and Marshall, 1961 cited by Ahlgren, 1974; Hurst, 1971) maybe because of: 1) recolonization from adjacent unburned areas or survival in patches of unburned land; and, 2) warm daytime temperatures and lush early postfire herbaceous recovery (Ahlgren, 1974). It is believed that periodic burning contributes to the diversity of grasshopper and leafhopper species (Gillon, 1971).

Although some authors have reported decreases in ant populations after fire (Pearse, 1943; Buffington, 1967; French and Keirle, 1969; Abbott, 1984), ants are less affected by fire than many other groups of insects because of their adaptations to the hot, xeric conditions of early post-fire topsoil (Ahlgren, 1974). Furthermore, their cryptic habits enable them to survive fire below the level of intense heat. Their colonization habits and social organization adapt them to rapid re-establishment on burned land (Ahlgren, 1974). Reports of increases of ant populations after fire are frequent (Rice, 1932; Heyward and Tissot, 1936; Hurst, 1971) and are attributed to rapid recolonization and survival in lower soil layers (Ahlgren, 1974).

Most forest beetle species are negatively affected by fire, at least temporarily (Heyward and Tissot, 1936; Pearse, 1943; Buffington, 1967; French and Keirle, 1969; Ahlgren, 1974). Less intense grassland and prairie fires do not affect beetle populations as much, partly because soil temperatures are lower than during forest fires. The effects of either prescribed burning or wildfire on carabid beetles have been studied for subtropical pine forests in Australia (French and Keirle, 1969) and Florida (Harris and Whitcomb, 1974), boreal forest in Manitoba (Richardson and Holliday, 1982; Holliday, 1984, 1991, 1992) and Finland (Muona and Rutanen, 1994), shrubs steppes in southeastern Washington (Rickard, 1970), pine forest in Germany (Winter, 1980 cited by Holliday, 1991), and a jack pine stand in eastern Ontario (Duchesne and McAlpine, 1993). Fire itself may also attract carabid beetles (Evans, 1972).

The effect of burning upon pot worms mainly depends on the initial thickness of the humus. Burning would apparently improve their nutritional requirements and if a sufficiently deep humus layer remains, the soil can temporarily support denser populations than usual (Huhta *et al.* 1967).

Despite such variations among results, two generalizations are apparent. First, the effect of fire is greater in forests than in grasslands. There are several possible reasons: 1) grassland species may be more initially adapted to xeric conditions than forest species found in cooler and moister environments; 2) fire intensity may be greater in forests because of more abundant fuel in forested areas; and, 3) most of the grassland studies were made on small burned areas where recolonization from unburned land could be rapid (Ahlgren, 1974). Second, with the exception of the mesofaunal species (mainly consisting of mites and spring tails) and spiders, the population reductions do not seem to be directly caused by heat of fire. More important in these decreases are post-fire changes in the environment. The transition to xeric conditions is frequently mentioned, along with lack of food, and greater temperature fluctuations (Ahlgren, 1974). By burning part or all of soil litter, fire causes changes in food supplies, moisture content, temperature, and pH of the soil which in turn cause great reductions in number and diversity of soil fauna (Pearse, 1946). Gill (1969) as shown that soil microclimatological properties are more important in controlling abundance and migration of soil organisms than nutritional properties of the litter. After burning, forest food supplies on the soil surface diminish, moisture decreases, and temperature and pH increase. These changes cause a 3- to 10-fold reduction in numbers of most organisms (Heyward and Tissot, 1936; Pearse, 1946) and require three to five years to reach pre-fire equilibrium (Abbott, 1984).

Higher plants

Herbs, grasses, and shrubs characteristically proliferate after fire in many areas due to the fertilizing action of nutrients released by burning and, in the case of shrubs, the heat may stimulate the germination of seeds of some species (Ahlgren and Ahlgren, 1960).

Early stages of conifer growth are generally believed to be favoured in post-fire environments because of improved seedbed conditions (Ahlgren and Ahlgren, 1960). Furthermore, some tree species, such as lodgepole pine (*Pinus contorta*

Dougl.) and jack pine are well adapted to fire as their serotinous cones will open when heated (Wright and Bailey, 1982). In addition, the bark of some tree species acts as a good insulator (western larch, Ponderosa pine (*Pinus ponderosa*), and Douglas fir) (Wright and Bailey, 1982). Several other tree species are recognized as colonizers of burned areas (white pine, red pine, paper birch (*Betula papyrifera* Marsh.), aspen, black spruce) (Ahlgren and Ahlgren, 1960).

VI. EFFECTS OF SOIL SCARIFICATION

Physical and chemical soil properties

Soil scarification after logging is a site preparation method that either mixes mineral and organic layers or removes a certain depth of organic matter. In Canada, it was utilized on more than 2/3 of treated areas at the beginning of the 1980's (Sutherland, 1987) and is the most frequently applied treatment to facilitate seedling establishment in Québec (Prévost, 1992). Weber *et al.* (1985) found after 8 years of complete removal of the forest floor of an eastern Ontario jack pine ecosystem: 1) reduction in total soil nitrogen; 2) reduction in the mineral soil of both NO_3-N and NH_4-N; and, 3) reduced site productivity as indicated by lower diameter growth. After an intensive site preparation practice that removed almost all of the organic matter of the soil surface, Vitousek and Matson (1985) found: 1) increased maximum soil temperatures; 2) lower moisture-holding capacity in the surface soil during summer drought; 3) greater net N mineralization late in the first summer; 4) increased soil NO_3-N; and, 5) lower N immobilization.

Higher soil temperatures are generally reported after scarification compared with unscarified sites (Malkonen, 1972; Dobbs and McMinn, 1973; Plamondon *et al.* 1980; Palmgren, 1984; Bassman, 1989; Ohtonen *et al.* 1992) and are mainly due to increased direct solar radiation reaching the soil surface because of the removal of slash and vegetation (Prévost, 1992). Soil temperatures vary greatly according to the scarification method used and also the type of soil, climate, and forest (Sims, 1975; Morris and Pritchett, 1983 cited by Prévost, 1992; Bassman, 1989). Four years after blade scarification, which removed all the forest humus, and planting of eastern white pine and white spruce in eastern Ontario, Munson *et al.* (1993) found increased nitrification, evaporation, and maximum mineral soil temperatures. Blade scarification also had a negative effect on resin sorption of NH_4^+, NO_3^-, PO_4^{3-}, and Ca^{2+} thus decreased nutrient availability as Krause and Ramlal (1986) also reported. Greater soil water conservation capability due in part to increased precipitation reaching the surface soil compensate for increased seedling evaporation (McMinn, 1984 cited by Prévost, 1992). Muelder *et al.* (1963) reported that conifer seedlings were not affected by increased evaporation when soil water content was high. But when evaporation is elevated, exposed soil can then dry rapidly (Sims, 1975) and thus inhibit germination or jeopardize seedling survival. It is generally recognized that scarification methods which incorporate organic matter to mineral soil will produce a layer with good water retention capability and aeration for a long time (Orlander *et al.* 1990 cited by Prévost, 1992). Scarification also amplifies temperature extremes in daily and annual cycles (Prévost, 1992). Several studies showed that exposing mineral soil reduces nutrients (Morris and Pritchett, 1983 cited by Prévost, 1992; Ezell and Arbour, 1985; Stransky *et al.* 1985; Tuttle *et al.* 1985; Vitousek and Matson, 1985). Soil scarification which mixes organic matter with mineral soil can allow for the conservation of an adequate source of nutrients for seedlings (McMinn, 1984 cited by Prévost, 1992), and also favour mineralization (Burger and Pritchett, 1984; Palmgren, 1984; Orlander *et al.* 1990 cited by Prévost, 1992) through more favourable soil temperature and moisture conditions. Munson *et al.* (1993) concluded that scarification removes a significant amount of nutrients from the organic layer and reduces nutrient availability as well as encourages important nitrogen losses (Krause et Ramlal, 1986).

Soil microorganisms

The increase in soil temperature after scarification should promote microbial activity, organic matter decomposition, and nitrogen mineralization (Munson *et al.*

1993). Moisture conditions, together with increased soil temperatures, determine the degree of response of these processes. Studying the soil microbial community response 5 years after scarification in coniferous plantation (white pine) ecosystems, Ohtonen *et al.* (1992) found: 1) increased ratio of microbial to total organic carbon (C_{mic}/C_{org}) in the new organic horizon; 2) unaffected microbial biomass N and C; 3) nutrient limitation which tended to increase the C/N of microbial biomass; 4) increased soil temperature; 5) increased soil moisture tension; 6) reduced total nutrients in the F/H horizon; 7) reduced total N and Ca; 8) markedly reduced phosphate levels; 9) unchanged microbial volume; 10) unaffected tree growth; and, 11) unaltered proportion of bacteria and fungi. Total litter removal from a longleaf pine forest floor reduced the average rate of CO_2 evolution by approximately 22% compared with undisturbed sites and reflected decreased biological activity of the forest floor and a reduction in decomposition rates (Reinke *et al.* 1981). Furthermore, the amount of CO_2 produced was related to rainfall and air temperature, showing declines in periods of drought and cool temperature.

Soil fauna

To date, little is known about the influence of forest soil scarification on soil fauna in boreal ecosystems. In Scotland, removal of the ground vegetation and acid humus in a natural Caledonian pine forest by scarification greatly increased the number of carabid beetles in comparison with untreated areas (Parry and Rogers, 1986). In western Canada, more carabid species were found in regenerating boreal forest sites that were previously clear-cut and scarified than in mature forest (Niemelä *et al.* 1993).

Higher plants

By exposing mineral soil, scarification provides excellent seedbed conditions for coniferous tree species such as red spruce (*Picea rubens* Sarg), white spruce, black spruce, and balsam-fir (Prévost, 1992). Scarification in boreal ecosystems also improves natural regeneration of jack pine (Demers, 1978; Mattice and McPhee, 1979), black spruce (Frisque, 1977 cited by Prévost, 1992; Jeglum, 1980; Orynik, 1985 cited by Prévost, 1992), lodgepole pine and white spruce (Wright, 1985 cited by Prévost, 1992). So far, studies demonstrate that, for the first years, all types of soil scarification allow good seedling establishment or seed germination (Derr and Mann, 1970; Haines *et al.* 1975; Stafford *et al.* 1985 cited by Prévost, 1992; Wilhite and McKee, 1985; Ross *et al.* 1986; Wittwer *et al.* 1986; Orlander, 1987 cited by Prévost, 1992; Brand, 1990, 1991; Roberts and Dong, 1993). Still, some studies show that seedling establishment after scarification does not necessarily insure a good growth (Ballard, 1978; Hall, 1985; Ross *et al.* 1986). There are some indications that scarification also favours the establishment of competitive vegetation (Robitaille, 1978 cited by Prévost; Durand *et al.* 1988). Although scarification did not reduce foliar nutrient levels 4 years after its application, Weber *et al.* (1985) found significant reductions of foliar N and growth increments of jack pine 8 years after complete removal of forest humus in central Ontario. Reductions in nutrient availability that were evident in resin sorption may become apparent once tree demand reaches higher levels (Munson *et al.* 1993). Brand (1991) found that scarification increased the root zone temperature, considerably affected soil moisture and its nutrient content (e.g. reduced foliar N concentration), and increased soil pH during the first two growing seasons after planting of coniferous seedlings. On the other hand, survival of planted seedlings was greater where scarification was applied. Brand and Janas (1988) found warmer soil temperatures where scarification was applied and it was beneficial to the growth of both white pine and white spruce the first growing season. Lunt (1950), studying the effect of 20 years of litter raking on sandy soils in Connecticut planted to red pine and white pine found only little damaging effects on tree growth. It is not known if N losses through scarification can be balanced by forest humus development during a rotation and only long-term monitoring will provide useful indications (Munson *et al.* 1993). Litter removal may adversely affect timber production because it affects soil nutrient and water balance (Ginter *et al.* 1979;

Reinke *et al.* 1981). Trees in a longleaf pine plantation where litter was removed a few weeks earlier had the lowest xylem potential (i.e. greater water stressed) and showed growth reductions (Ginter *et al.* 1979). In addition, litter removal permitted a relatively high soil water content after rainfall but this capacity was not maintained during dry periods (Ginter *et al.* 1979). It is expected that sandy soils would be more negatively affected by litter manipulation than clay soils because of their low water holding capacity (Ginter *et al.* 1979). At the same site, McLeod *et al.* (1979) found reduced tree growth for the first two years after litter removal. By the third year, tree growth was similar in control and treated plots.

CHAPTER 2

MATERIALS AND METHODS

STUDY AREAS

Frontier Lake Experiment

One study site was located at Frontier Lake (46°00'N and 77°33'W) of the Petawawa National Forestry Institute, in Chalk River, eastern Ontario. The site is located within the Middle Ottawa Forest Section (L.4c) of the Great Lakes-St.Lawrence Forest Region (Rowe, 1972). Its landscape was influenced by glacial and postglacial stream deposits of the Ottawa Valley that left a uniformly fine-grained sand 10 to 30 m deep (Gadd, 1962 cited by Weber *et al.* 1987). The bedrock, which is part of the Canadian Shield, consists of Precambrian granite, gneiss, and schists (Weber *et al.* 1987; Weber, 1990), and the soil is a Humo-Ferric Podzol with poorly developed horizons (Anonymous, 1974 cited by Weber *et al.* 1987). The climate, continental in character, is moist-humid at the local level (Hills, 1959 cited by Weber, 1991). The Petawawa National Forestry Institute receives on average 832 mm of precipitation each year: 621 mm as rain and the rest in the form of snow (Anonymous, 1993). The growing season of 180 days has 112 frost-free days (Hills, 1959 cited by Weber, 1991). During the sampling period, i.e. in the summer of 1992, mean maximum temperatures were lower than normal except in May and September; mean minimum and mean monthly temperatures were both lower than normal, except in September; precipitation was lower than normal in May and June but higher than normal in July, August, and September (Table 1).

Trees with a diameter of 17.5 cm or more were cut at the study site in 1942 and 1943. After dendrochronological analyses, it was found that the site experienced several fires, including one in 1943 due to broadcast slash burning

Table 1 Weather data for the 1992 sampling period at Petawawa, Ontario.

Month	Mean maximum temperature (°C)	Mean minimum temperature (°C)	Mean temperature (°C)	Total precipitation (mm)
May	19.9(19.2)*	2.3(4.5)	11.0(11.9)	58.3(68.7)
June	22.4(23.3)	7.2(9.0)	14.8(16.2)	27.4(86.8)
July	22.7(26.4)	9.8(11.9)	16.3(19.2)	167.2(74.2)
August	22.8(24.6)	9.7(10.8)	16.3(17.7)	127.4(76.1)
September	19.2(19.0)	6.3(6.2)	12.8(12.6)	110.2(78.8)

*: numbers in parentheses indicate normals calculated over a 30-year period, i.e. from 1961 to 1990 and obtained from: Anonymous. 1993. Canadian climate normals, 1961-1990: Ontario. Vol. 4, Atmospheric Environment Service, Environment Canada.

(E. Stechishen, cited by Duchesne and McAlpine, 1993). Prior to clear-cutting, the forest of the study site was composed of jack pine, white pine, and red pine (Table 2). Several other plant species were also observed before clear-cutting: *Amelanchier sp.*, *Comptonia peregrina* (L.) Coult., *Gaultheria procumbens* L., *Kalmia angustifolia* L., *Lycopodium complanatum* L., *Maianthemum canadense* Desf., *Polygonatum pubescens* (Willd.) Pursh., *Pteridium aquilinum* (L.) Kuhn., and *Prunus pumila* L. (Duchesne and McAlpine, 1993).

In 1990, the forest of the study site was clear-cut (150 m x 1000 m) with residual slash (limbs and treetops) left in place (Duchesne and McAlpine, 1993). The area was divided into 44 plots of 30 m x 70 m each (Figure 1). All plots were surrounded by a 8 m-wide fire line. In 1991, 10 plots were burned-over between June 14 and August 8, 10 were scarified in October using a disk trencher creating strips 50 cm wide of bare mineral soil 2 m apart, and the other 24 plots were left clear-cut. All 44 plots were planted with 50% white and 50% red pine seedlings in May 1992, at a density of 10,000 seedlings/ha. In 1992, the plant cover in all plots was mainly composed of *Pteridium aquilinum* (L.) Kuhn., *Vaccinium angustifolium* Ait., *Vaccinium myrtilloides* Michx., *Amelanchier* sp., *Prunus pumila* L., *Comptonia peregrina* (L.) Coult., *Kalmia angustifolia* L., and several grass and sedge species (Tellier, 1994). In order to have control plots, 34 plots (30 m x 70 m each), each surrounded by a 8 m-wide fire line, were established in an adjacent undisturbed area of forest (Duchesne and McAlpine, 1993).

Weather data necessary to obtain the indices and codes of the Canadian Forest Fire Weather Index System were gathered with an on site automatic fire weather station (Table 3) and fuel consumption was calculated by subtracting post-burn fuel loads from pre-burn fuel loads (slash and duff) (Duchesne and McAlpine, 1993). To measure the rate of fire spread, each burned plot had a pin grid network so that fire distance and time data were collected (Duchesne and McAlpine, 1993). Fire intensity was determined using Byram's (1959) fire intensity formula:

$$I = H \cdot w \cdot r$$

Table 2[+] Dendrometric characteristics of the forest at the Frontier Lake research site before clear-cutting in 1990.

Species	Age (years)	DBH[*] (cm)	Density Stems/ha	Volume m^3/ha
Pinus banksiana Lamb.	53	17.1	505	81
Pinus resinosa Ait.	105	37.5	50	45
Pinus strobus L.	55	28.7	100	57

+ from Duchesne and McAlpine, 1993.
* diameter at breast height.

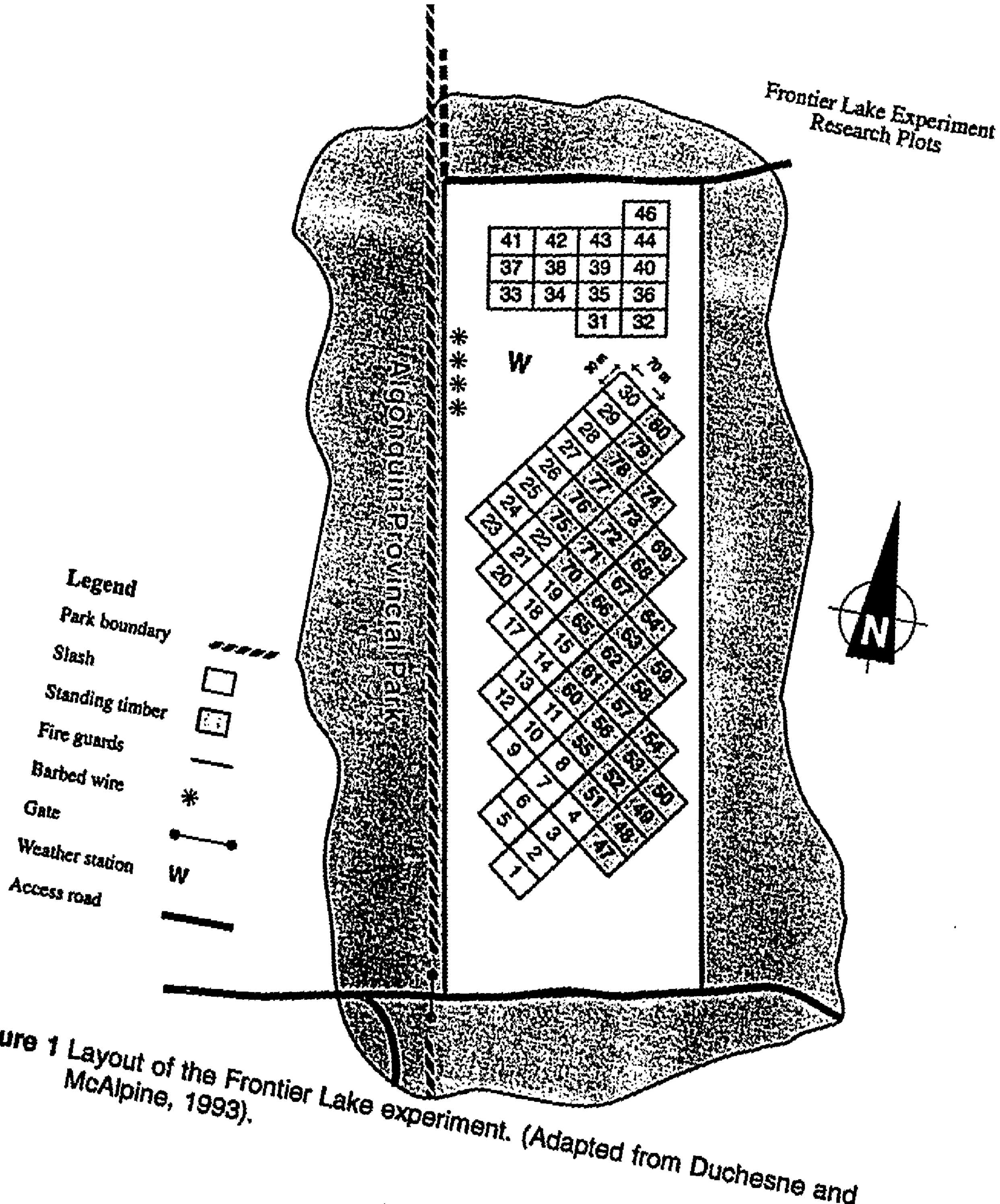


Figure 1 Layout of the Frontier Lake experiment. (Adapted from Duchesne and McAlpine, 1993).

Table 3$^+$ Prescribed burning data for the 10 burned-over plots at Frontier Lake Experiment Research Plots.

Plot No.	Fire date (dd/mm/yr)	Temperature (°C)	Relative Humidity (%)	10-m wind (km/h)	Fire Weather Index	Total[1] fuel consumption (kg/m^2)	Depth of burn (cm)	Rate of spread (m/min)	Frontal Fire Intensity (kW/m)
2	08-08-91	25.2	53	5.3	6	2.05	0.37	1.2	446
7	08-08-91	25.2	53	5.3	6	1.78	0.38	2.1	1,063
44	24-06-91	27.3	32	1.3	22	4.35	2.37	1.7	2,097
40	10-07-91	20.0	60	5.2	7	4.86	2.78	3.0	4,132
32	12-07-91	26.0	49	3.6	14	3.57	1.85	5.5	5,565
26	14-06-91	22.6	40	4.3	18	3.80	3.50	9.4	10,143
46	24-06-91	27.3	32	3.7	22	4.95	1.95	7.9	11,077
36	10-07-91	20.0	60	5.6	7	6.31	2.71	6.3	11,176
43	12-07-91	26.0	49	3.8	14	6.41	2.64	9.5	17,259
24	14-06-91	22.6	40	16.6	18	3.18	1.79	22.0	19,854

+: data obtained from L.C. Duchesne (personal communication)
1: Slash and duff

where I is the frontal fire intensity (Kw/m), H is the fuel low heat of combustion assumed to be equal to 18,000 kJ/kg, w is the weight of fuel consumed in the active flaming area (kg/m^2), and r is the rate of spread of the fire (m/s) (Duchesne and McAlpine, 1993). The burned-over plots were exposed to fire intensities ranging from low to high (Table 3).

La Mauricie National Park

The other study took place in La Mauricie National Park (**LMNP**) (limit north: 46°55'N; south: 46°39'N; east: 73°11'W; west: 72°46'W), north of the St.Lawrence River, in Québec (Anonymous, 1992) (Figure 2). Approximately half of the park's surface is characteristic of the Laurentian Forest Section (L.4a) of the Great Lakes-St.Lawrence Forest Region and the remainder corresponds to a transition zone between southern deciduous and northern boreal forests as indicated by the abundance of balsam-fir and paper birch (Rowe, 1972; Anonymous, 1992; Del Degan *et al.* 1993). According to Grandtner's (1966) classification, Rowe's (1972) Laurentian Forest Section is situated in the northern part of the ecological region 3g - Middle Laurentians of La Mauricie and belongs to the "domaine de l'érablière à bouleau jaune" (*Betula alleghaniensis* Britton) and to the "sous-domaine de l'érablière à bouleau jaune et hêtre" (*Fagus grandifolia* Ehrh.) (Grandtner, 1966; Anonymous, 1992; Del Degan *et al.* 1993). Balsam-fir represents the most abundant tree species (31.8%) followed by larch (13%) (*Larix laricina* (Du Roi) Koch), paper birch (12.5%), red maple (9.3%) (*Acer rubrum* L.), and sugar maple (7.7%) (*Acer saccharum* Marsh.) (Del Degan *et al.* 1993). White pine and red pine are also abundant (Del Degan *et al.* 1993). The landscape consists of numerous hills and valleys shaped by glaciations (Anonymous, 1992; Del Degan *et al.* 1993). The Precambrian bedrock, which is part of the Canadian Shield, is composed of massive and crystalline metamorphic rocks and is covered with a variety of glacial deposits of variable depths, with till being the most abundant (Anonymous, 1992; Del Degan *et al.* 1993). Podzolic soils have developed over most of the park area (Del Degan *et al.* 1993). Mean temperature variations are in the order of 2°C from

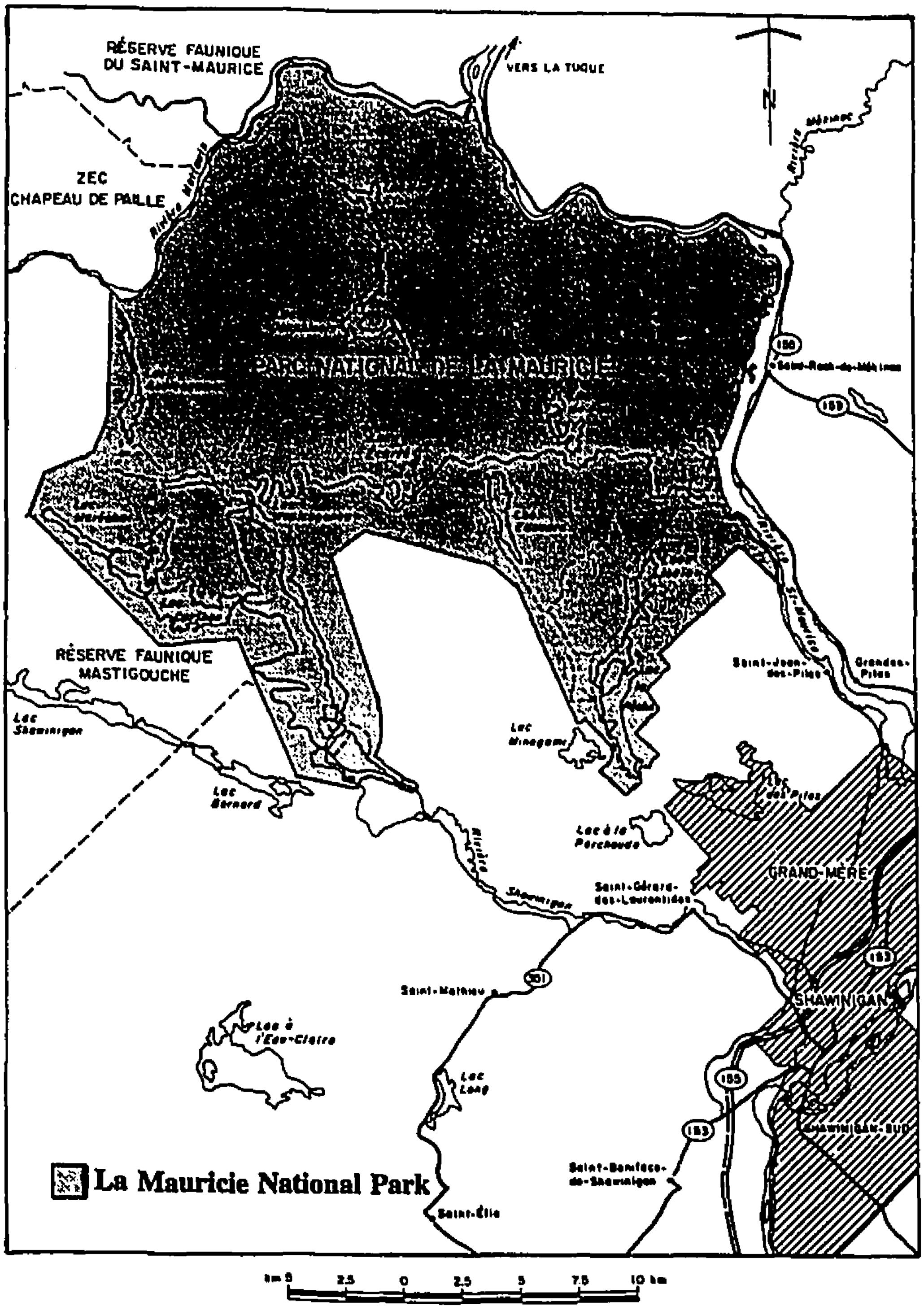


Figure 2 Location of La Mauricie National Park, Québec, Canada. (Adapted from Del Degan *et al.* 1993).

north to south and contribute to the presence of both boreal and meridional vegetation types (Del Degan *et al.* 1993). The mean annual temperature is between 2°C and 3°C with a growing season of 160 to 180 days of which 100 to 120 are frost-free, and annual precipitations vary from 900 to 1,300 mm (Del Degan *et al.* 1993). During the sampling period, i.e. in the summer of 1993, available climatic data for the locality nearest to the sampled sites (i.e Saint-Joseph-de-Mékinak, 46°55'N and 72°41'W) indicate that the mean maximum temperatures were higher than normal except in May and October; mean minimum and mean monthly temperatures were both higher than normal; precipitation was higher than normal except in May and August (Table 4).

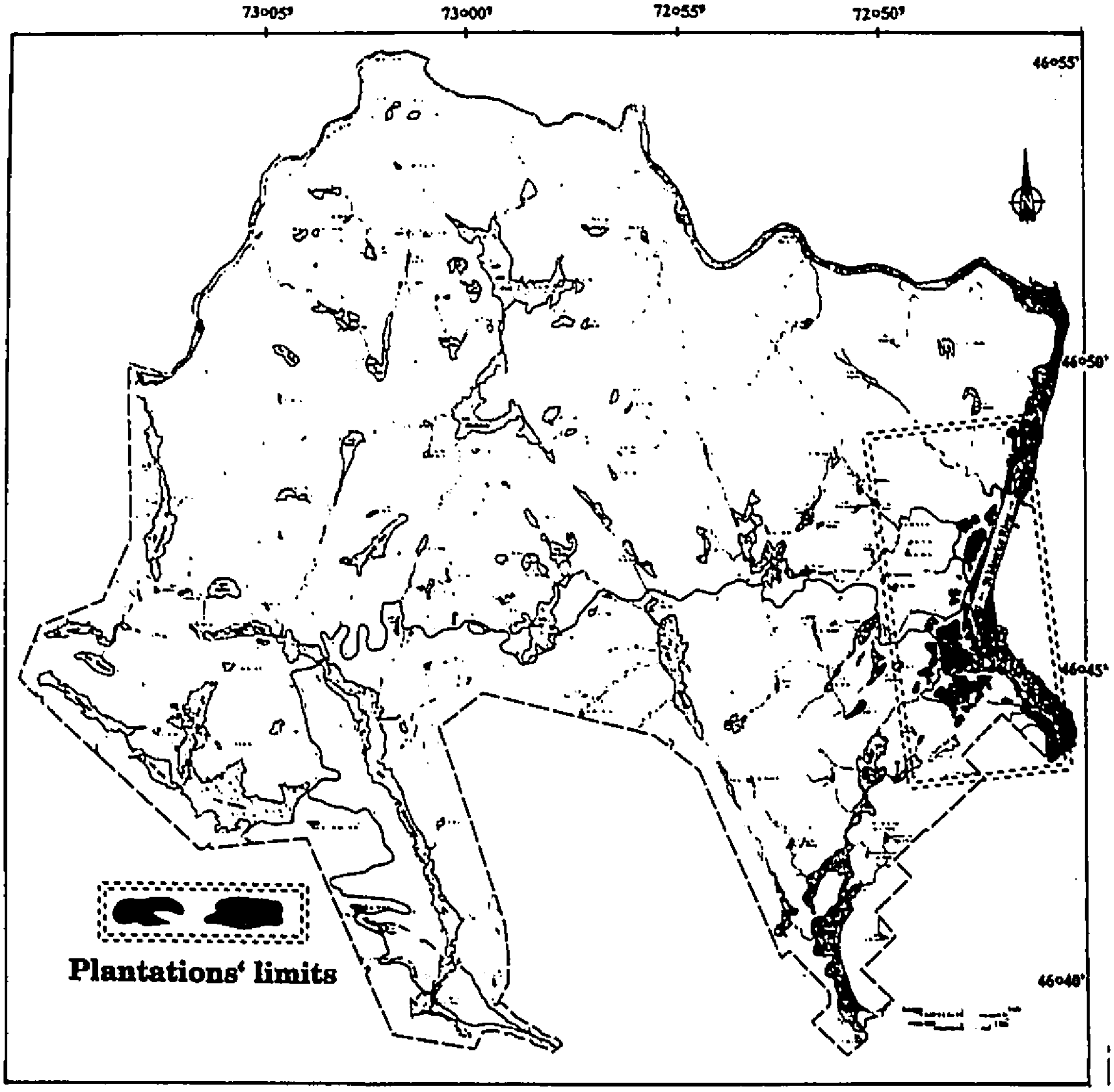
Three major disturbances influenced the park's vegetation, namely logging, forest fires, and spruce budworm outbreaks (Del Degan *et al.* 1993). Logging operations affected more than 50% of the park's surface over the last forty years (Anonymous, 1992) and favoured the regeneration of already established and pioneer tree species such as paper birch, red maple, and balsam-fir (Anonymous, 1992; Del Degan *et al.* 1993). Most of the park's area supports stands of 50 years old or more (Del Degan *et al.* 1993). The absence of younger stands is mainly due to the interruption of natural and anthropogenic disturbances since the creation of the park in 1970 (Del Degan *et al.* 1993).

The sampling area was located in the southeastern sector of the park, along the west coast of the St.Maurice River. This area is occupied by white spruce plantations covering 426 ha and established between 1930 and 1932 (Anonymous, 1992) (Figure 3). They were established on relatively flat terrain on river terraces formed by clay and sand deposits of the Champlain sea (Anonymous, 1992). White spruce was planted every 1.5 m at a density of 3,700 to 4,400 seedlings/ha (Veillette and Boivin, 1987). Dead seedlings were replaced and these plantations became commercially exploitable. The understorey vegetation, mainly composed of conifers, is not well developed due to the dense canopy (Anonymous, 1992). Baguette and Gérard (1993) have also noticed that the lack of light under the canopy of spruce plantations hinders the growth of other plants. Soils are mainly

Table 4 Weather data for Saint-Joseph-de-Mékinak, Québec, 1993.

Month	Mean maximum temperature (°C)	Mean minimum temperature (°C)	Mean temperature (°C)	Total precipitation (mm)
May	17.9(18.2)	3.9(2.9)	10.9(10.6)	86.2(93.9)
June	22.9(22.6)	8.5(8.1)	15.7(15.4)	141.4(102.6)
July	25.9(25.5)	13.0(11.2)	19.5(18.4)	123.3(96.4)
August	25.9(21.0)	12.8(8.9)	19.4(14.0)	70.6(90.9)
September	18.5(16.8)	5.4(5.1)	11.9(10.8)	100.0(94.0)
October	9.9(11.0)	N/A(-0.3)	N/A(5.4)	N/A(71.8)

*: numbers in parentheses indicate normals calculated over a 17- or 18-year period, i.e. from 1973 to 1990 and obtained from: Luc Mercier, (Environment Canada, Atmospheric Environment Service, personal communication).



Scale: 0.35 cm = 1 km

Figure 3 White spruce plantation areas in La Mauricie National Park. (Adapted from Veillette and Boivin, 1987).

composed of Humo-Ferric Podzols and Brunizols (Veillette and Boivin, 1987) and are little affected by erosion (Anonymous, 1992). It appears that all sampled sites experienced wild fires between 1870 and 1900 (Anonymous, 1992). Since their establishment, almost 70% of white spruce plantations in LMNP were submitted to commercial silvicultural treatments before the park's creation and to rehabilitation treatments subsequently (Veillette and Boivin, 1987). These treatments mainly consisted of thinnings, single tree harvesting, group selection cuttings, and, since 1990, clear-cutting and prescribed burning (Anonymous, 1992) (Figure 4). These forestry practices favoured the establishment of balsam-fir, paper birch, and aspen (*Populus tremuloïdes* Michx) (Veillette and Boivin, 1987).

The even-aged structure, almost pure stand composition, and high density of these plantations impeded natural vegetation evolution by preventing the establishment of a natural succession. Furthermore, the presence of these plantations decreases floral and faunal diversity, and increases risks of wildfires, insect outbreaks, and damage by diseases (Veillette and Boivin, 1987). Since white spruce plantations are not part of the natural forest landscape of LMNP and interfere with natural vegetation succession and evolution, it was decided that they would gradually be eliminated using three forestry practices: 1) logging; 2) thinning through girdling; and, 3) prescribed burning (Veillette and Boivin, 1987; Anonymous, 1992). The primary objective of these interventions in the plantations is to open up the canopy, to different degrees, permitting proper light conditions for a short- and mid-term natural and diversified regeneration (Veillette and Boivin, 1987).

Four sites were sampled for carabid beetles (Figure 5). Site R (46°45'30"N and 72°48'15"W) was used as a control site and is a pure white spruce plantation of 13.7 ha (Veillette and Boivin, 1987). Commercial thinnings were done on this site in 1968 (Anonymous, 1992). Site T (46°46'50"N and 72°48'15"W) covers 6.0 ha and was also used as a control. It is dominated by naturally regenerated tree species (peupleraie dentée à pin rouge et épinette blanche) (Veillette and Boivin, 1987). Site U (46°47'30"N and 72°47'45"W) is a pure white spruce plantation and

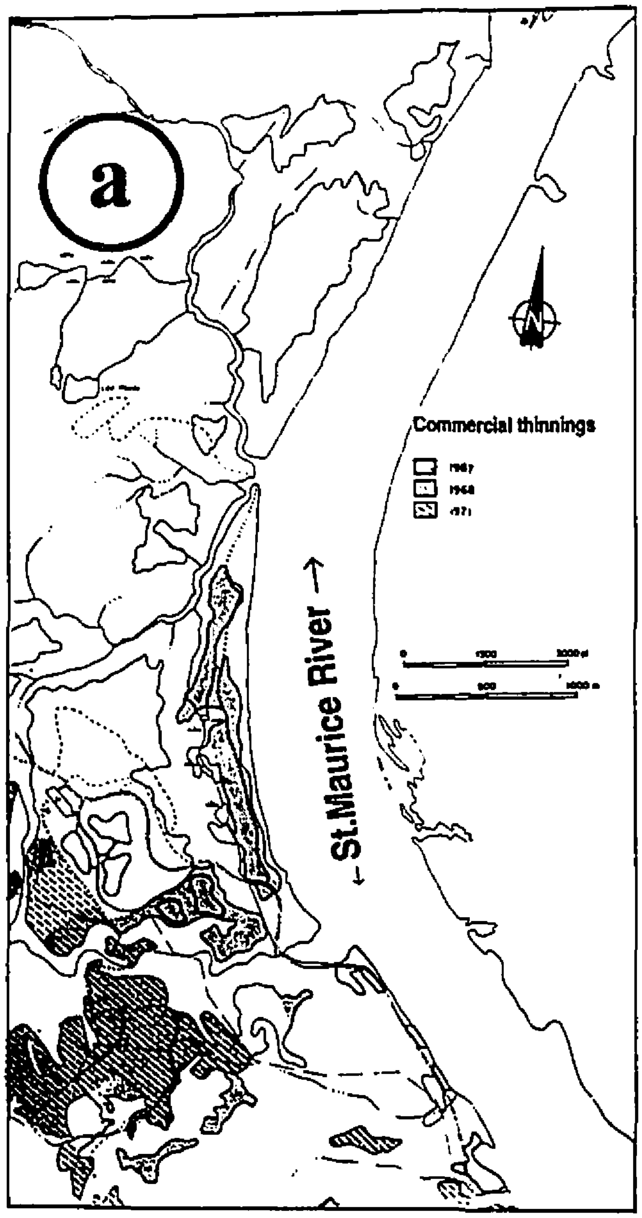
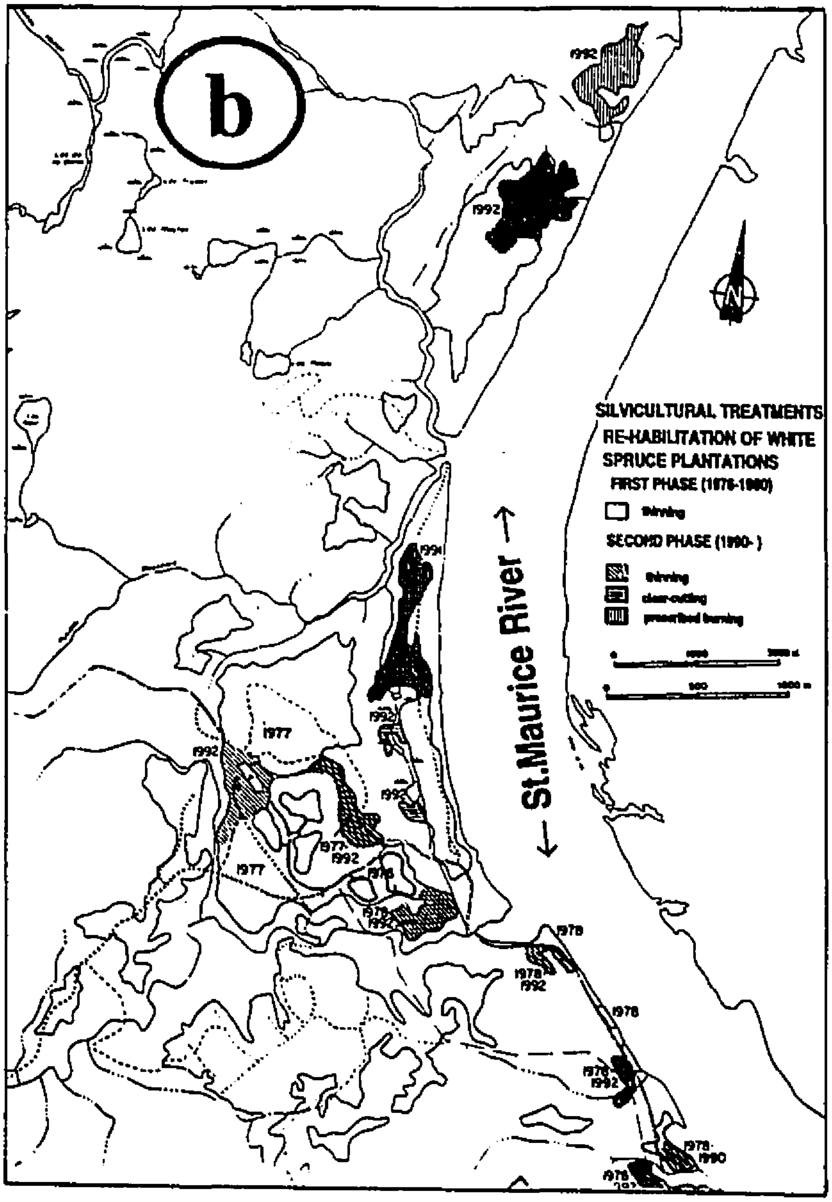


Figure 4 Silvicultural treatments practiced or planned in the white spruce plantations at La Mauricie National Park: a) between 1967 and 1971; b) first phase (1976-1980) and second phase (1990-); c) proposed in the 1987 re-habilitation plan. (Adapted from Anonymous, 1992).



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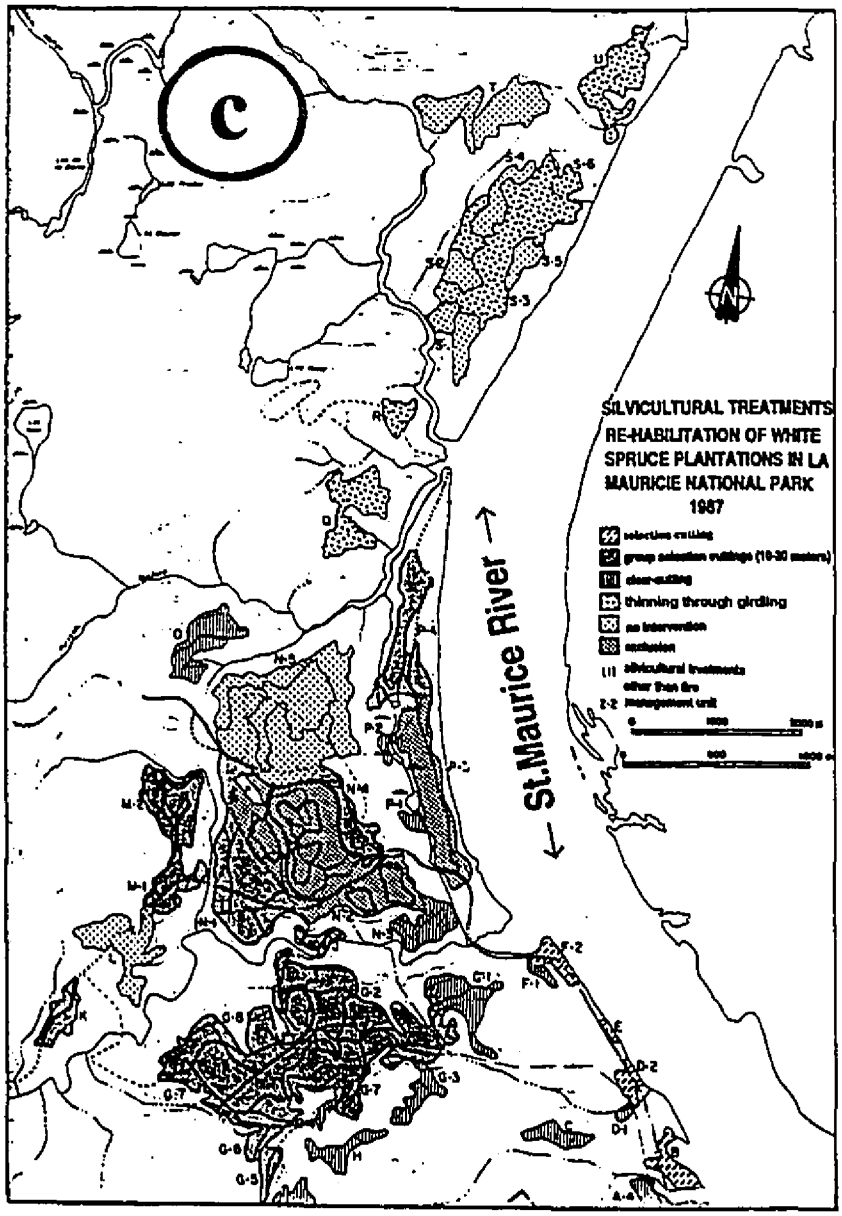

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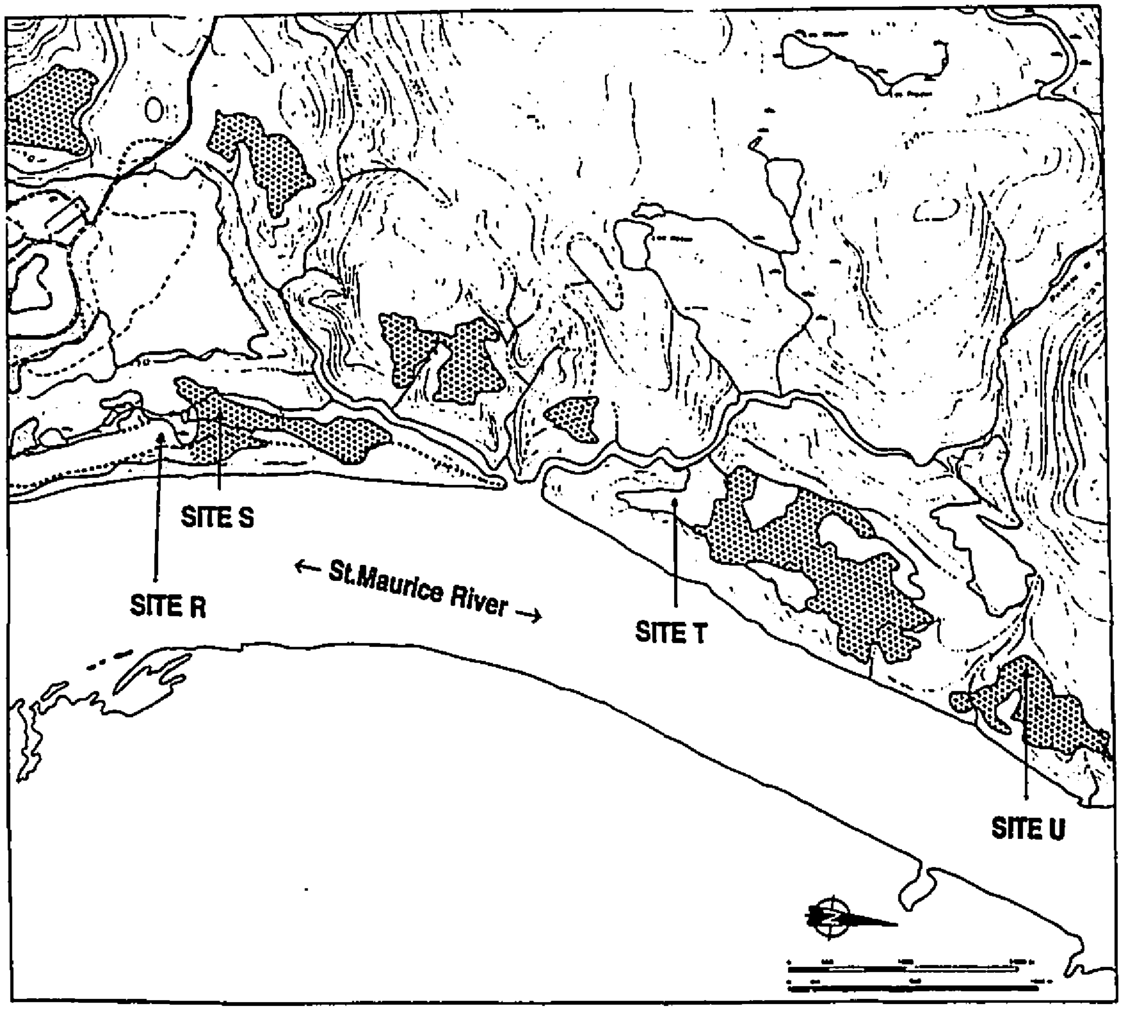


Figure 5 Location of the four sampled sites within the white spruce plantations at La Mauricie National Park. (Adapted from Veillette and Boivin, 1987).

covers 14.1 ha (Thériault and Van Dijk, 1993). Between April 30 and May 20 1992, 30% of stems were cut and uniformly placed to insure maximum energy release and elimination of white spruce seeds and stems during burning (Thériault and Van Dijk, 1993). At the same time, a fire line 5 m wide to the east and west and 7.5 m wide to the north and south was established around the site (Thériault and Van Dijk, 1993). Of the 14.1 ha that covers the site, 8.9 ha was burned on July 24 1992 (Thériault and Van Dijk, 1993). Site S (46°45'40"N and 72°48'15"W) is also a pure white spruce plantation and covers 12.8 ha (Quenneville and Van Dijk, 1991). Commercial thinnings were done on this site in 1968 (Anonymous, 1992). It was then clear-cut between November 5 1990 and January 10 1991 and a fire line was established around it (Quenneville and Van Dijk, 1991). Before burning, the plant cover was mainly composed of young aspen, raspberry (*Rubus idaeus* L.), and other shrubs (Quenneville and Van Dijk, 1991). For experimental purposes, in section P-4.1, 50% of logs of commercial value were left on place, and in section P-4.2, where the sampling of carabids was done, 100% of logs of commercial value were removed (Quenneville and Van Dijk, 1991) (Figure 6). Residual slash was uniformly distributed on the site and burning took place on September 3 1991 (Quenneville and Van Dijk, 1991).

Weather data necessary to obtain the different indices and codes of the Canadian Forest Fire Weather Index System (CFFWIS) were gathered with an on site automatic weather station (Table 5). Fuel loads were evaluated following the method proposed by McRae *et al.* (1979). Fuel consumption was calculated by subtracting post-burn fuel loads from pre-burn fuel loads (slash and duff). Due to erratic fire behaviour (site S), intense smoke and ignition method (i.e spiral) used (site U), it was not possible to measure the rate of fire spread nor the frontal fire intensity. For site U, they were determined using the simulation software FBP91 (Fire Behaviour Preparedness) and collected weather data (Thériault and Van Dijk, 1993). For site S, they were roughly estimated (Quenneville and Van Dijk, 1991). The burned-over sites were exposed to fire intensities ranging from moderate to high (Table 5).

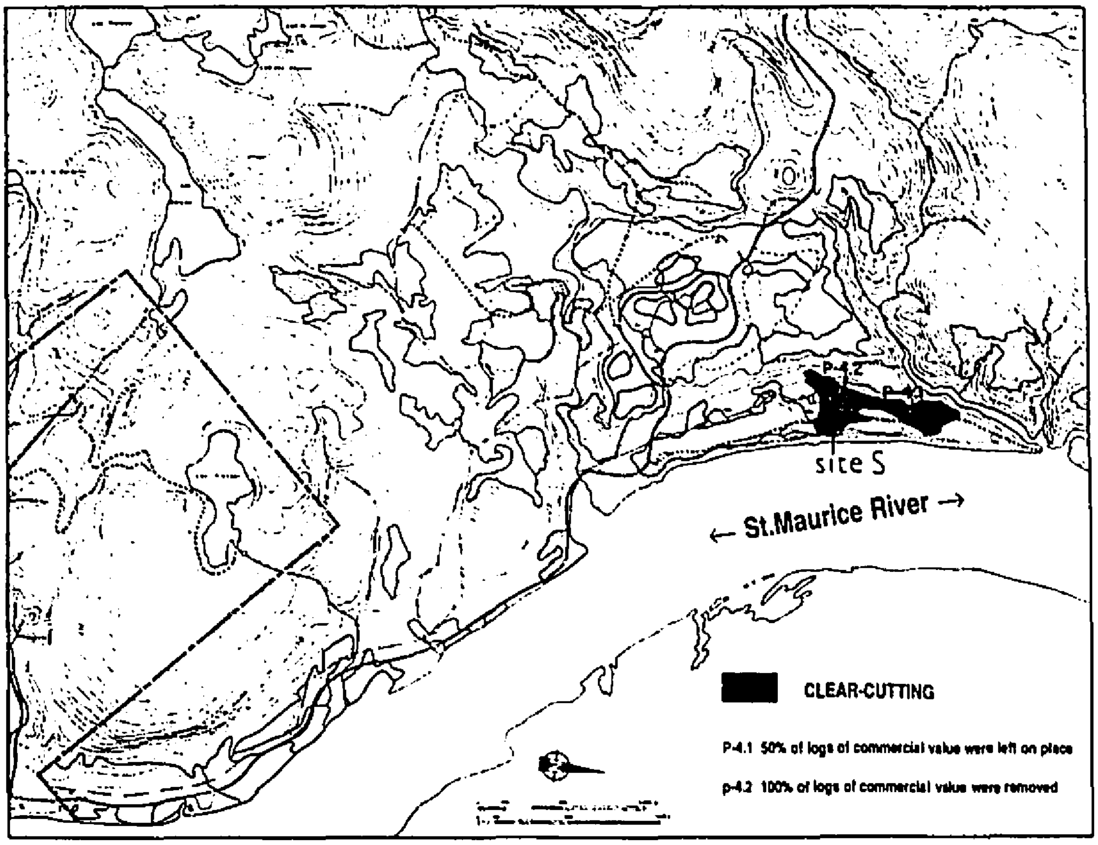


Figure 6 Experimental trials for the area burned on September 3 1991, including sampled site S, at La Mauricie National Park. (Adapted from Quenneville and Van Dijk, 1991).

Table 5[+] Prescribed burning data for the burned-over sites at La Mauricie National Park.

Site	Fire date (dd/mm/yr)	Temperature (°C)	Relative Humidity (%)	Wind (km/h)	Fire Weather Index	Total[1] fuel consumption (kg/m^2)	Depth of burn (cm)	Estimated Mean Rate of spread (m/min)	Estimated Frontal Fire Intensity (kW/m)
S(P-4.2)	03/09/91	22.4	68	17.0	8	3.1	0.5	3.0	3,000
U	24/07/92	26.8	54	2.6	8	7.7	1.5	7.0	4,000-8,000

+: data obtained from Quenneville and Van Dijk (1991), and Thériault and Van Dijk (1993).
1: Slash and duff

SAMPLING OF CARABID BEETLES

Continuous pitfall trapping during the snow-free season was used to collect adult carabid beetles. Pitfall catch data were used to compare relative abundances of species between treatments, as suggested by Niemelä *et al.* (1986, 1990, 1993) and Bombosch (1962, cited by Refseth, 1980). The traps consisted of 350 ml plastic containers (8 cm diameter and 14 cm high) sunk in the soil so that their rims were level with the soil surface (Greenslade, 1964; Southwood, 1978). Each container had drain holes in the bottom (Luff, 1975). At the Frontier Lake study site, the carabid beetles were collected from 10 burned-over, 3 clear-cut, 3 scarified, and 4 control plots for a total of 20 plots. Twenty pitfall traps were used in each of the 20 plots for a total of 400 traps. The 20 unbaited traps were placed at intervals of 2 m along a transect line laid out in the middle of each plot in order to minimize edge effects. In the case of the white spruce plantation sites, the carabid beetles were collected from 2 burned-over sites i.e. sites S and U, and 2 control sites i.e. sites R and T, for a total of 4 sites. Thirty pitfall traps were used in each of the 4 sites for a total of 120 traps. Three transect lines of 10 unbaited traps placed at intervals of 2 m and forming a Y were laid out at least 50 m inside each site in order to minimize edge effects. No preservatives were used in the traps because of their probable differential attractant or repellant effects on carabid species (Southwood, 1966; Luff, 1968; Greenslade and Greenslade, 1971; Holopainen, 1990, 1992). For comparison purposes, catches from all traps from each sampled plot/site were pooled for the entire sampling period. At Frontier Lake, traps were set up on May 11 1992 and carabid beetles were collected weekly from May 19 1992 to September 8 1992. The sampling effort (i.e. number of traps x number of trapping days) was 2420 trap-days for all plots. No preservatives were used to keep carabids because they were pinned and air-dried on the same day of their collection from the traps. At LMNP, traps were set up on May 21 1993 and carabid beetles were collected weekly from May 28 1993 to October 4 1993. The sampling effort was 4110 trap-days for all sites. Carabids were kept in a solution made of 85% ethanol and 15% methanol until they could be pinned and air-dried. Beetles were identified to the species using Lindroth (1961-1969) and Larochelle (1976). Nomenclature follows Bousquet and Larochelle (1993).

Species diversity was assessed using the Shannon-Wiener index (Shannon and Weaver, 1949). The Shannon-Wiener formula is:

$$H' = -\sum_{i=1}^{s} p_i \cdot \ln(p_i)$$

where H' is the species diversity index, p_i is the relative abundance of species number i, and s is the total number of species. This index has been used in several studies on carabid beetles (e.g. Refseth, 1980; Lenski, 1982a; Sustek, 1984; Holliday, 1992; Niemelä *et al.* 1992; Duchesne and McAlpine, 1993). When conditions of homogeneity of variance are met, it is thus possible to use analyses of variance to compare the species diversity index of different habitats (Magurran, 1988).

STATISTICAL ANALYSES

Because the number of species (species richness) increases with sample size (Magurran, 1988), the rarefaction method (Sanders, 1968) was used to standardize all samples to a common size. For the Frontier Lake and LMNP study sites, the number of species was estimated in subsamples of 117 and 224 individuals respectively (smallest samples size coming from control plot/site) for each plot/site. The program RAREFACT in Krebs (1989), which is a modified version of a program presented by Simberloff (1978), was used to obtain the rarefaction data.

Regressions were calculated using SYSTAT (1992) to predict the mass of carabid specimens using body length as the independent variable. To do so, 28 pinned-dried carabids taken at random from all the catches of the Frontier Lake site were measured and weighted. The length range of the measured specimens was from 2.8 to 23.5 mm; the range in mass was from 0.7 to 223.5 mg. In the same manner for the catches of LMNP, 31 pinned-dried carabids taken at random were also measured and weighted. The length range in this case was from 5.9 to 25.2 mm; the range in mass was from 1.7 to 390.5 mg. The species length ranges found in Gariépy *et al.* (1977) were used to obtain an average body length for each sampled species and subsequently calculate the total dry mass of carabids/plot (or site). After regression analyses, the carabids' dry mass was found to respond in the following manner:

1) for the Frontier Lake area:

$$M = 0.01047 \cdot L^{3.0882}$$

2) for La Mauricie National Park:

$$M = 0.00239 \cdot L^{3.70976}$$

where M is the dry mass in mg and L is the body length in mm. The corrected R^2 for Frontier Lake and LMNP were equal to 0.89 and 0.96 respectively. Similar power functions were found for insects in general (Rogers *et al.* 1976) and for carabid beetles (Jarosik, 1989). Nevertheless, specific regressions such as those calculated above are considered to be more accurate than a generalized regression (Rogers *et al.* 1976).

The effects of forestry practices on the average number of catches, dry mass, number of species, number of species after rarefaction, and diversity index of carabid assemblages were tested using ANOVA followed by Least Significant Difference (LSD), modified for unequally replicated means (Steel and Torrie, 1980) (**Note**: LSD was only used for data from the Frontier Lake research plots since 4 treatments were studied, whereas only 2 treatments were studied at LMNP). In addition, regression analyses were done to assess the effect of fire intensity on the number of catches, dry mass, number of species, number of species after rarefaction, and diversity index of carabid assemblages of the Frontier Lake study area. Homogeneity of variances was tested using the statistic F_{max} (Kirk, 1968). Homogeneity of variances was met for all independent variables except for the number of catches data of Frontier Lake where a $\log_{10}$ transformation was used. At Frontier Lake, the levels of significance were set at 0.01 when testing for homogeneity of variances and for analyses of variance and at 0.05 for LSD tests and regression analyses. For LMNP, the levels of significance were set at 0.01 when testing for homogeneity of variances and at 0.05 for analyses of variance.

CHAPTER 3

RESULTS

FRONTIER LAKE EXPERIMENT

Effects of forest site preparation methods on carabid assemblages

Silvicultural methods had a significant effect on the number of catches ($P < 0.0003$), total dry mass ($P < 0.0054$), number of species ($P < 0.0001$), number of species after rarefaction ($P < 0.0001$), and the diversity index ($P < 0.0011$) of carabid assemblages (Table 6). Clear-cutting and clear-cutting followed by prescribed burning had a significantly higher number of catches and carabid dry mass than undisturbed forest. The number of species was lowest in undisturbed forest although after rarefaction, it was significantly higher only in two of the three forestry practices studied, i.e. burned-over and scarified sites, when compared with undisturbed forest. Prescribed burning resulted in the highest diversity index (Table 6).

The number of catches increased linearly with increasing fire intensity (Figure 7). However, no regressions were found to be significant between fire intensity and dry mass, number of species, number of species after rarefaction, and diversity index of carabid assemblages.

Species responses to forest site preparation methods

In all, 5970 specimens were collected in the course of this study, representing 26 genera and 83 species (Appendix A).

Out of 15 *Amara* and 20 *Harpalus* species collected in this study, 14 and 18 species, respectively, were trapped only in clear-cut sites (i.e. including burned-over and scarified sites) (Appendix A). In addition, seven major species (i.e. representing 2% or more of the total catches of a treatment) were collected more abundantly or solely on clear-cut plots (including burned-over and scarified plots), namely *Calosoma calidum* (F.), *Harpalus affinis* (Schrank), *H. laticeps* LeC., *H.*

Table 6 Effect of three forestry practices on 5 characteristics of carabid assemblages at Frontier Lake Experiment Research Plots, 1992.

Treatment	Number of catches*	Dry mass (g)	Number of species	Number of species after rarefaction	Diversity index
Undisturbed forest	145b	3.0b	12b	11b	1.9b
Clear-cutting followed by prescribed burning	367a	8.3a	34a	21a	2.4a
Clear-cutting followed by scarification	210ab	6.0ab	29a	22a	2.1ab
Clear-cutting alone	363a	8.3a	29a	18ab	1.9b

*: statistical analyses were done using the transformed data set ($\log_{10}$).
Note: numbers in this table represent average values/treatment/sampling season.
Note: within column values followed by different letters differ significantly at $P < 0.05$.

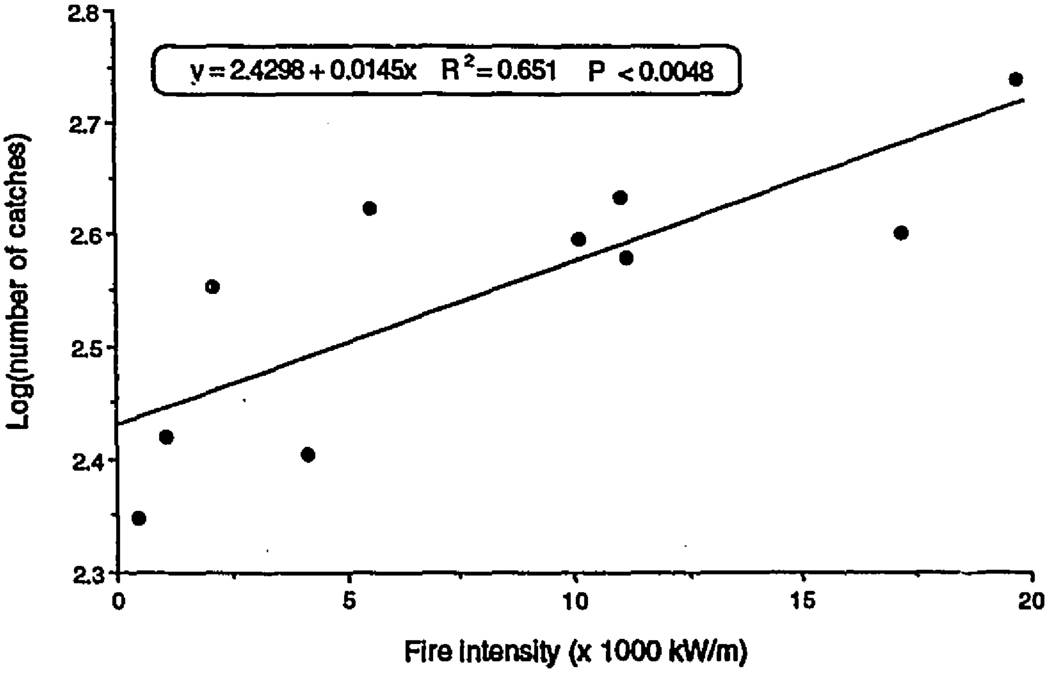


Figure 7 Effect of fire intensity on the number of carabid beetles, Frontier Lake experiment, 1992.

lewisii LeC., *H. pensylvanicus* (DeGeer), *Poecilus lucublandus* (Say), and *Pterostichus mutus* (Say). As a major species, *Syntomus americanus* (Dej.) occurred in all treatments in 1992 including control sites but was not reported the previous year (Duchesne and McAlpine, 1993). *Synuchus impunctatus* (Say) was the most abundant species trapped, representing almost 40% of the total catches in this study. It was collected in all sites and was abundant in 1991 (Duchesne and McAlpine, 1993) and 1992. Of the four major species more abundant in control sites in 1991, i.e. *Calathus ingratus* Dej., *Carabus nemoralis* O. F. Müll., *Myas cyanescens* Dej., and *Pterostichus adoxus* (Say) (Duchesne and McAlpine, 1993), only *Calathus ingratus* Dej. is still abundant in control sites in 1992 along with *Calathus gregarius* (Say), *Pterostichus tristis* (Dej.), and *Sphaeroderus stenostomus lecontei* Dej. which are all forest species (Lindroth, 1961-1969; Gariépy *et al.* 1977). Both *Carabus nemoralis* O. F. Müll. and *Pterostichus adoxus* (Say) were not sampled in 1992. *Myas cyanescens* Dej., on the other hand, became a major species in all but burned-over sites in 1992. No species recognized as being "pyrophilous" (attracted to fire) were collected in this study.

Effects of forest site preparation methods on the dry mass distributions of carabids

Dry mass distributions (Figure 8) show that there are 4 dominant species common to all treatments, including undisturbed forest: *Syntomus americanus* (Dej.) (0-1 mg class), *Synuchus impunctatus* (Say) (10-20 mg class), *Myas cyanescens* Dej. (40-50 mg class), and *Calosoma calidum* (F.) (150-160 mg class).

In the 1-2 mg class, *Notiophilus aeneus* (Hbst) is dominant in all treatments except in burned over sites where *Bembidion nitidum* (Kby) is dominant. Clear-cutting alone is without any species in the 2-4 mg class, whereas undisturbed forest and scarified sites both have *Agonum retractum* LeC. and burned over sites have *Amara convexa* LeC. as dominant species. Undisturbed forest does not have any species belonging to 4-6 mg class, whereas all 3 silvicultural methods have at least one species represented in this class. Three dominant species

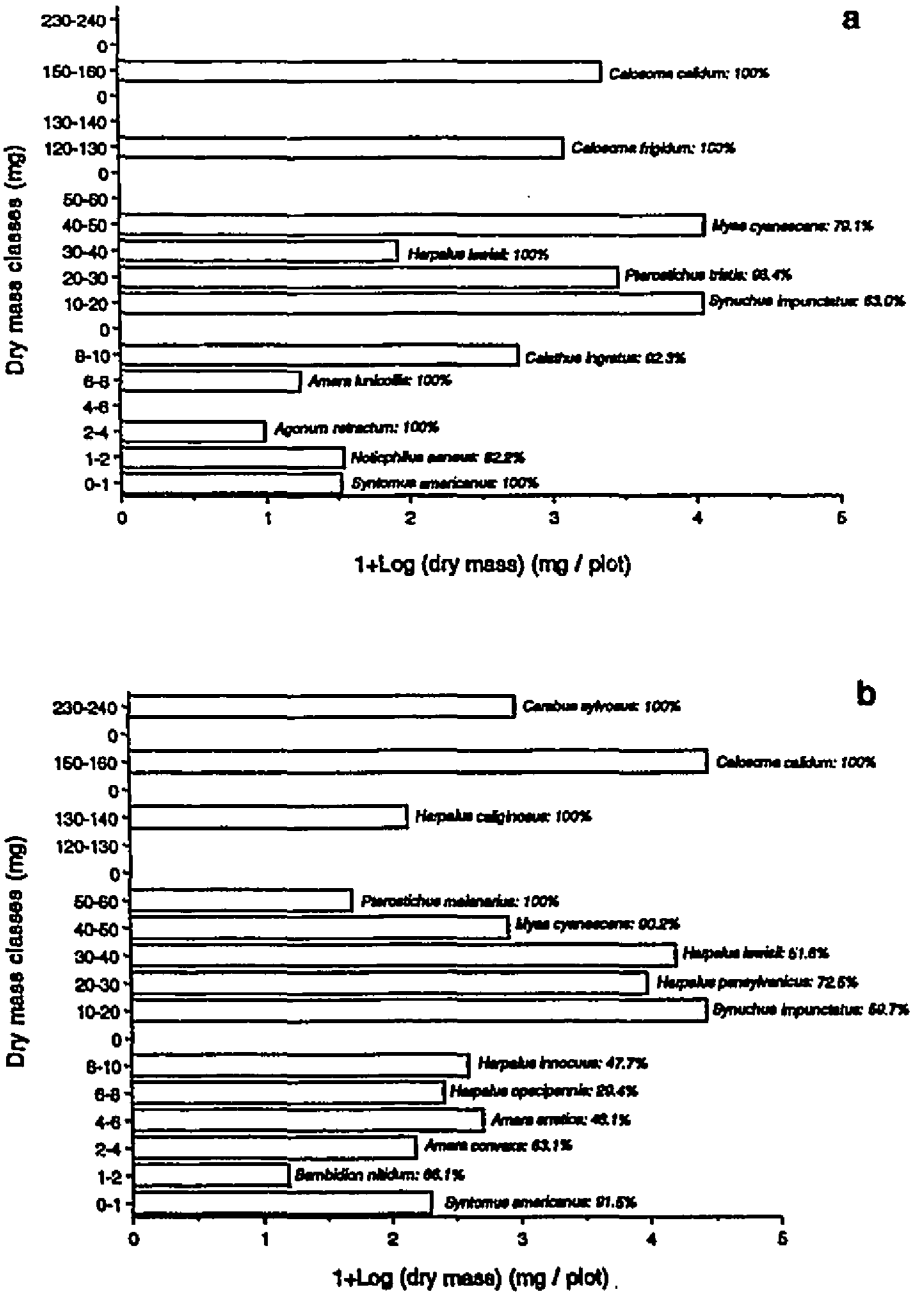
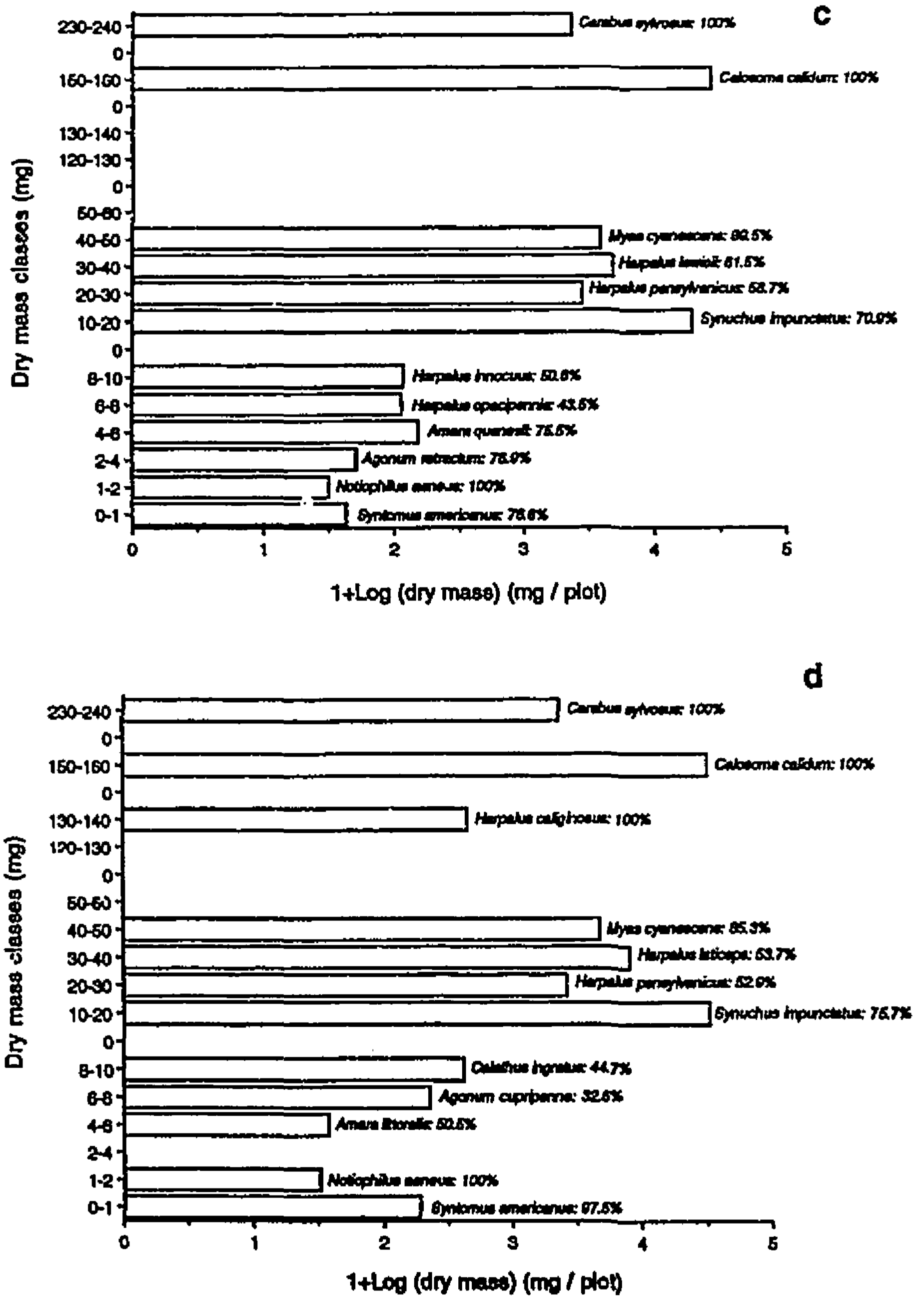


Figure 8 Dry mass distributions of carabid assemblages according to treatment applied at Frontier Lake Experiment Research Plots, 1992: a) undisturbed forest; b) clear-cutting followed by prescribed burning; c) clear-cutting followed by scarification; d) clear-cutting alone. Note: for each dry mass class, the dominant species is indicated followed by its relative mass contribution in percentage.



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characterize the 6-8 mg class: *Harpalus opacipennis* (Hald.) in burned over and scarified sites; *Amara lunicollis* Schiö. in undisturbed forest; *Agonum cupripenne* (Say) in clear-cut sites. *Calathus ingratus* Dej. is the dominant species of the 8-10 mg class in undisturbed forest and clear-cut sites whereas *Harpalus innocuus* LeC. is the dominant species for burned over and scarified sites. For the 20-30 mg class, *Harpalus pensylvanicus* (DeG.) is the dominant species for all treatments except for undisturbed forest where the dominant species is *Pterostichus tristis* (Dej.). The dominant species in 30-40 mg class is *Harpalus lewisii* LeC. in all treatments except for clear-cutting alone where *Harpalus laticeps* LeC. is dominant. There are no species representing the 50-60 mg class, except *Pterostichus melanarius* (Ill.) in burned over sites. *Calosoma frigidum* Kby, in the undisturbed forest, is the only species present in the 120-130 mg class. For the 130-140 mg class, *Harpalus caliginosus* (F.) is the only species in burned over and clear-cut sites. In the largest mass class, i.e. 230-240 mg, *Carabus sylvosus* Say is the only species present in all treatments except in undisturbed forest where no species was found in this class.

Furthermore, dry mass classes of 50 mg or more are invariably represented by single species. Burning and scarification share the same dominant species for dry mass classes from 6-8 mg up to 40-50 mg inclusively.

LA MAURICIE NATIONAL PARK

Effects of logging followed by prescribed burning on carabid assemblages

Logging and burning significantly affected the number of species before and after rarefaction ($P < 0.0125$ and $P < 0.0289$ respectively), and the diversity index ($P < 0.0274$) of carabid assemblages. On the other hand, these treatments did not significantly affect the number of catches or the total dry mass of the carabid fauna. With logging and burning, the number of species, either before or after rarefaction significantly increased by a factor of 2. The diversity index was significantly greater in cut and burned-over sites (Table 7).

Table 7 Effect of logging followed by prescribed burning on 5 characteristics of carabid assemblages at La Mauricie National Park, 1993.

Treatment	Number of catches	Dry mass (g)	Number of species	Number of species after rarefaction	Diversity index
Control	265a	8.3a	14b	13b	1.8b
Logging followed by prescribed burning	279a	9.3a	28a	26a	2.4a

Note: numbers in this table represent average values/treatment/sampling season.
Note: within column values followed by different letters differ significantly at $P < 0.05$.

Species responses to logging followed by prescribed burning

The total sample includes 1,087 adult carabid beetles belonging to 18 genera and 44 species (Appendix B).

All *Amara* and *Harpalus* species were trapped exclusively in cut and burned-over sites (Appendix B). In addition, four major species were found to be collected only on cut and burned sites, namely *Harpalus laticeps* LeC., *H. pleuriticus* Kby, *Poecilus lucublandus* (Say), and *Pterostichus mutus* (Say). *Pterostichus adstrictus* Eschz and *P. coracinus* (Newm.) occurred in both control and burned-over sites and were the most abundant species in this study, representing almost 19% and 17% of the total catches respectively. Other major species caught in both control and burned-over sites include *Myas cyanescens* Dej., *P. melanarius* (Ill.), *P. pensylvanicus* LeC. and *Synuchus impunctatus* (Say). Three major species were more abundantly caught in control sites: *Calathus gregarius* (Say), *C. ingratus* Dej., and *Sphaeroderus stenostomus lecontei* Dejean. In addition, no species recognized as being pyrophilous were collected in this study.

Effects of logging followed by prescribed burning on the dry mass distributions of carabids

The dry mass distributions (Figure 9) indicate 4 dominant species common to both control and burnt over sites: *Calathus ingratus* Dej. (8-10 mg class), *Pterostichus adstrictus* Eschz (10-20 mg class), *Sphaeroderus nitidicollis brevoorti* LeC. (30-40 mg class), and *Pterostichus coracinus* (Newm.) (60-70 mg class).

Burned-over sites have *Syntomus americanus* (Dej) as a dominant species in the 0-1 mg class whereas control sites have no species representing this class. Control sites have *Notiophilus aeneus* (Hbst) dominating 1-2 mg class and no species were found in burnt sites. *Agonum retractum* LeC. and *Loricera pilicornis* F. dominate in 2-4 mg and 4-6 mg classes respectively in control sites, whereas *Amara laevipennis* Kby and *Amara impuncticollis* (Say) dominate in burnt sites. *Harpalus pleuriticus* Kby dominates the 6-8 mg class in burnt sites. No species were found representing this latter dry mass class in control sites. In the 20-30 mg

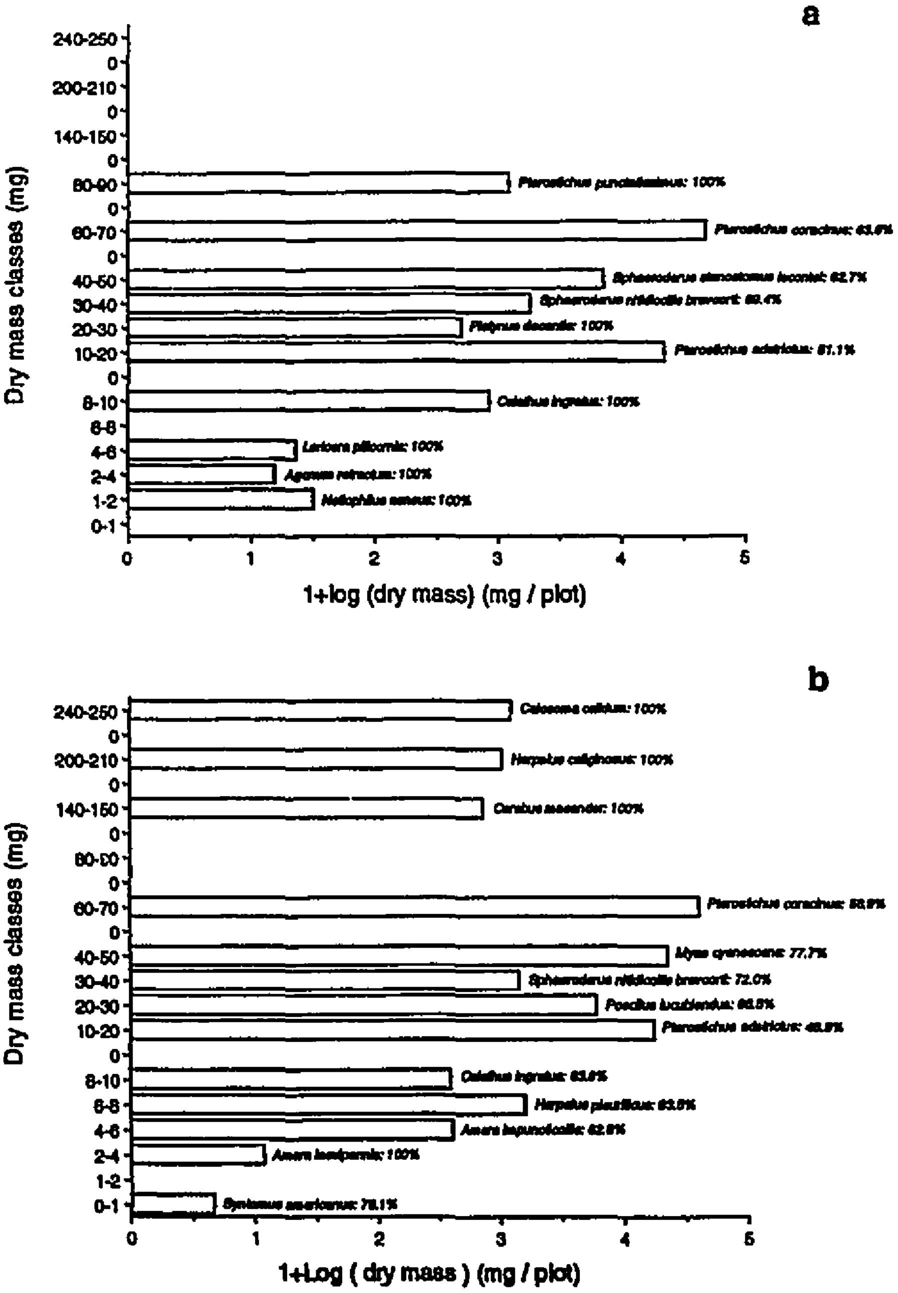

Figure 9 Dry mass distributions of carabid assemblages according to treatment applied at La Mauricie National Park, 1993: a) control sites, and b) forest cutting followed by prescribed burning. Note: for each dry mass class, the dominant species is indicated followed by its relative mass contribution in percentage.

class, *Platynus decentis* (Say) is the only species in control sites whereas *Poecilus lucublandus* (Say) is the dominant species in burnt over sites. Both *Sphaeroderus stenostomus lecontei* Dej. and *Myas cyanescens* Dej. are dominant in 40-50 mg class in undisturbed and burnt sites respectively. The 80-90 mg class is only represented by *Pterostichus punctatissimus* (Rand.) in control sites. The three largest dry mass classes i.e. 140-150, 200-210, and 240-250 mg are invariably represented by single species and solely in burned sites: *Carabus maeander* Fischer von Waldheim, *Harpalus caliginosus* (F.), and *Calosoma calidum* (F.) respectively.

CHAPTER 4

DISCUSSION

Although carabid assemblages of disturbed sites differed from those of undisturbed sites, our results suggest that the silvicultural methods investigated increased or maintained carabid assemblages' characteristics i.e. number of catches, dry mass, species richness, and diversity compared with undisturbed forest. Except for the comparison of dry mass and fire intensity analyses, these findings are in general agreement with other investigations conducted in other forest types (Arnoldi and Matveev, 1973; Szyszko, 1983 both cited by Niemelä *et al.* 1993; Jennings *et al.* 1986a; Niemelä *et al.* 1988; Duchesne and McAlpine, 1993). In fact, the lower measure of species diversity in undisturbed than in regenerating forests seems to be the general response observed for carabids in both temperate and boreal ecosystems (Niemelä *et al.* 1993).

Niemelä *et al.* (1993) observed three general carabid species responses to logging. The first response is for species of rather dry and open conditions to increase in cut areas. This reaction was well demonstrated by Sustek (1981) and Niemelä *et al.* (1993) who reported increased activity for both *Harpalus* and *Amara* species after logging. These two species groups are more characteristic of open areas (Lindroth, 1961-1969; Gariépy *et al.* 1977). Our results also suggest the same response of open country carabid species after logging, as, for example, *Amara* and *Harpalus* species were found almost exclusively in disturbed sites (Appendices A & B). According to Sustek (1981), the increase of *Amara* and *Harpalus* species in cut areas, which are considered pests of herbage and cereals (Vasiliev et al. 1973 cited by Sustek, 1981) can be beneficial in forestry. They could be considered as biological control agents of weeds in cut forests (Sustek, 1981). In addition, the seven major species that were collected more abundantly or solely on clear-cut plots at Frontier Lake (including burned-over and scarified plots) (*Calosoma calidum* (F.), *Harpalus affinis* (Schrank), *H. laticeps* LeC., *H.*

lewisii LeC., *H. pensylvanicus* (DeGeer), *Poecilus lucublandus* (Say), and *Pterostichus mutus* (Say)) and the four major species uniquely sampled in cut and burned sites at LMNP, namely *H. laticeps* LeC., *H. pleuriticus* Kby, *Poecilus lucublandus* (Say), and *Pterostichus mutus* (Say), are also all commonly found on rather dry and open terrain (Lindroth, 1961-1969; Lévesque *et al.* 1976; Gariépy *et al.* 1977). Furthermore, these results support previous observations that found *H. laticeps* to be associated with burned-over sites (Richardson and Holliday, 1982; Holliday, 1984, 1991). *P. lucublandus* has previously been associated with open areas such as meadows and cut forests (Lévesque *et al.* 1976; Niemelä *et al.* 1992; Duchesne and McAlpine, 1993). *H. lewisii* LeC. was previously reported as a major species uniquely collected from clear-cut and burned-over plots in 1991 (Duchesne and McAlpine, 1993). It is not the first time for *H. pleuriticus* to be associated with open terrain (Niemelä *et al.* 1992). On the other hand, *H. pensylvanicus* (DeGeer) and *P. mutus* (Say) were both forest generalist species according to Duchesne and McAlpine (1993) but Lévesque *et al.* (1976) have characterized *P. mutus* with open grounds as in the present study. The increased activity of open ground species in cut forest sites may be explained by the close relationship between the carabids' preferred light intensity and moisture conditions and their habitat selection (Thiele, 1977). For example, forest carabids are mostly night-active and prefer moister conditions than field species who are generally day- or day- and night-active and prefer drier conditions (Thiele, 1977). Logging operations modify the soil's temperature, moisture, and light regime and, at the same time, seem to have favoured, among others, the establishment of open country carabid beetles.

The second response of carabids to logging is characterized by an initial decrease of forest generalist species that re-establish with forest regeneration and canopy closure. At Frontier Lake, it is surprising to observe *Syntomus americanus* (Dej.) as a forest generalist since it is known more for being a xerophilous species of open ground conditions seeking direct sun exposition (Lindroth, 1961-1969; Gariépy *et al.* 1977). Jennings *et al.* (1986a) found *Syntomus americanus* almost exclusively in clear-cut strips of spruce-fir forests of Maine, while Lévesque *et al.* (1976) found it to be exclusive of clearings. *Synuchus impunctatus* Say, on the other hand, has already been reported as a forest generalist species by Lévesque *et al.* (1976) and Jennings et al. (1986a). Even though it prefers rather dry conditions, *S. impunctatus* is found in both open terrain and various forest types (Lindroth, 1961-1969; Gariépy et al. 1977). As an initial study on the effects of forestry practices on carabid beetles at LMNP, it is not possible to compare our results with earlier species composition. However, it is interesting to note, at this stage, that all major species occurring in both control and treated sites i.e. *Myas cyanescens* Dej., *Pterostichus adstrictus* Eschz, *P. coracinus* (Newm.), *P. melanarius* (Ill.), *P. pensylvanicus* LeC., and *Synuchus impunctatus* (Say) (Appendix B), are found in wooded and open areas and also near or in open forests (Lindroth, 1961-1969; Lévesque *et al.* 1976; Gariépy *et al.* 1977). It was not surprising to find *P. adstrictus* as the most abundantly sampled species since it is one of the most widely distributed carabids (Goulet, 1974). All of these species, except for *Myas cyanescens* (Say), were previously reported as forest or habitat generalists (Lévesque *et al.* 1976; Jennings *et al.* 1986a; Martel *et al.* 1991; Niemelä *et al.* 1992; Duchesne and McAlpine, 1993; Appendix A). *Myas cyanescens* (Say) was reported more abundant in undisturbed plots in 1991 by Duchesne and McAlpine (1993), and, the following year, became a major species in all but burned-over plots (Appendix A). Several mutually exclusive factors seem to facilitate the co-existence of these major species in the same forest types. For instance, *Syntomus americanus*, *P. adstrictus* Eschz, and *P. pensylvanicus* LeC. are spring breeders while *Synuchus impunctatus*, *P. coracinus* (Newm.), *P. melanarius* (Ill.) are summer breeders (Bousquet and Pilon, 1977; Lévesque *et al.* 1979; Lévesque and Lévesque, 1986). The separation in time of maximum activity periods may serve as a means to lessen competition between similar species (Greenslade, 1965; Dennison and Hodkinson, 1984). Also, by their difference in size, they will more likely have a different diet (Loreau, 1983; Wheater, 1988). This niche differentiation according to size allows ground beetles to use a wide range of prey with many species co-existing in the same habitat (Loreau, 1983). In addition, *P. adstrictus* and *P. pensylvanicus*, who are presumed closely related, were both found to be major species occurring in the same forest types at LMNP. However, Goulet (1974) reported differences in their preferred habitats as *P. pensylvanicus* seems to be restricted to forest litter whereas *P. adstrictus* can be found in both litter and open habitats and also in their oviposition behaviour and sites.

Dry mass distributions and structures indicated differences as well as similarities between carabid beetle assemblages. Similarities in dry mass distributions may indicate certain patterns of resistance or adaptations of species to a wide range of conditions as already indicated for: 1) *Pterostichus coracinus* (Newm.) in Québec Appalachian maple forests affected by canopy dieback (Martel *et al.* 1991); 2) *Calathus ingratus* Dej. in boreal forest in Alberta affected by clear-cutting (Niemelä *et al.* 1993); and, 3) *S. impunctatus* (Say) in Ontario and in Québec affected by different forestry practices (Duchesne and McAlpine, 1993; Appendices A & B). Underwood (1989) relates the absence of response of dominant species to their adaptation to a wide variety of environmental conditions or their rapid dispersal and colonization after disturbance.

The third response of carabids to logging concerns forest specialist species who seem unable to re-establish populations in cut over forests. Niemelä *et al.* (1992, 1993) classified *C. ingratus* as a forest generalist species because it occurred abundantly in all forest types. But at Frontier Lake and LMNP, it appears to be more sensitive to disturbance since it is mainly active in undisturbed sites (Appendices A & B). Holliday (1991) also found *C. ingratus* to be most frequently caught in an undisturbed conifer forest compared with a burned forest site. *Calathus gregarius* (Say) and *S. stenostomus lecontei* Dej. were both previously associated with coniferous forest types (Lévesque *et al.* 1976) as observed at the Frontier Lake study site (Appendix A). *Carabus nemoralis* O. F. Müll. and *Pterostichus adoxus* (Say) appear not able to establish persistent populations in any type of forest sites at Frontier Lake and might be negatively affected by human-caused habitat change, as mentioned for other mature forest specialist carabid species by Niemelä *et al.* (1993). *Myas cyanescens* Dej., on the other hand, seems capable of establishing populations in disturbed forest. Again, no comparison with previous species composition at LMNP study area is possible, but, interestingly, it can be noted that *Calathus gregarius* (Say), *C. ingratus* Dej., and *Sphaeroderus stenostomus lecontei* Dej., which are forest species (Lindroth, 1961-1969; Lévesque *et al.* 1976; Gariépy *et al.* 1977), were major species more abundantly caught in control sites. The same results for these three species are reported at Frontier Lake (Appendices A & B).

Evans (1972) listed three pyrophilous carabid species, including *Agonum obsoletum* Say. Apparently, such species are attracted to the heat and/or smoke of fire (Evans, 1972). Interestingly, this latter species was found in 1991 at Frontier Lake shortly after burning (Duchesne and McAlpine, 1993), but not in 1992, suggesting that their occupation of burned sites is of short duration as observed by Holliday (1984). In LMNP, no such species were identified. The delay between burning and sampling may explain their absence. Nevertheless, pyrophilous species play an important role in processes such as decomposition of dead trees into humus by starting to feed and borough through them during or very shortly after a fire and they also contribute to initial increases in species diversity at burned areas (Evans, 1972; Muona and Rutanen, 1994).

As secondary treatments, scarification and prescribed burning did not seem to further enhance the carabid assemblages' differences between clear-cut and undisturbed Frontier Lake studied sites, except for the species diversity index (Table 6). Although the average number of catches and species richness for clear-cut only and burned plots were not statistically different, the diversity index of burned over plots was significantly higher than the one of clear-cut only plots. By taking into account both the number and relative abundance of species, the Shannon-Wiener index permits normalized comparisons of species diversity. Thus, species of clear-cut sites are less abundant and evenly distributed than species of burned sites as indicated by a lower diversity index for clear-cut sites.

The increase in abundance in cut sites of groups of open country species like *Amara* spp., *Harpalus* spp., *Bembidion* spp., *Cicindela* spp., *Poecilus lucublandus*, *Calosoma calidum*, and *Pterostichus mutus* along with the capability of some forest generalists like *M. cyanescens*, *P. adstrictus*, *P. coracinus*, *P. melanarius*, *P. pensylvanicus*, *S. impunctatus*, and *Syntomus americanus* to establish populations in regenerating sites contributed to maintain or even increase studied carabid assemblages' characteristics in regenerating sites compared to control sites.

It appears from the effects of logging, fire and scarification on carabid beetles that they are affected by either immediate (Rice, 1932; French and Keirle, 1969) or long-lasting changes of environmental conditions (Harris and Whitcomb, 1971; Richardson and Holliday, 1982). Factors such as differences in environmental conditions (habitat diversity and heterogeneity, food resources, microclimate), interspecific interactions, and autecological species characteristics (dispersal power and habitat preferences) have been mentioned to try to explain observed differences in carabid assemblages composition and structure (Harris and Whitcomb, 1974; Lenski, 1982a,b; Niemelä *et al.* 1985; Jennings *et al.* 1986a; Holliday, 1991; Martel *et al.* 1991). It is suggested that the colonization of disturbed areas by early colonists like certain bacteria, fungi and other soil organisms may contribute to initiate the establishment of open country as well as forest generalist carabid beetles.

A wide range of food webs are believed to display scale invariance (Briand and Cohen, 1984). Assuming that carabid species number follow this phenomenon, the present results indicate that short-term effects of logging, prescribed burning, and soil scarification do not reduce the diversity of the forest soil communities at the studied sites. Many investigations show that physical and chemical changes in the environment brought primarily by logging and secondarily by prescribed burning and scarification do in fact affect other forest soil invertebrates and microorganisms in a variety of forest types (Ahlgren and Ahlgren, 1965; Huhta *et al.* 1967; Huhta *et al.* 1969; Jorgensen and Hodges, 1970; Huhta, 1971; Reichert and Reeder, 1971; Ahlgren, 1974; Huhta, 1976; Niemelä and Sundman, 1977; Laudelout *et al.* 1978; Sundman *et al.* 1978; Bååth, 1980; Coyle, 1981; Lundgren, 1982; Jennings *et al.* 1986b; McIver *et al.* 1992; Ohtonen *et al.* 1992; McSorley, 1993). Nonetheless, more studies are necessary in order to verify this assumption.

The present results support the hypothesis that disturbance increases species diversity (Levin and Paine, 1974). Similar trends of increased species diversity after disturbance have been reported for bryophytes in a boreal spruce forest affected by uprooting in Sweden (Jonsson and Esseen, 1990), and insects in managed apple orchards in Hungary (Szentkiralyi and Kozar, 1991). By increasing habitat heterogeneity, disturbances may allow less competitive species to use limited resources now available to them (Levin and Paine, 1974). It has already been postulated that natural disturbance contribute to maintain species diversity in forests by creating spatial heterogeneity that species could partition (Grubb, 1977). The two most important hypotheses for insect diversity are the "resource diversity hypothesis" (RDH) and the "intermediate disturbance hypothesis" (IDH) (Szentkiralyi and Kozar, 1991). For RDH, the greater diversity of available resources, the higher the insect species richness (Price, 1984). The IDH predicts greater number of species at intermediate levels of disturbance (Petraitis *et al.* 1989). More specifically, two main suggestions have been mentioned to explain increased carabid diversity in disturbed forests: 1) disturbance may disrupt processes of competition exclusion (Lenski, 1982a); and, 2) carabid diversity may be related to habitat heterogeneity (Niemelä *et al.* 1988).

Finally, the tendency for the number of catches to increase with fire intensity might indicate that more food resources, either vegetal and/or animal, are favoured or stimulated as fire intensity increases, which in turn would permit an increasingly large number of carabid beetles to colonize burned areas. For example, in eastern Québec, vegetation diversity in plant frequency and density both increased as the intensity of mechanical site preparation methods increased (Jobidon, 1990). In addition, more herbaceous species occurred where high-intensity site preparation took place compared with low-intensity treated sites.

CONCLUSION

It has been suggested that maximizing habitat diversity would contribute to the conservation of biological diversity (Hunter, 1990). Our results support this approach as the presence of regenerating sites among the natural landscape increased carabid beetle diversity. However, extensive regenerating areas could be detrimental to mature forest specialists. A balance between the different forest types and age classes may ensure the maintenance of a proper level of biological diversity.

Furthermore, the sensitivity and rapid response of carabids to environmental changes, as suggested by our study and others, would give further evidence for their use as bioindicators for the evaluation of the impact of habitat disturbance.

Long-term ecological and biological studies through monitoring programs are still necessary in order to assess not only the extent and nature of the effects of habitat disturbances but also to distinguish natural variations from those caused by human influences (Spellerberg, 1991). More studies on other forest types are needed if we are to include information concerning the effects of habitat disturbances on the biodiversity of the soil community in forest management programs.

"If we are seriously interested in the challenge of maintaining biological diversity and ecological integrity of forest systems, we cannot afford to ignore invertebrates."

(Niemelä *et al.*1993)

THESIS CONCLUSION

This research was mainly intended to further document the ecological impact of forestry practices such as logging and harvesting, prescribed burning, and soil scarification on carabid beetle assemblages' diversity. To do so, carabids were sampled, using pitfall traps, in two different forest types, namely a jack pine stand in eastern Ontario and white spruce plantations in Québec in 1992 and 1993 respectively. The short-term effects of such forest disturbances maintained or even increased the diversity of carabid assemblages. In addition, the number of catches, dry mass, and number of species (either before or after rarefaction) all responded in the same way as diversity. Furthermore, it was also possible to examine carabid species responses and dry mass distributions. Several similarities in response patterns of species or groups of species were observed in both study areas.

Although the results of this study are comparable with those reported in previous studies, too little is presently known on the short-, mid-, and long-term impact of forest disturbances, such as forest site preparation methods, on the diversity of carabids and other arthropods. More research is needed before generalizations can be drawn and knowledge incorporated in forest management programs and applied to a variety of forest types.

It is now widely recognized that terrestrial arthropods display certain characteristics (diversity and functional roles, wide distribution, rapid growth and response to environmental changes) that contribute to their increasing consideration as useful indicator groups (Kremen *et al.* 1993). Used in such a way, terrestrial arthropods such as carabids would contribute more and more to our knowledge on the impact of natural as well as anthropogenic disturbances on ecosystems by being part of long-term environmental monitoring programs.

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APPENDICES

APPENDIX A. Sampled carabid species for the entire sampling period at Frontier Lake Experiment Research Plots, 1992.

Species	Body length (mm)	Undisturbed forest (4 plots)		Clear-cutting followed by prescribed burning (10 plots)		Clear-cutting followed by scarification (3 plots)		Clear-cutting alone (3 plots)	
		n	%	n	%	n	%	n	%
Agonum cupripenne (Say)	7.6-9.2	-	-	9	0.25	1	0.16	3	0.28
A. placidum (Say)	6.9-8.8	-	-	10	0.27	-	-	-	-
A. retractum LeConte	6.1-7.6	1	0.17	-	-	3	0.48	-	-
Amara avida (Say)	7.5-9.8	-	-	1	0.03	-	-	-	-
A. convexa LeConte	5.4-7.9	-	-	26	0.71	1	0.16	-	-
A. cupreolata Putzeys	6.6-9.1	-	-	1	0.03	1	0.16	3	0.28
A. discors Kirby	6.1-8.7	-	-	8	0.22	-	-	-	-
A. erratica (Duftschmid)	6.6-8.7	-	-	43	1.17	2	0.32	1	0.09
A. familiaris (Duftschmid)	5.7-7.1	-	-	1	0.03	-	-	-	-
A. impuncticollis (Say)	7.1-9.1	-	-	3	0.08	-	-	-	-
A. laevipennis Kirby	5.8-7.0	-	-	12	0.33	-	-	-	-
A. latior (Kirby)	7.9-10.7	-	-	31	0.84	11	1.75	2	0.18
A. littoralis Mannerheim	6.2-9.2	-	-	1	0.03	-	-	1	0.09
A. lunicollis Schiödte	7.4-9.0	1	0.17	-	-	-	-	-	-
A. obesa (Say)	9.0-12.3	-	-	54	1.47	4	0.64	5	0.46
A. quenseli (Schönherr)	6.1-8.6	-	-	34	0.93	7	1.11	-	-
A. rubrica Haldeman	5.3-7.3	-	-	3	0.08	-	-	-	-
A. sinuosa (Casey)	5.7-9.0	-	-	5	0.14	-	-	-	-
Amphasia sericea (T.W. Harris)	8.9-11.0	1	0.17	1	0.03	-	-	-	-

APPENDIX A. Continued...

Species	Body length (mm)	Undisturbed forest (4 plots)		Clear-cutting followed by prescribed burning (10 plots)		Clear-cutting followed by scarification (3 plots)		Clear-cutting alone (3 plots)	
		n	%	n	%	n	%	n	%
Anisodactylus merula (Germar)	11.0-12.6	1	0.17	29	0.79	2	0.32	5	0.46
A. rusticus (Say)	8.9-11.0	-	-	3	0.08	-	-	1	0.09
Bembidion mutatum Gemminger & Harold	2.7-3.5	-	-	2	0.05	2	0.32	-	-
B. nitidum (Kirby)	4.2-5.3	-	-	8	0.22	-	-	-	-
B. quadrimaculatum oppositum Say	2.9-3.7	-	-	20	0.54	2	0.32	2	0.18
B. tetracolum Say	5.0-6.0	-	-	2	0.05	-	-	-	-
Calathus gregarius (Say)	8.3-10.8	27	4.65	2	0.05	9	1.43	15	1.38
C. ingratus Dejean	7.0-11.0	23	3.96	3	0.08	1	0.16	6	0.55
Calosoma calidum (Fabricius)	20.0-25.0	6	1.03	179	4.88	52	8.27	61	5.60
C. frigidum Kirby	16.0-26.0	4	0.69	-	-	-	-	-	-
Carabus sylvosus Say	24.0-27.0	-	-	4	0.11	3	0.48	3	0.28
Chlaenius tomentosus (Say)	12.7-17.6	-	-	-	-	-	-	1	0.09
Cicindela limbalis Klug	14.0-15.0	-	-	-	-	1	0.16	-	-
C. longilabris Say	13.3-15.0	-	-	14	0.38	-	-	7	0.64
C. punctulata Olivier	10.0-12.0	-	-	19	0.52	3	0.48	2	0.18
C. purpurea Olivier	13.5-14.0	-	-	21	0.57	1	0.16	-	-
C. scutellaris lecontei Haldeman	12.5-13.7	-	-	1	0.03	-	-	-	-
C. tranquebarica Herbst	13.0-15.0	-	-	4	0.11	3	0.48	-	-
Cymindis cribricollis Dejean	8.4-11.1	-	-	16	0.44	-	-	4	0.37

APPENDIX A. Continued...

Species	Body length (mm)	Undisturbed forest (4 plots)		Clear-cutting followed by prescribed burning (10 plots)		Clear-cutting followed by scarification (3 plots)		Clear-cutting alone (3 plots)	
		n	%	n	%	n	%	n	%
C. limbatus Dejean	8.3-10.4	4	0.69	1	0.03	-	-	-	-
Dyschirius globulosus (Say)	2.7-3.2	-	-	4	0.11	1	0.16	-	-
Elaphrus olivaceus LeConte	7.3-8.0	-	-	1	0.03	-	-	-	-
Harpalus affinis (Schrank)	8.6-12.1	-	-	119	3.24	4	0.64	3	0.28
H. caliginosus (Fabricius)	18.0-25.0	-	-	1	0.03	-	-	1	0.09
H. faunus Say	8.5-12.7	-	-	14	0.38	4	0.64	4	0.37
H. herbivagus Say	8.7-11.0	-	-	43	1.17	4	0.64	-	-
H. indigens Casey	7.3-10.2	-	-	19	0.52	1	0.16	6	0.55
H. innocuus LeConte	8.2-9.6	1	0.17	21	0.57	2	0.32	1	0.09
H. laevipes Zetterstedt (= *H. egregius* Casey)	10.7-12.4	-	-	1	0.03	-	-	-	-
H. laticeps LeConte	13.0-15.4	-	-	161	4.39	10	1.59	34	3.12
H. lewisii LeConte	12.7-14.7	1	0.17	236	6.43	26	4.13	25	2.29
H. nigritarsis C.R. Sahlberg	7.0-9.1	-	-	1	0.03	-	-	2	0.18
H. ochropus Kirby	7.0-7.7	-	-	1	0.03	-	-	-	-
H. opacipennis (Haldeman)	7.6-9.2	-	-	10	0.27	2	0.32	2	0.18
H. pensylvanicus (DeGeer)	10.0-15.0	-	-	269	7.33	19	3.02	16	1.47
H. plenalis Casey	7.6-8.4	-	-	1	0.03	-	-	-	-
H. providens Casey (= *H. viduus* LeConte)	12.0-13.4	-	-	8	0.22	3	0.48	5	0.46

APPENDIX A. Continued...

Species	Body length (mm)	Undisturbed forest (4 plots)		Clear-cutting followed by prescribed burning (10 plots)		Clear-cutting followed by scarification (3 plots)		Clear-cutting alone (3 plots)	
		n	%	n	%	n	%	n	%
H. puncticeps (Stephens)	6.5-9.0	-	-	1	0.03	-	-	-	-
H. reversus Casey (= *H. funerarius* Csiki)	10.6-13.0	-	-	4	0.11	2	0.32	1	0.09
H. solitaris Dejean (= *H. fuliginosus* Duftschmid)	8.9-10.4	-	-	18	0.49	2	0.32	3	0.28
H. fallax LeConte (= *H. somnulentus* Dejean)	7.9-10.9	-	-	1	0.03	2	0.32	-	-
H. pleuriticus Kirby (= *H. somnulentus* Dejean)	8.1-9.7	-	-	-	-	-	-	1	0.09
Miscodera arctica (Paykull)	6.2-9.5	-	-	2	0.05	-	-	-	-
Myas cyanescens Dejean	13.6-15.6	89	15.32	18	0.49	25	3.97	29	2.66
Notiobia terminata (Say)	8.7-9.0	1	0.17	1	0.03	-	-	-	-
Notiophilus aeneus (Herbst)	5.1-5.7	6	1.03	1	0.03	5	0.79	5	0.46
N. aquaticus (Linné)	4.6-5.9	-	-	1	0.03	-	-	-	-
N. intermedius Lindroth	4.4-5.0	2	0.34	-	-	-	-	-	-
N. semistriatus Say	4.8-5.4	-	-	1	0.03	-	-	-	-
Poecilus lucublandus (Say)	9.3-13.8	-	-	75	2.04	3	0.48	5	0.46
Pterostichus commutabilis (Motschulsky) (= *P. lecontelanus* Lutshnik)	7.3-8.5	-	-	-	-	1	0.16	-	-
P. corvinus (Dejean)	11.7-14.8	-	-	1	0.03	-	-	-	-
P. luctuosus (Dejean)	8.0-11.8	-	-	1	0.03	-	-	-	-
P. melanarius (Illiger)	12.2-19.0	-	-	1	0.03	-	-	-	-

APPENDIX A. Continued...

Species	Body length (mm)	Undisturbed forest (4 plots)		Clear-cutting followed by prescribed burning (10 plots)		Clear-cutting followed by scarification (3 plots)		Clear-cutting alone (3 plots)	
		n	%	n	%	n	%	n	%
P. mutus (Say)	9.6-12.9	5	0.86	333	9.07	52	8.27	50	4.59
P. pensylvanicus LeConte	9.6-12.1	76	13.08	11	0.30	9	1.43	57	5.23
P. tristis (Dejean)	10.7-13.4	50	8.61	6	0.16	5	0.79	-	-
Scaphinotus bilobus (Say)	10.0-13.7	1	0.17	-	-	-	-	-	-
Selenophorus gagatinus Dejean	6.5-7.4	-	-	1	0.03	-	-	-	-
S. opalinus (LeConte)	9.6-10.7	-	-	1	0.03	-	-	1	0.09
Sphaeroderus stenostomus lecontei Dejean	12.0-17.0	24	4.13	2	0.05	2	0.32	4	0.37
Stenolophus conjunctus (Say)	3.2-4.2	-	-	11	0.30	2	0.32	1	0.09
Syntomus americanus (Dejean)	2.8-3.6	35	6.02	474	12.92	26	4.13	145	13.30
Synuchus impunctatus (Say)	8.8-11.3	222	38.21	1224	33.35	308	48.97	567	52.02
TOTAL	-	581	100	3670	100	629	100	1090	100
NUMBER OF SPECIES	-	22	-	74	-	44	-	41	-

n = number of specimens caught
% = relative species abundance in percentage
Note: body size ranges from Gariépy *et al.* (1977) and nomenclature according to Bousquet and Larochelle (1993).
Note: *Harpalus fallax* LeConte and *Harpalus pleuriticus* Kirby have been considered as seperate species even though Noonan (1991) has considered both to be *Harpalus somnulentus* Dejean. They would appear to be still considered as seperate species (Y. Bousquet, personal communication).

APPENDIX B. Sampled carabid species for the entire sampling period at La Mauricie National Park, 1993.

Species	Body length (mm)	Control forest (2 sites)		Logging followed by prescribed burning (2 sites)	
		n	%	n	%
Agonum cupripenne (Say)	7.6-9.2	-	-	2	0.36
A. retractum LeConte	6.1-7.6	1	0.19	-	-
Amara cupreolata Putzeys	6.6-9.1	-	-	1	0.18
A. erratica (Duftschmid)	6.6-8.7	-	-	3	0.54
A. impuncticollis (Say)	7.1-9.1	-	-	9	1.61
A. laevipennis Kirby	5.8-7.0	-	-	1	0.18
A. latior (Kirby)	7.9-10.7	-	-	2	0.36
A. lunicollis Schiødte	7.4-9.0	-	-	1	0.18
A. obesa (Say)	9.0-12.3	-	-	10	1.79
Bembidion quadrimaculatum oppositum Say	2.9-3.7	-	-	1	0.18
Calathus gregarius (Say)	8.3-10.8	43	8.13	7	1.25
C. ingratus Dejean	7.0-11.0	21	3.97	6	1.08
Calosoma calidum (Fabricius)	20.0-25.0	-	-	1	0.18
Carabus maeander Fisher von Waldheim	15.0-24.0	-	-	1	0.18
Cymindis borealis LeConte	7.6-10.0	-	-	1	0.18
C. cribricollis Dejean	8.4-11.1	3	0.57	5	0.90
Harpalus affinis (Schrank)	8.6-12.1	-	-	2	0.36
H. caliginosus (Fabricius)	18.0-25.0	-	-	1	0.18

APPENDIX B. Continued...

Species	Body length (mm)	Control forest (2 sites)		Logging followed by prescribed burning (2 sites)	
		n	%	n	%
H. compar LeConte (= *H. bicolor* Fabricius)	10.8-14.1	-	-	2	0.36
H. fallax LeConte (= *H. somnulentus* Dejean)	7.9-10.9	-	-	1	0.18
H. fulvilabris Mannerheim	8.9-10.8	-	-	1	0.18
H. herbivagus Say	8.7-11.0	-	-	1	0.18
H. laticeps LeConte	13.0-15.4	-	-	19	3.41
H. lewisii LeConte	12.7-14.7	-	-	2	0.36
H. nigritarsis C.R. Sahlberg	7.0-9.1	-	-	1	0.18
H. pleuriticus Kirby (= *H. somnulentus* Dejean)	8.1-9.7	-	-	37	6.63
H. solitaris Dejean (= *H. fuliginosus* Duftschmid)	8.9-10.4	-	-	8	1.43
Loricera pilicornis Fabricius	7.0-8.3	1	0.19	-	-
Myas cyanescens Dejean	13.6-15.6	11	2.08	70	12.54
Notiophilus aeneus (Herbst)	5.1-5.7	5	0.95	-	-
Platynus decentis (Say)	9.1-13.8	5	0.95	4	0.72
Poecilus lucublandus (Say)	9.3-13.8	-	-	50	8.96
Pterostichus adoxus (Say)	12.1-15.4	1	0.19	-	-
P. adstrictus Eschscholtz	9.6-13.1	117	22.12	85	15.23
P. coracinus (Newman)	12.7-18.0	104	19.66	79	14.16

APPENDIX B. Continued...

Species	Body length (mm)	Control forest (2 sites)		Forest cutting followed by prescribed burning (2 sites)	
		n	%	n	%
P. melanarius (Illiger)	12.2-19.0	56	10.59	52	9.32
P. mutus (Say)	9.6-12.9	-	-	32	5.73
P. pensylvanicus LeConte	9.6-12.1	27	5.10	31	5.56
P. punctatissimus (Randall)	15.3-18.2	3	0.57	-	-
Sphaeroderus nitidicollis brevoorti LeConte	12.5-13.8	10	1.89	6	1.08
S. stenostomus lecontei Dejean	12.0-17.0	19	3.59	3	0.54
Syntomus americanus (Dejean)	2.8-3.6	-	-	4	0.72
Synuchus impunctatus (Say)	8.8-11.3	102	19.28	14	2.51
Xestonotus lugubris (Dejean)	9.3-11.0	-	-	2	0.36
TOTAL	-	529	100	558	100
NUMBER OF SPECIES	-	17	-	39	-

n = number of specimens caught
% = relative species abundance in percentage
Note: body size ranges from Gariépy *et al.* (1977) and nomenclature according to Bousquet and Larochelle (1993).
Note: *Harpalus fallax* LeConte and *Harpalus pleuriticus* Kirby have been considered as seperate species even though Noonan (1991) has considered both to be *Harpalus somnulentus* Dejean. They would appear to be still considered as seperate species (Y. Bousquet, personal communication).