

IMPACT OF REGENERATION TECHNIQUES ON ECOLOGICAL
DIVERSITY IN PLANTED AND NATURAL FOREST STANDS:
SPECIES AND ECOSYSTEM DIVERSITY AMONG CARABID
BEETLES (COLEOPTERA:CARABIDAE) IN JACK PINE STANDS

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Submitted to the Faculty

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98

Graduate Studies

The University of Manitoba

by

Rhéal Christian Lafrenière

In Partial Fulfilment of the
Requirements for the Degree

of

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Department of Entomology

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BY

RHEAL CHRISTIAN LAFRENIERE

A Thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

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Dedicated
To my wife, Carmelle

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ABSTRACT

Lafrenière, R. C., M.Sc., The University of Manitoba, 1994
Impact of Regeneration Techniques on Ecological Diversity in
Planted and Natural Forest Stands: Species and Ecosystem
Diversity Among Carabid Beetles (Coleoptera:Carabidae) in
Jack Pine Stands.

Major Professor: N.J. Holliday

In 1991 and 1992, carabid beetles were collected in naturally (fire) regenerated and planted stands of jack pine, *Pinus banksiana* Lamb. from four different age classifications, (5, 15, 25, 40 years after establishment) using pitfall traps. Species diversity (α) was measured using the Shannon-Wiener and log series α indices, and ecosystem diversity (β) was measured using Jaccard's coefficient and Kendall's τ rank correlation coefficient. Ordination analysis was conducted on the common carabid species and environmental data: dominant vegetation, light intensity, and soil and litter temperatures, using Correspondence Analysis and Canonical Correspondence Analysis.

Number of carabid beetles, number of carabid species, α and β diversity were not significantly affected by type of regeneration. However, the log series α indicated that

planted sites may reach their peak in carabid species diversity earlier than the natural regenerated sites. In the planted sites the highest level of carabid α diversity occurred in the 15 year age class, whereas in the natural sites, carabid α diversity peaked in the 15 to 25 year age classes. It also appears that natural stands maintain a higher level of diversity after the peak and for longer than planted sites.

Kendall's τ indicated that the similarity in carabid species abundance between site replicates was generally greater among planted stands than natural stands, and were therefore lower in ecosystem diversity.

Correspondence analysis indicated that the difference in carabid species composition between stand ages was greater than the difference between type of regeneration, with the carabid beetles separating into groups according to site age. The carabid species assemblages in the 5 year old sites, many of which belonged to the genera *Harpalus* and *Amara* were consisted dry open habitat species typically associated with early successional vegetation. The carabid species in the 15 and 25 year old sites generally consisted of open forest carabid species (e.g. *Carabus taedatus* F. and *C. serratus* Say.) which were associated with intermediate successional vegetation. The carabid species assemblages in the 15 year old sites also included several open habitat species, whereas the carabid assemblages in the 25 year old

sites included more of the mature forest carabid species. The carabid species assemblages in the 40 year old sites consisted mainly of mature forest carabid species such as *Calathus ingratus* Dejean, *Synuchus impunctatus* Say, *Dicaelus sculptilis* Say and *Pterostichus pensylvanicus* Leconte and *P. adstrictus* Eschscholts, which were associated with the cool shaded conditions and the late successional vegetation species of closed forests.

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 the sites. Large symbols indicate high light
 intensity and litter temperatures. The first
 axis, (horizontal) has an eigenvalue of 0.420
 = 37.3 % and the second axis, (vertical) has
 an eigenvalue of 0.152 = 13.5 %. The carabid
 species are: AP = *Agonum placidum*, ALAE =
Amara laevipennis, ALAT = *Amara latior*, AO =
Amara obesa, CA = *Calosoma calidum*, CI =
Calathus ingratus, CS = *Carabus serratus*, CT
 = *Carabus taedatus*, DS = *Dicaelus sculptilis*,
 HF = *Harpalus fuliginosus*, HLA = *Harpalus*
laticeps, HLE = *Harpalus lewisi*, PA =
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 intensity and litter temperatures. The first
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 an eigenvalue of 0.079 = 8.8 %. The carabid
 species are: AP = *Agonum placidum*, ALAE =
Amara laevipennis, ALAT = *Amara latior*, AO =
Amara obesa, CA = *Calosoma calidum*, CI =
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CHAPTER I

Introduction

Ecological diversity is a measure of community information that expresses diversity in terms α and β diversity (Pielou, 1975). Measures of α diversity utilize the number and relative abundance of species within a single habitat, whereas measures of β diversity depend on the change in species diversity or composition between two or more habitats (Pielou, 1975; Magurran, 1988).

Diversity measures are used to give insight into the internal mechanisms of a community as well as into the effects of the environmental changes on the ecosystem (Kempton and Taylor, 1976). The importance of studying the ecological diversity of an area after a dramatic disturbance is to:

- 1) Provide a better understanding how the environment will respond after the disturbance and whether different types of disturbances exhibit different responses (Frambs, 1990; Kimmins, 1991).
- 2) Provide insight into ways of reducing the stress caused by the disturbance (Niemelä et. al.,

1988).

A problem with studying forest diversity is that forests are slow developing, complex and diverse ecosystems in which studies may require decades to yield meaningful results (Powers and Van Cleve, 1991). Chrono-sequence and retrospective studies, which utilize sites of different ages to imitate forest succession, have been used to overcome this problem. Although these types of studies are unfortunately plagued by large numbers of concerns about matching of sites, they still provide an accurate interpretation of what typically occurs during forest succession (Powers and Van Cleve, 1991). Another problem associated with diversity studies after a disturbance is that few successional studies encompass both floristic and faunal aspects during succession (Brown and Hyman, 1986).

The effects of modern forestry on faunal diversity is still poorly understood (Heliovaara and Varsonen, 1984). We are able to gain insight into the effect of anthropogenic disturbances on the forest fauna by comparing managed forest sites to forests that have been subject only to natural disturbances (Chandler, 1991). Human manipulation of the forest such as logging has increased the frequency of disturbance in today's forests. For these, the rate of disturbance is often greater than the rate of forest maturation and therefore many of the forest's climax species are becoming extinct (Loucks, 1977). Forest management

activities such as planting have also affected the biological integrity of today's forest. For example, Orme et. al. (1990), indicate that "even-aged" plantations of monoculture conifers lack the structural diversity and floristically have fewer species than forests resulting from natural regeneration after a disturbance.

Carabid beetles have been used as indicators of changes to the environment under many different circumstances. The majority of the studies have compared habitat systems that would be considered profoundly different, such as before and after a large disturbance. For example, they have been used to determine how insecticidal spraying affects the natural enemy populations in the field (Richardson, 1982), or to indicate the significant changes in the biota after a major disturbance such as clearcutting forests (Sustek, 1981; Lenski, 1982) or excavating peat bogs (Frambs, 1990). Many studies have shown that carabid beetles are a good indicator of the diversity of a system. As a generalist predator, carabids tend to respond to the overall conditions of the environment, rather than to specific components such as the presence of a special food item (Greenslade, 1964). The family Carabidae has been used frequently in forest ecological research, including diversity studies for the following reasons (Greenslade, 1964). Carabid beetles are a characteristic component in most forest ecosystems, they are found in all types of forests and throughout the

successional sequence from recently disturbed habitats to old growth forests (Thiele, 1977). Adult carabid beetles are taxonomically well known and easily collected using pitfall traps (Thiele, 1977).

Jack pine, *Pinus banksiana* Lamb., is a conifer tree that grows on well-drained soils (Anderson, 1960; Smith et al. 1964). In jack pine, high temperatures are needed to cause the serotinous cones to open and release their seeds, therefore quick regeneration often occurs after exposure to fire (Ahlgren, 1959). In situations where the level of natural regeneration is low, commercial foresters may plant jack pine seedlings to reforest a burned area (Cayford, 1963). Over the last 40 years, planting has become an increasingly important means of jack pine reforestation in certain areas of Manitoba (Glen Peterson pers. commun.). Because of its long planting history and the abundance of naturally regenerated stands in the upland areas of the southern Boreal forest. Jack pine would be a good candidate for a study, which examines the effects of different regeneration techniques on carabid beetle ecological diversity.

The objectives of this thesis are:

- i) To determine whether the α diversity of carabid beetles differs between and naturally regenerated jack pine stands of similar age and composition.
- ii) To determine whether differences in carabid α

diversity associated with the type of regeneration increases or decreases with stand maturity.

- iii) To examine whether the β diversity of carabid beetle assemblages in planted and naturally regenerated stands differ.
- iv) To measure the relationship between carabid beetle composition and the environmental variables of the sites in order to better explain the differences between carabid assemblages in planted and naturally regenerated sites at different levels of maturity.

CHAPTER II

Literature Review

Section A - Biodiversity/Ecological diversity

Biodiversity is an ambiguous term used to express habitat vitality. It has been used as an indicator of the effectiveness of conservation practices in maintaining characteristic populations of species and ecological processes of an ecosystem in a healthy state (Orme et. el. 1990). It is most often used in the context of species richness, which is simply the number of species in the habitat (Pielou, 1975; Magurran, 1988). It can also be used to signify ecological diversity, which is a measure of community content that expresses diversity in terms of the number and relative abundance of the species within an area (Magurran, 1988).

Ecological diversity is divided into two major categories based on community scale (Pielou, 1975; Magurran, 1988; Wilson and Shmida, 1984). Species diversity or α diversity is the number and relative abundance of the species within a single habitat. Ecosystem diversity or β diversity is the change in species composition between two

or more habitats (Pielou, 1975; Magurran, 1988). Species diversity is most commonly used to express the health of a system, while ecosystem diversity is used to indicate the degree a habitat has been partitioned by the species (Pielou, 1975; Whittaker, 1972). According to Wilson and Shmida (1984), it is important to identify both α and β diversity to get a better estimate of the overall diversity of an area. A system that is dominated by only a few species or is uniform over a large area is susceptible to disturbances such as pest outbreaks or sudden changes in climate because it may lack the necessary resources to respond (Kimmins, 1991).

Alpha diversity indices.

The concept of quantifying a habitat based on species diversity information has given rise to a large number of measures or indices (Pielou, 1966; 1975; Southwood, 1978). Magurran (1988) evaluated α diversity indices based on their statistical and theoretical properties, ability to discriminate between sites, dependency on sample size, and whether the index is widely used and understood. Magurran's evaluations of some common indices are summarized here.

The Shannon-Wiener index, which assumes that individuals are randomly sampled from an infinitely large population, is the most commonly used index and is relatively easy to calculate. However, it has only moderate

discriminating abilities, is highly sensitive to sample size, and is unduly influenced by the most abundant species (Magurran, 1988).

The log series alpha index considers the relationship between the number of species and the number of individuals in the habitat. It has only recently become popular, especially among entomologists. It appears to be the least biased towards too much emphasis on the most abundant species and is one of the best indices for discriminating between different sites (Kempton and Taylor, 1976; Magurran, 1988). In the future, it is expected that the popularity of log series alpha's will increase. Currently, for mainly comparative reasons, many researchers continue using the more traditional indices (Magurran, 1988).

Beta diversity indices.

Ecological criteria of good performance of an index of β diversity are that the index accurately reflect the range of community composition contained within an area; that the index is additive along a gradient, for example [$\beta(a,c) = \beta(a,b) + \beta(b,c)$]; and that the index is independent of sample size and of α diversity. Wilson and Shmida's (1984) review of six differentiation diversity measures on theoretical and field presence or absence data indicated that Whittaker's beta diversity and beta turnover seem to adequately fulfil these criteria. Whittaker's beta

diversity is the most widely used measure because it does not assume a gradient structure in its formulation. It should be used when the data cannot be arranged along an environmental gradient (Wilson and Shmida, 1984).

The Jaccard index is one of the most widely used and simplest means of measuring differences in species composition between sites, based on presence and absence data. Sites that are identical in terms of species would produce a coefficient value of 1, and 0 when they are completely different (Magurran, 1988). The major drawback with this index is that important community structure information is lost when the abundance of the species is not taken into account (Magurran, 1988; Southwood, 1978).

An alternative approach to beta diversity is to measure the degree of similarity between habitats (Magurran, 1988). Huhta (1979) reviewed how sixteen similarity measures performed in a comparison of clearcut areas to intact forest stands. He found that Kendall's τ and the modified form of Sørensen coefficient, (Bray and Curtis, 1957), were the most efficient similarity measures in that they did not change when two stable communities were compared and they showed a consistent change when a changing community was compared to a stable community (Huhta, 1979).

Section B - Ordination Analysis

Ordination Analysis is a multivariate technique that

represents a multi-dimensional data set in a space with a smaller number of dimensions, while preserving as much of the data's variation as possible (Orlóci, 1978; Pielou, 1984). This allows the major trends to be displayed in a simple, yet comprehensive ordination diagram (Pielou, 1984). In the ordination diagram, the data are plotted as a multidimensional scattergram in which the distance between the data points indicates their degree of similarity. The farther the points are apart the lower the similarity (Greenacre, 1984). The eigenvector elements in an ordination diagram are the weights of the variables on the axes, which indicates the principal direction of the variates. The axes in the diagram are arranged in an orthogonal manner in such a way as to explain the maximum possible amount of variance in the data. The eigenvalue of each of the axis describes the amount of linear variance that can be explained by the axes (Bernstein, 1988). Therefore, axis 1 has the largest eigenvalue and axis 2 would explain the next greatest amount of variance (Green and Carroll, 1976). The signs on the axes are arbitrarily assigned and are simply used for orientation purposes, therefore mirror images in ordination diagrams will have the same meanings (ter Braak, 1985). If the amount of variance explained by the first two axes is relatively large and the major trends in the data have been revealed the other axes may be dropped from the ordination diagram (Pielou, 1984).

Correspondence analysis, (CA) is a form of ordination analysis which expresses the observed associations between two quantitative variables, (e.g. species relative abundance in several sites) (Greenacre, 1984). The ordination diagram produced using CA provides the option of plotting the sites and species scores in the same diagram (Benzécri, 1992). The position of the species and sites relative to each other, is that generally the sites lie in the direction of the species which are the most prominent (Greenacre, 1984; Benzécri, 1992).

Canonical Correspondence Analysis, (CCA) is similar to Correspondence Analysis in that both produce species and site scores, but in CCA the site scores are also constrained by the environmental variables introduced into the equation (ter Braak, 1986). The function of the axes and the general appearance of the ordination diagram remains the same with the exception of the environmental variables, which are represented by vectors and whose direction and length are indicative of increasing "importance" (ter Braak, 1986; 1987). Palmer (1993) suggests that the linear combination (LC) sites score are the most appropriate scores to use in the ordination diagram. Conversation with Norman Kenkel, indicate that the LC sites scores are overshadowed by the environmental variables and that the weighted average (WA) sites scores show a more equitable distribution of species and environmental variable influences. For a complete

description of the mathematical mechanics for CA and CCA consult {Greenacre, 1984 or Benzécri, 1992} and ter Braak, 1986 respectively.

Section C - Effects of Natural and Man-Made Disturbances on Biodiversity

The first step to understanding the effects of natural and man-made disturbances on biodiversity is to understand how the environment has changed since the disturbance (Solbrig, 1991). No matter what the type of disturbance, the outcome is that there will be a change in the relative abundance and distribution within the floral and faunal community (Lenski, 1982; Frambs, 1990). The term succession has been coined to describe the sequence of vegetation or animal turnover after a disturbance.

Most species occupy a certain niche and are competitively superior within certain environmental situations (Solbrig, 1991; Drury and Nisbet, 1973). For example, the pioneer species that recolonize a site after a disturbance are known as r-strategists; they are usually small, fast-growing, short-lived organisms with good dispersing abilities and low competitive ability. In contrast, the later species to colonize a site after a disturbance are the k-strategists; they are typically large, long-lived, competitive organisms with reduced dispersal and lower reproductive capabilities. The k-strategists, over

time, out-compete the r-strategist for the dominant position in the community (Solbrig, 1991). In forest systems, succession typically continues until the species composition best suited for the habitat and climate (i.e. climax) is attained or until the next disturbance (Clements, 1977). In the southern Boreal forest, the frequency of fires has limits the age of most jack pine stands to less than 100 years, therefore there are few pyric climax forest left in this area (Rowe, 1956).

The typical distribution in species richness for most floral and faunal communities during a forest succession is that it will be low immediately after the disturbance and also at climax. This is because both stages generally place strong limitations on the species capable of inhabiting them (McLeod, 1980; Petraitis et. al., 1989). In the early stages of succession, the disturbed area is frequently dominated by a small number of r-strategist species, suited to open habitats with limited vegetation. In the late successional stages, a small number of shade-tolerant k-strategist species, adapted for cool, moist habitat conditions typically dominate the mature forest (McLeod, 1980; Petraitis et. al., 1989). The highest level of species richness typically occurs during the "transition" stages between major structural and climatic changes in the habitat (Loucks, 1977). Esseen (1983) reported an initial increase in ground vegetation species diversity followed by

a gradual decrease in a post-felling and post-fire succession in a dry lichen-pine forest in northern Sweden. In planted pine forests in Poland, ground vegetation species diversity is highest in the 13 - 14 year old sites and then decreases before increasing slightly in the oldest (>76 year old sites) (Faltynowicz, 1980). After 44 years of research on floral species richness in a Boreal forests succession, Shafi and Yarranton (1973) observed that the number of plant species decreases immediately after a fire then suddenly begins to increase and peaks at between 4 and 11 years after the fire. It then falls again and levels off approximately 16 to 18 years after the fire. For many arthropods in a forest succession, the highest level of species richness occurs just prior to canopy closure because the number of shade tolerant species are on the rise and the number of open habitat species are on the decline, but not yet absent from the habitat (Loucks, 1977).

In most situations, disturbance enhances the species richness of a system as long as it does not occur too frequently. If disturbance is very frequent, late successional species populations would not have the opportunity to develop and may ultimately disappear from the area (Loucks, 1977). The intensity of the disturbance is also important in plant succession, in that the disturbance may eliminate species such as *Populus tremuloides* Michx. which would otherwise return quickly (Petraitis et. al.,

1989; Powers and Van Cleve, 1991). Therefore the highest level of diversity will occur at intermediate levels of disturbances (Petraitis et. al., 1989).

In many ways, the effects from natural disturbances such as those caused by fire, and man-made disturbances on a forest habitat and its floral and faunal diversity are not very different (Heliovaara and Varsonen, 1984). Clearcutting, forest logging, and fire all alter the habitat by removing the vertical stratification of the stand, thereby allowing more light to penetrate to the soil surface (Heliovaara and Varsonen, 1984; Oksanen, 1986). Denitrification caused by a nutrient flush after clearcutting is similar to that observed after disturbances caused by fire, insects, and wind (Kimmins, 1991). Timber harvesting has been known to cause a rise in the water table, lower nitrogen reserves and increase ammonium, nitrate, phosphorous and potassium levels in the soil (Burger and Pritchett, 1988). In a ponderosa pine succession initiated by fire, reductions in carabid species richness were attributed to decreased organic matter and moisture holding capacity in the soil caused by the fire (Wagle and Kitchen, 1972). Both fire and clearcutting can cause forest fragmentation which deters the movement of small animals from one habitat to the next (Samson and Knopf, 1982; Klein, 1989; Orme et al., 1990). Sustek's (1984) study on the effects of human activity on beta

diversity of Carabidae and Staphylinidae found that beta diversity is reduced by clearcutting because the dramatic changes in the habitat structure are a barrier, inhibiting the movement between the surrounding forests and the clearing. The frequency of rare species and of extinction is much greater in fragmented forest than in a contiguous one (Klein, 1989).

The major difference between natural disturbances and human-initiated disturbances is that the trees in the natural sites are not removed whereas in clearcuttings the trunks of the trees are normally removed from the site. The group of organisms most profoundly affected by this removal are the microflora that grow on the rotting wood and the fauna that feed on their fruiting bodies (Heliovaara and Varsonen, 1984). Chandler (1991) found that for beetles that eat slime-mold and fungus, although the species composition was not the same, the diversity in a managed forest was nearly identical to that found in an old growth forest.

Section D - Carabid Beetles in a Forest Succession

Most forest carabid beetles are generalist predators feeding on other arthropods and are unspecialized in their requirements for specific forest types (Sustek, 1981; Buse, 1988; Niemelä et. al., 1988). Forest carabid beetle distribution appears to be more dependent on microclimate

characteristics and plant ecology of the habitat than on specific vegetation species (Thiele, 1977). Carabid species richness seems to be correlated to plant diversity in that the greater the plant diversity, the greater the variety of microhabitats available (Buse, 1988). Southwood et al. (1979) maintains that faunal species diversity is related to the structural diversity of the flora rather than to floral species diversity. In black spruce, post-fire succession, carabid species richness responded positively to habitat structural diversity (Holliday, 1991).

During forest succession there may be a change in the dominant carabid species. After the logging of an oak forest, the once abundant, brachypterous, snail-eating carabid beetles are succeeded by prairie, macropterous species, such as *Harpalus pensylvanicus* De Geer, which then dominate the habitat (Lenski, 1982). Similarly, the frequency of brachypterous carabid species is reduced in the Boreal forest after forest fire (Holliday, 1991).

In non-forest areas, Rushton et al. (1990) studied the effect of grassland management on the occurrence of carabid beetles. The authors found that different species react differently to disturbances caused by management strategies. R-strategists like *Amara plebeja* (Gyll), *Nebria brevicollis* (F.) and *Loricera pilicornis* (F.) are most frequently caught in intensively managed grasslands while k-strategists, like *Pterostichus niger* (Schaller), *P madidus* (F.) and *Carabus*

nemoralis Mueller, are less common when there is any type of disturbance.

CHAPTER III

Materials and Methods

Section A - General Study Area Description.

The study was conducted in the Sandilands Provincial Forest, situated in southeastern Manitoba. This forest reserve is the most southern portion of the Boreal forest in Manitoba, and the most western portion of the Great Lakes Forest (Rowe, 1956). The northern limit of Sandilands Provincial Forest is located at 49° 45' N between 96° 15' W and 96° W. The southern limit is located at 49° N and 96° 49' E; the reserve occupies 886,977 ha (Smith et. al., 1964).

The surface geology of the area is a mixture of mineral deposits from two glacial ice sheets during the last ice-age. The glacial till from the first ice sheet ranges from calcareous clay loam to clay with large fragments of limestone and dolomite. The second ice sheet deposited a sandy till with fragments of Pre-Cambrian rock (Johnston, 1946). The topography of the area is primarily flat with undulating colloid-sandy ridges and wet lowland bogs and swamps (Anderson, 1960; Smith et. al., 1964). Jack pine, *Pinus banksiana* Lamb. is the dominant tree species in the dry

uplands of the area, whereas black spruce, *Picea mariana* [Mill.] B.S.P., is dominant in the wet lowlands (Mueller-Dombois, 1964; Smith et. al., 1964). The most striking physiographic feature in the Sandilands Provincial Forest is the large sickle-shaped ridge located in the mid-western portion of the forest reserve, locally known as the Bedford Hills - Whitemouth lake plateau, at an elevation of just over 430 m a.s.l. (Smith et. al., 1964).

The soils of the Sandilands region have been well described by S.M. Anderson in her Ph. D. thesis, (Anderson, 1960) and secondly by Smith et. al., (1964) as part of the Manitoba Soil Survey of the southeastern region of Manitoba. Therefore, I will not go into the details of the soil classifications, only to indicate that the majority of the soils in the study sites have a high sand content and belong to either the Sandilands series, Woodridge series or a mixture of the two. Soils from the Sandilands series are sandy well-draining soils with a minimal podzol profile development. Soils from the Woodridge series are also well-draining soils originating from calcareous, stratified sand and gravel deposits. In both series the dominant tree species is *P. banksiana* (Anderson, 1960; Smith et al., 1964).

The climate in Sandilands Provincial Forest is generally milder than the typical boreal forest climate, mainly because of its southern location (Rowe, 1956). The annual mean temperature is 2 °C, with mean summer temperatures, (May -

September) of 22 °C and mean winter temperatures, (October - April) of approximately -12 °C (Anderson, 1960; Smith et. al., 1964). The growing season in this area is approximately 130 days above a 10 °C threshold and therefore the vegetation in this area is less limited by the number of degree days than the more northern boreal forest (Anderson, 1960). The amount of precipitation, in the form of rain and snow this area receives is relatively high, approximately 55 cm per annum. During the summer months approximately 55 cm of rain falls, with most of that occurring in July. During the winter, the mean yearly snow fall is approximately 135 cm (Anderson, 1960; Smith et. al., 1964)

Section B - Experimental Design and Site Description

Experimental design.

The two types of sites used were natural and planted stands of jack pine, with natural stands being the result of natural regeneration after a forest fire. In this study planted stands were not differentiated according to planting technique and were generally considered to be initially planted with two year old seedlings. Each stand type included two sites from each of the following age classes: 5, 15, 25, 40. The 5 year age class included sites with dominant tree ages between two to five years old; the 15 year age class included 10 to 15 year old trees; the 25 year age class consisted of 20 to 30 year old trees; and the 40 year age

class was composed of 30 to 50 year old trees.

Details of Sites.

Study sites were established in the spring of 1991, with the aid of fire maps and plantation records supplied by Manitoba Department of Natural Resources. Sites were all in the Bedford Hills - Whitemouth Lake Plateau physiographic area of the Sandilands Provincial Forest (Smith et al., 1964), between the hamlets of Marchand and Badger, Manitoba. Five increment borer samples were taken per site to determine whether the age of the trees corresponded with the information in the historical records for the area.

Selected sites were square plots 100 m x 100 m in stands of a minimum of 2 ha in size, with the site located at least 20 m from any major discontinuity such as roadways or vehicular trails. The sites were positioned to best represent the entire stand. To be considered as a study site, the tree composition of the stand had to be >75 % jack pine. Of the 16 sites required by the experimental design, only 15 were found because only one 15 year old natural site met the selection criteria.

Sites were give code names which correspond to the type of regeneration and approximate year of planting or number of years after a fire. For example PL89A indicates that this site is the first replicate of the sites planted in 1989. B5B indicates that it is the second replicate of the

natural sites which were burned approximately 5 years ago. A summary of descriptive information on site location, the year planted or burned, and the dominant soil type (Anderson, 1960) are provided in Table 1 and Figure 1. Specific site information on each of the sites tended to be somewhat unpredictable because historical information for specific sites was extremely variable.

The 5 year old planted sites (PL89A, PL89B) (Fig. 2) and the 5 year old natural sites (B5A, B5B) (Fig. 3) were open areas with no living trees above 2 m. The greatest difference between planted and natural sites was that in the planted sites a large proportion of the slash was removed prior to planting.

The 15 year old planted sites (PL76A, PL76B) (Fig. 4) and the 15 year old natural site (B15A) (Fig. 5) were generally open forest sites, whose canopy was just beginning to close. The greatest difference between planted and natural sites was that because there is no predetermined distance between the trees in the natural sites, the trees in these sites tended to grow aggregations. Whereas the tree distribution in the planted sites was more uniform, with equa-distance between the trees.

The 25 year old planted sites (PL67A, PL67B) (Fig. 6) and the 25 year old natural sites (B25A, B25B) (Fig. 7) were intermediately open forest with partial canopy closer. With the exception of B25A, which had been mechanically thinned,

the greatest difference between planted and natural sites in this age class was the greater degree of canopy cover in the tree aggregated areas in the natural sites. The spacial distribution of naturally regenerated jack pine seedlings after a fire is typically in the form of aggregates (St-Pierre et. al., 1991). While planted stands generally have uniform (1.2 m) distances between planted seedlings (Cayford and Bickerstaff, 1968).

The 40 year planted old sites (PL52A, PL52B) (Fig. 8) and the 40 year old natural sites (B40A, B40B) (Fig. 9) were generally cool shaded forest with substantial canopy closure. Planted and natural sites in this age class were very similar, in that because of natural thinning which occurs in mature jack pine forest 25 to 40 year into their succession had created greater uniformity in the tree distribution in the natural sites (Ahlgren, 1974).

Section C - Vegetation Sampling

In 1992, the three levels of vegetation: ground, shrub and trees, were identified and their percent cover estimated in the field. The ground vegetation consisted of all herbaceous plants, and woody plants < 30 cm in height. The shrub vegetation included all woody plants > 30 cm but less than 2 m in height, whereas tree vegetation was comprised of all woody vegetation higher than 2 m. The ground vegetation sampling was conducted over two sampling periods, late

spring/early summer and late summer/early fall. In each period, 25 1 m x 1 m quadrat samples, (Fig. 10), were taken per site, using a stratified random design. The site was stratified into five 20 m x 100 m blocks, and five quadrat samples were taken per block. Shrub and tree vegetation was sampled only once. Twenty-five 2 m x 2 m quadrat samples were taken for the shrubs, (Fig. 11), and ten 10 m x 10 m quadrat samples for the trees (Fig. 12). The sample selection for the shrubs was identical to that for ground vegetation. Tree vegetation samples were again drawn from strata of 20 m x 100 m blocks, but only two quadrat samples were taken per block. Also, the number of trees, diameter at breast height (DBH), and the mean height of five previously selected trees per quadrat were recorded during the tree vegetation sampling. DBH and mean height of the trees were measured using a DBH tape and a clinometer, respectively.

Section D - Environmental Sampling

Temperature. Air temperature was recorded continuously from June to October in 1991, and in 1992 from May to September, using a Cole Parmer hygrothermograph placed in a Stevenson's screen at the Marchand Natural Resources Forestry Station, 10 km east of Marchand, Manitoba. Soil and litter temperatures were recorded at five randomly selected locations in each site each week.

New locations were selected weekly from a total of 16 possible locations. Soil and litter temperatures were measured using a Cole Parmer Digi-Sense® hand-held thermistor thermometer and temperature probe (Fig. 13).

Light intensity. In 1992 under clear sky or minimal cloud conditions, light intensity, measured in μ einstein $m^{-2} s^{-1}$, was recorded at the same five randomly selected locations as the temperature measures in each site. Light intensity was measured at ground level and at 2 m above the ground level using a Li-Cor 185 Quantum / Photometer with a photometer probe (Essenburg, 1991).

Section E - Carabid Beetle Sampling

Carabid beetles were collected using 8.5 cm diameter pitfall traps set with their rims flush with ground. Each trap consisted of two plastic "beer" cups, the inner was a 450 ml cup, which was nested in a 500 ml cup to facilitate the emptying of the traps. The traps were covered by a 30 cm x 30 cm square 0.3 cm plywood cover with 12 cm nails as legs. Each site contained 16 pitfall traps arranged in a 4 x 4 grid pattern with approximately 20 m between each trap (Fig. 14) Two types of pitfall traps were used: "wet traps" which contained a preservative mixture of equal parts ethylene glycol and water, (Fig. 15), and "dry traps" which contained no preservative and had small holes drilled into

the bottom to allow for water drainage (Fig. 16). Equal numbers of each type of trap were used to determine if trap type significantly affected beetle catch and if so, to analyze trap catches according to trap type. Since preliminary results suggested that there was no significant difference between the number of carabid beetles and species collected in dry and wet pitfall traps this was not necessary. The pitfall traps in B5B were exclusively dry traps because the wet traps were repeatedly dug up by deer, and so did not yield any results.

From June 26 to October 8 in 1991, and from May 11 to September 11 in 1992, the pitfall traps were emptied weekly and the carabid beetles brought back to the laboratory for identification. To discourage wildlife from disturbing the wet traps and ingesting the preservative, Nova-Quinine capsules, (200 mg quinine sulphate / capsule), at a rate of 20 capsules per litre or 4 g / l, were added to the preservative mixture. Despite this precaution, wildlife disturbance of wet traps in site B5B was so troublesome that after July 28, 1991 all traps in this site were changed to dry traps.

Section F - Statistical Analysis

The number of carabid beetles collected and the number of carabid species were used as general indicators of species occurrence and species richness. The Shannon-

Wiener, (H') and log series α were used to measure α diversity of the carabid beetle assemblage in each of the sites.

The Shannon-Wiener index was calculated from the equation:

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

Where S is the total number of species found in that site and p_i is the number of individuals found in the i^{th} species divided by the total number of individual found in the site (Krebs, 1989).

The log series α of the equation:

$$S = \alpha \ln \left(1 + \frac{N}{\alpha} \right) \quad (2)$$

was obtained for each site by a two stage process. Firstly the logarithmic series parameter, x was estimated using least squares minimization in the NONLIN module of SYSTAT, (Wilkinson, 1988), for the equation:

$$\frac{S}{N} = \frac{(1-x)}{x} [-\ln(1-x)] \quad (3)$$

Where N is the total number of individuals and S is the number of species. The value of x is usually between 0.9 and 1.0 (Williams, 1964).

The log series α was derived from N and the estimate of x using:

$$\alpha = \frac{N(1-x)}{x} \quad (4)$$

Jaccard's coefficient, (C_j) and Kendall's τ rank correlation coefficient were used to measure carabid β diversity between site replicates. The Jaccard index (C_j) was obtained from the equation:

$$C_j = \frac{j}{(a+b-j)} \quad (5)$$

Where j is the number of species present in both sites A and B, and a is the number of species present only in site A, and b is the number of species present only in site B (Southwood, 1978).

The Kendall's τ rank correlation coefficient (Kendall, 1962) index of β diversity (Bullock, 1971) was calculated using the CORR module of SYSTAT (Wilkinson, 1988). Species abundance data for the pair of replicates of each treatment-age combination, were used in the rank correlation. Species

presence was not used in the calculation.

Repeated measures analysis of variance, using the univariate repeated measures analysis in SYSTAT (Wilkinson, 1988) was used to determine the effects of field season bias on the number of species, total number of individuals collected in the sites and the indices α and β diversity. In situations where significant differences between the two years existed, 1991 and 1992 data were analyzed and reported separately. Fixed effects analysis of variance, using the MGLH module of SYSTAT (Wilkinson, 1988) was used to determine the significance of the effect of stand type, stand age and the interaction between the two on the data. The only exception was the analysis of β diversity in each year; these data were analyzed using a paired t-test. The level considered significant for all statistical analysis, if not otherwise indicated, was $P \leq 0.05$.

The CA and CCA analyses were carried out using the default settings of the CANOCO software, (ter Braak, 1987-1992) with the exception of the following:

- (1) To reduce the dominating effect of the extremely abundant species, all data were transformed using the logarithmic transformation provided in the CANOCO program.
- (2) The sample scores used in the canonical correspondence analysis ordination diagram were those determined by weighted averaging, (WA

scores) rather than those produced by the linear combination of the variables, (LC scores), which are the current default settings in the CANODRAW program, (ter Braak, 1987-1992) (Norman Kenkel, pers. commun.).

In this study, for representation purposes, only the first two ordination axes were used in all of the ordination diagrams. To simplify the ordination diagrams and to avoid the influence of incidental species, only the most common species were used (ter Braak, 1986). Common species of carabid beetles were defined as those species which occurred in both field seasons, and whose number of beetles collected divided by the total number of beetles collected was greater than 10 %. The definition of a common vegetation species is any species that occurred in 1992 with a sum of the percent cover of all the sites was greater than 20 %.

The unrestricted Monte Carlo permutation test was used to assess levels of significance of the relationship between the environmental variables and the carabid assemblage data (ter Braak, 1986; Prentice and Cramer, 1990; Rejmánková et al., 1991). For each test, 99 environmental sample numbers were generated randomly and their trace eigenvalues calculated and compared to the observed environmental trace eigenvalues. If these observed values were higher than 95 % of the randomly generated values, then the species abundance was considered to be significantly related to the

environmental variables (ter Braak, 1987; Prentice and Cramer, 1990). For a complete description of the correspondence analysis technique, consult Hill (1973); for canonical correspondence analysis see ter Braak (1986).

CHAPTER IV

Results

Section A - Vegetational and Environmental Factors of the Sites

Vegetation. The results of the 1992 vegetation sampling are contained in Appendix I. Only the vegetation species that had a sum total ≥ 1 percent have been included. The table includes 45 ground level species, 15 shrubs and 3 tree species. The most common ground vegetation, shrubs, trees and average DBH in each site have been summarized in Table 2.

In the 5 year old sites, there were no "trees" *per se*, none of the woody vegetation in these sites could be classified as a tree based on the criteria that woody plants had to be at least 2 m in height to be considered a tree. The shrub cover in these young sites was minimal. The dominant shrub species in this age class all belonged to the Rosaceae. *Prunus pensylvanica* L. was only found in the burn sites while *Prunus virginiana* L. was restricted to the plantations. The ground vegetation in sites of this age

class resembled a grassland habitat more than a forest habitat because it was dominated by graminoids species.

In the 15 year old age class, the percent shrub cover was greater than in the younger sites, the most abundant shrub species being the same. The ground cover was notably different between the 5 and 15 year old sites; the vegetation in the 15 year old sites was more typical of an open forest. The ericaceous plants, such as the *Vaccinium* genus and *Arctostaphylos uva-ursi* (L.) Spreng., were the dominant vegetation followed by the graminoids.

In the 25 year old sites, the planted sites tended to have a greater percent cover of shrubs than the naturally regenerated sites. The ground vegetation in the 25 year old sites was very similar to that of the 15 year old sites. The major difference was in the increased presence of the moss, *Pleurozium schreberi* (BSG.) Mitt., and herbs adapted to moister conditions, such as *Anemone quinquefolia* L. and *Maianthemum canadense* Desf.

The shrub species in the majority of the 40 year old sites were very similar to those of the two previous age classes with the exception of B40A. In B40A, *Cornus stolonifera* Michx., *Corylus cornuta* Marsh., and *Alnus rugosa* (Du Roi) Spreng were all exclusively found in this site. The ground vegetation in this age class was similar to that of the 15 and 25 year old sites, with the exception of a strong reduction in grass cover, and the increased dominance

of *P. schreberi* as the principal ground cover.

Temperature. The mean soil and litter temperature (Table 3) and the seasonal temperature fluctuations (Fig. 17, 18, 19, 20) indicated that as a stand matured, soil and litter temperatures decreased and became less variable throughout the season. Because temperatures at different sites were taken at different times, site temperatures were related to those of the permanent Stevenson's screen in order to calculate the "mean base line difference" of each site. The mean base line differences in soil and litter temperatures were calculated by subtracting the temperature of the Stevenson's screen from the corresponding mean site temperature for the appropriate date and time of day. The results were then plotted with the mean base line difference in temperatures against the age of the stand (Fig. 21, 22, 23, 24). An analysis of variance of the mean base line differences for the soil and litter temperatures indicated that both temperatures were significantly affected by age, but not by the type of regeneration (Table 4). The interaction of the stand age and regeneration type on the mean soil base line difference temperature was only marginally significant in 1991, but was not significant in 1992.

Light intensity. Mean light intensity in a 5 year old stand measured at ground level and 2 meters above ground level, was 2-4 times as intense as that of a 40 year old stand (Fig. 25, 26). An analysis of variance, (Table 4), illustrated that light intensity in the stand was strongly influenced by age and that type of regeneration and the interaction between stand type and age had no significant effect.

Section B - Pitfall Catches of Carabid Beetles

Number of carabid beetles and most common species.

A total of 4861 beetle representing 50 species were collected during the course of the study: 1998 beetles in 40 species were collected in 1991 and 2863 beetles in 42 species in 1992 (Appendix II, III). The 15 most frequently caught species represented over 90 percent of the total catch (Table 7). The 5 year sites were dominated by carabid species that are typically associated with open dry grassland habitats (e.g. *Amara obesa* and *A. latior*), (Lindroth, 1968) and by species (e.g. *Harpalus laticeps* and *H. lewisi*), which invade recently burned forest areas (Holliday, 1991). All are considered to be macropterous, (Lindroth, 1968) with the exception of *A. obesa*, which is wing dimorphic (Lindroth, 1968). However in these sites, out of a total of 35 dissections of *A. obesa*, all had wings large enough to suggest flight capability, with a wing

length to elytra length ratio of 1.4:1 (Table 8). Even though wing muscle development was not assessed, it is probable that these insects could fly. The most commonly collected carabid species in the 15 year old sites were the for-mentioned *Amara* species, which are characteristic of grasslands, and forest species such as *Carabus taedatus*, *Pterostichus pensylvanicus*, and *Dicaelus sculptilis* (Lindroth, 1961; 1968). In the 25 year old sites, the most frequently collected carabid species were similar to those in the 15 year old sites, but species characteristic of open dry habitats were relatively less prevalent than those such as *Calathus ingratus* and *Synuchus impunctatus*, favouring cool, moist forest habitats (Lindroth, 1968). In the 40 year old sites, the most frequently caught carabid species were *P. pensylvanicus*, *C. ingratus*, *S. impunctatus*, and *D. sculptilis*, which are typical of cool, moist habitats (Lindroth, 1966; 1969).

Lindroth, (1949) indicates that carabid beetles capable of flying are usually the first colonizers after a disturbance. In that respect, the majority of the dominant species in the 15, 25, and 40 year old sites, with the exception of the few grassland associated species, were brachypterous species or the brachypterous morph of species that exhibit wing dimorphism (Table 7, 8).

In 1991, type of regeneration, ($F_{1,7}=0.14;p=0.72$); stand age, ($F_{3,7}=3.9;p=0.06$); and the interaction of the two,

($F_{3,7}=0.04;p=0.99$) had no significant effect on the mean number of beetles per site (Fig. 27). A contrast of the 5 year old sites against the remaining age classes indicated a significant difference in the number of beetles collected in the youngest sites ($F_{3,11}=5.9;p=0.01$); differences among the older three age classes were not significant ($F_{3,7}=4.1;p=0.09$). In 1992, the effect of stand age on the number of beetles per site was significant ($F_{3,7}=6;p=.02$) (Fig. 28). As stand age increased the number of beetles collected decreased.

Carabid beetle species richness. Neither the type of regeneration, ($F_{1,7}=0.6;p=0.47$), age of the stand, ($F_{3,7}=2.6;p=0.14$), nor their interaction, ($F_{3,7}=1.4;p=0.32$) had a significant effect on the mean number of species per site in 1991, (Fig. 29) but in 1992, stand age was found to have a marginally significant effect ($F_{3,7}= 4.4;p=.05$) (Fig. 30). A contrast of the 5 year old sites against the three older age classes was significant in 1992 ($F_{3,11}=4.7;p=.02$), but not in 1991 ($F_{3,11}= 2.6;p=.11$). The age effect among the 15, 25 and 40 year old sites was not significant in 1991, or 1992, ($F_{3,7}=1.4;p=0.34$).

Section C - Carabid Beetle α and β Diversity

Carabid beetle α diversity. In 1991 and 1992, carabid beetle alpha diversity using the Shannon-Wiener index was

not significantly affected by stand type, ($F_{1,7}=0.8;p=0.41$), age, ($F_{3,7}=2.3;p=0.17$), or their interaction, ($F_{3,7}=0.1;p=0.95$), (Fig. 31, 32).

In 1991, the log series alpha index for carabid beetles, was not significantly affected by type of stand, ($F_{1,7}=0.8;p=0.41$), or stand age, ($F_{3,7}=2.5;p=0.14$). Diversity was significantly affected by the interaction of stand age and stand type, ($F_{3,7}=4.4;p=0.05$), (Fig. 33). In 1992, alpha diversity was not significantly affected by stand type, ($F_{1,7}=0.9;p=0.39$), stand age, ($F_{3,7}=2.2;p=0.18$), or by the interaction between the two, ($F_{3,7}=1.1;p=0.41$), (Fig. 34). The significant interaction in 1991 may have been attributed to successional differences between planted and naturally regenerated sites. Planted stands peaked in α diversity during the 15 year age class, whereas in natural stands α diversity peaked during the 25 year age class. This pattern was not seen in 1992. The most obvious difference between the two years was that in the 15 year old natural site, the log series α more than doubled from a value of 3 in 1991 to 7.5 in 1992. This may be related to the marked increase in the number of species in this site. Because the 15 year old site was unreplicated, the analysis of this age class is particularly sensitive to perturbations. When a repeated measures design was used on the log series α data for both years there was no interaction ($F_{3,7}=1.7;p=0.26$) and that both planted and

natural sites peaked in carabid α diversity during the 15 year age class. In all cases, the rate of declining carabid α diversity after the peak was greater in planted sites than in naturally regenerated sites. By the time the sites were 40 year old α diversity in planted and natural sites were again similar (Fig. 33, 34).

Carabid beetle β diversity. The analysis of the 1991 and 1992 Jaccard's index measures using a repeated measures design indicated no significant difference between the two field seasons, ($F_{1,2}=0.01;p=0.98$). A paired t-test indicated that there was no significant difference between the degree of replicate similarity for planted stands and that of natural regeneration in 1991 ($t_2=-1.79;p=0.22$) (Fig. 35), and 1992 ($t_2=-0.94;p=0.45$) (Fig. 36). In both cases, the pattern of changing beta diversity over stand age was similar, with the 25 year old stands having the highest level of beta diversity.

In 1991, a paired t-test of Kendall's τ showed that planted stands had a greater degree of similarity between replicates, ($t_2= -11;p<0.05$), than did natural stands, and so plantations were significantly lower in beta diversity than naturally regenerated stands (Fig. 37). In 1992, the difference between planted and natural stands was not quite significant, ($t_2= -2.44;p=0.14$), even though the pattern of changing diversity was very similar to that in 1991

(Fig. 38). Because there was a significant field season effect on β diversity, repeated measures analysis was not used to interpret the data.

Section D - Ordination Analysis of the Most Common Carabid Beetle Species

Correspondence Analysis. In 1991, the Correspondence Analysis of the most common carabid species in the sites produced an ordination diagram in which the combined eigenvalue of the first two axes was 0.672, and thus explained 59.7 % of the ordinates' variance around the axes (Fig. 39). The axes separated the sites primarily by age: Axis 1 separated the 5 and 40 year old site scores on opposed ends of the axis. Axis 2 separated the 15 and 25 year old sites from the rest of the site scores. The eigenvectors of some of the carabid species characteristic of open dry habitats such as *Amara latior*, *Amara laevipennis*, *Amara obesa* (Lindroth, 1968), along with *Harpalus laticeps* and *Harpalus lewisi*, which invade recently burned areas, (Holliday, 1991), and *Agonum placidum* which invade recently cultivated fields, (Lindroth, 1966), have a strong positive correlation to axis 1 and were the main carabid species responsible for dictating the distribution of the 5 year old sites at the positive end of the first axis. Meanwhile, the eigenvectors of some of the

cool adapted, forest carabid species, such as *Synuchus impunctatus*, *Calathus ingratus*, *Dicaelus sculptilis*, *Pterostichus pensylvanicus* and *P. adstrictus*, (Lindroth, 1966; 1969), were strongly negatively correlated to the first axis and were responsible for placing the 40 year old sites at the negative end of axis 1. In the intermediate sites, the eigenvectors of the two open forest *Carabus* species (Lindroth, 1961), *C. taedatus* and *C. serratus* have a strong negative correlation with axis 2 and were therefore instrumental in the placement of the 15 and 25 year old sites on the negative side of this axis. An exception was one of the 25 year old natural sites, B25B which was closer the 40 year old sites than to the sites in its own age class.

In 1992, the ordination diagram was very similar to that of the previous year. The first two axes again explained a large proportion of the variation in the carabid species data, 69.4 %, and again the distribution pattern of the sites scores were separated based on the age of the stand (Fig. 40). The carabid species score distribution was also very similar, with the exception of the greater separation between the 5 year old natural and planted sites. This was mainly because of the strong association of the natural sites with the carabid species, *H. laticeps* and *H. lewisi*. For example, the number of *H. laticeps* collected in the natural 5 year old sites was significantly greater than

the number collected in the 5 year old planted sites ($F_{1,2}=42.8;p=0.02$) (Table 7).

Canonical Correspondence Analysis

Vegetation species as environmental variables.

The Canonical Correspondence Analysis of the most common carabid beetles and vegetation species produced an ordination with a high degree of covariability between the environmental variables. Forward selection was used to determine the most important environmental variable that could explain the trends in the carabid species data. Variables were tested on a stepwise basis using the unrestricted Monte Carlo permutation test to determine the cumulative contribution of significance of the variables (ter Braak, 1986). From the original nine most common vegetation species only June grass, *Koeleria gracilis* Pers., a grass species of open dry habitats, such as prairies or open glades in the boreal forest (Looman, 1982; 1983) and Schreberi moss, *Pleurozium schreberi* (Brid.) Mitt, a common feathermoss in boreal forest, particularly in upland conifer forests (Baldwin and Sims, 1989), were significant. *Cladina mitis* (Sandst.) Hale & Culb., is a reindeer lichen species that occurs in a broad range of habitats but is most prevalent in exposed locations of conifer dominated forests (Baldwin and Sims, 1989) and is also one of the dominant intermediate vegetation species in the succession from a

grass to a moss dominated habitat (Sims et. al., 1989). Although its contribution was not considered significant, it was added to the environmental variables list because it contributed to the visual presentation of the data.

In the Canonical Correspondence Analysis ordination diagram, the first two axes accounted for 50.8 % of the variance in the species data in 1991 and 56.8 % in 1992 (Fig. 41, 42). The arrangement of the sites and species scores in these two diagrams were almost mirror images of the Correspondence Analysis diagrams. The 5 year old sites and the open habitat carabid species were all grouped together on the negative side of the first ordination axis with the early successional vegetation species, *K. gracilis*. The sites of intermediate age and the open forest carabid species, *C.taedatus*, *C. serratus*, and *P. adstrictus* were clustered together in the negative portion of the second axis with the intermediate successional vegetation species, *C. mitis*. The third environmental variable, the late successional vegetation species, *P. schreberi* was associated with the 40 year old sites and the mature forest carabid species.

Canonical Correspondence Analysis

Soil and litter temperatures and light intensity as environmental variables.

The Canonical Correspondence Analysis of the 15 most common carabid beetles and four environmental variables:

soil base temperature difference, litter base temperature difference, light intensity at ground level, and light intensity at 2 m above ground; produce an ordination with a high degree of covariability between the environmental variables. Forward selection reduced the number of significant environmental variables to a single variable. In order to maintain multidimensionality in the ordination diagram, two environmental variables were used: litter base line temperature difference and light intensity at ground level.

In 1991, the first two ordination axes of the canonical correspondence analysis explained 32.8 % of the variance in the species data and 40.6 % in 1992 (Fig. 43, 44). The separation of the sites and carabid species were reasonably similar to the Canonical Correspondence Analysis ordination diagrams with vegetation as the environmental variables. The first axis, which was positively correlated with the environmental variables, separated the sites according to age. Sites with negative litter base temperatures and low light intensity were negatively correlated to the axis. For example the 5 year old sites have a strong positive correlation, the 40 year old sites a strong negative correlation and the intermediate aged sites with little to no correlation with the first axis. The second axis to a lesser extent separated the 40 year old sites from the intermediate aged sites.

Table 1. Site description, location, soil series and plantation size

Site	Age Class (years)	Type of regeneration	Section Township Range	Year of Fire or Planting	**Soil Type (series or complex)	Plantation size (ha)
B5A	5	Natural	NW 24-5-10E	1987	Sandilands-Woodridge	N/A
B5B	5	Natural	NW 15-5-10E	1987	Sandilands	N/A
PL89A	5	Planted	SW 28-5-10E	1989	Sandilands	4
PL89B	5	Planted	SW 16-5-10E	1989	Sandilands	6
B15A	15	Natural	SW 13-4-10E	1974	Sandilands-Woodridge	N/A
PL76A	15	Planted	SE 24-6-10E	1978	Sandilands + shallow peat	11
PL76B	15	Planted	NE 26-4-9E	1976	Sandilands-Woodridge	8
B25A	25	Natural	NE 23-4-10E	1964	Sandilands-Woodridge	N/A
B25B	25	Natural	SE 16-3-9E	1963	Woodridge	N/A
PL67A	25	Planted	NE 3-5-9E	*1965	Woodridge	16
PL67B	25	Planted	SW 36-4-9E	*1964	Sandilands	25
B40A	40	Natural	NE 22-3-12E	1946	Woodridge-Lonesand-Kerry	N/A
B40B	40	Natural	NW 13-4-10E	1952	Woodridge	N/A
PL52A	40	Planted	SE 16-4-10E	1952	Sandilands	10
PL52B	40	Planted	NW 32-4-11E	1952	Woodridge	8

NOTE: * indicates sites that were partially refilled at a later date.

** Soil descriptions are based on the Manitoba Soil Survey soil classifications for south-eastern Manitoba. (Smith et. al., 1964).

Table 2. Most common vegetation species found in the sites in addition to the mean diameter at breast height, (DBH) of the dominant tree species.

Site	Age class	Stand type	VEGETATION			DBH (cm)
			Ground	Shrub	Tree	
B5A	5	Natural	Andropogon gerardi Koeleria gracilis Pteridium aquilinum	Pinus banksiana Populus tremuloides	N/A	N/A
B5B	5	Natural	Arctostaphylos uva-ursi Andropogon gerardi Koeleria gracilis	Pinus banksiana Salix spp.	N/A	N/A
PL89A	5	Planted	Andropogon gerardi Koeleria gracilis Arctostaphylos uva-ursi	Pinus banksiana Spireae alba	N/A	N/A
PL89B	5	Planted	Andropogon gerardi Koeleria gracilis Cyperus spp.	Pinus banksiana Spireae alba	N/A	N/A
B15A	15	Natural	Vaccinium spp. Arctostaphylos uva-ursi Cladina spp.	Vaccinium spp.	Pinus banksiana	6.6±1.1
PL76A	15	Planted	Vaccinium spp. Cladina spp. Arctostaphylos uva-ursi	Prunus virginiana	Pinus banksiana	6.7±1.5
PL76B	15	Planted	Andropogon gerardi Amorpha canescens Arctostaphylos uva-ursi	Prunus virginiana	Pinus banksiana	8.2±1.4
B25A	25	Natural	Cladina spp. Vaccinium spp. Andropogon gerardi	Ceanothus ovatus	Pinus banksiana	9.4±3.1
B25B	25	Natural	Andropogon gerardi Arctostaphylos uva-ursi Vaccinium spp.	Amelanchier alnifolia Prunus virginiana	Pinus banksiana	11.6±4.9
PL67A	25	Planted	Vaccinium spp. Andropogon gerardi Maianthum canadense	Amelanchier alnifolia	Pinus banksiana	9.6±2.0
PL67B	25	Planted	Symphoricarpos spp. Andropogon gerardi Rhus radicans	Symphoricarpos spp.	Pinus banksiana	10±3.0
B40A	40	Natural	Pleurozium scherberi Pteridium aquilinum Maianthum canadense	Corylus cornuta Alnus rugosa	Pinus banksiana	15.4±3.7
B40B	40	Natural	Vaccinium spp. Pleurozium scherberi Maianthum canadense	Vaccinium spp.	Pinus banksiana	13.1±3.5
PL52A	40	Planted	Pleurozium scherberi Vaccinium spp. Maianthum canadense	Lonicera spp.	Pinus banksiana	12.9±3.9
PL52B	40	Planted	Pleurozium scherberi Vaccinium spp. Maianthum canadense	Symphoricarpos spp.	Pinus banksiana	13.3±3.5

Table 3. Mean soil and litter temperatures ($^{\circ}\text{C}$) in the sites for June to September, 1991 and 1992.

SITE	REGENERATION TYPE	AGE CLASS	1991		1992	
			LITTER TEMPERATURE	SOIL TEMPERATURE	LITTER TEMPERATURE	SOIL TEMPERATURE
B5A	Natural	5	28.1 \pm 2.1	22.6 \pm 1.3	22.4 \pm 0.8	18.7 \pm 0.5
B5B	Natural	5	27.7 \pm 2.2	23.2 \pm 1.7	22.0 \pm 0.8	18.8 \pm 0.6
PL89A	Planted	5	24.0 \pm 2.2	20.0 \pm 1.3	20.5 \pm 0.7	17.7 \pm 0.5
PL89B	Planted	5	24.1 \pm 2.9	20.0 \pm 1.6	22.7 \pm 0.7	19.5 \pm 0.5
B15A	Natural	15	24.4 \pm 1.8	19.7 \pm 1.2	21.5 \pm 0.7	17.3 \pm 0.4
PL76A	Planted	15	23.2 \pm 2.3	18.3 \pm 1.3	20.6 \pm 0.7	16.4 \pm 0.4
PL76B	Planted	15	21.8 \pm 2.1	17.7 \pm 1.3	25.0 \pm 1.0	19.0 \pm 0.5
B25A	Natural	25	22.8 \pm 1.5	17.8 \pm 1.0	19.2 \pm 0.4	15.6 \pm 0.3
B25B	Natural	25	22.0 \pm 1.6	18.7 \pm 1.2	21.0 \pm 0.7	18.8 \pm 0.4
PL67A	Planted	25	19.7 \pm 1.5	16.9 \pm 0.9	19.2 \pm 0.7	15.6 \pm 0.4
PL67B	Planted	25	20.9 \pm 1.3	18.4 \pm 0.8	20.4 \pm 0.7	16.3 \pm 0.4
B40A	Natural	40	20.7 \pm 1.6	15.4 \pm 0.9	18.0 \pm 0.5	13.5 \pm 0.3
B40B	Natural	40	23.0 \pm 1.7	18.3 \pm 1.1	19.9 \pm 0.5	16.0 \pm 0.3
PL52A	Planted	40	19.3 \pm 1.3	16.3 \pm 1.0	19.1 \pm 0.7	14.8 \pm 0.3
PL52B	Planted	40	19.8 \pm 1.7	17.4 \pm 1.3	18.6 \pm 0.6	15.1 \pm 0.4

Table 4. F-values of the analysis of variance on the effects of regeneration type, stand age and the interaction of regeneration type and stand age, on site mean soil and litter base-line temperature differences and light intensity in 1991 and 1992.

	df	TEMPERATURE				LIGHT INTENSITY	
		1991		1992		1992	
		SOIL	LITTER	SOIL	LITTER	GROUND	2 METER
REGEN	1	0.691	3.596	0.201	0.257	1.095	0.03
AGE	3	*17.38	*17.405	*10.29	*4.634	*14.712	*17.035
REGEN + AGE	3	*5.924	2.898	0.166	0.348	3.208	2.21
ERROR	7						
MSE		0.522	0.758	1.159	1.935	0.011	0.012

Note: * Indicates a significant effect at a significance level of 0.05

Table 5. Carabid beetle species collected in both 1991 and 1992 with yearly catches greater than 15 individuals.

CARABID SPECIES	YEAR	5 year old				15 year old				25 year old				40 year old		SUM
		Natural		Planted		Natural		Planted		Natural		Planted		Natural	Planted	
		B5A	B5B	PL89A	PL89B	B15A	PL76A	PL76B	B25A	B25B	PL67A	PL67B	B40A	B40B	PL52A	
Agonum placidum	1991	0	3	10	0	0	0	0	2	0	2	0	0	0	0	17
Say	1992	2	0	15	5	1	0	3	0	1	0	0	0	1	1	29
Amara laevipennis	1991	1	4	1	8	0	1	1	0	0	0	0	0	0	0	16
Kirby	1992	5	1	6	25	1	2	2	0	0	0	1	0	1	0	44
Amara latior	1991	0	1	171	17	0	1	21	0	0	0	3	0	0	0	214
Kirby	1992	4	3	502	60	0	1	15	0	0	0	14	0	0	0	599
Amara obesa	1991	54	11	47	22	2	11	25	0	0	0	0	0	0	0	172
Say	1992	46	1	2	17	0	2	10	0	0	0	0	0	0	0	78
Calosoma calidum	1991	8	3	7	1	7	1	8	1	0	0	2	0	1	0	39
Fabricius	1992	14	6	9	6	5	1	14	2	0	0	3	0	0	0	60
Calathus ingratus	1991	2	0	2	2	1	0	1	8	0	0	1	12	21	68	118
Dejean	1992	2	0	0	0	1	0	0	3	0	0	1	8	2	10	39

Table 5. Continued

CARABID SPECIES	YEAR	5 year old				15 year old				25 year old				40 year old		SUM	
		Natural		Planted		Natural		Planted		Natural		Planted		Natural	Planted		
		B5A	B5B	PL89A	PL89B	B15A	PL76A	PL76B	B25A	B25B	PL67A	PL67B	B40A	B40B	PL52A		PL52B
<i>Carabus serratus</i>	1991	1	0	0	0	0	0	9	2	0	2	2	0	2	0	1	19
Say	1992	0	0	1	1	2	1	5	2	0	0	6	0	0	0	2	20
<i>Carabus taedatus</i>	1991	7	0	1	0	16	3	64	17	30	14	68	0	5	2	0	227
Fabricius	1992	13	0	5	3	7	6	50	7	10	10	60	4	3	0	14	192
<i>Dicaelus sculptilis</i>	1991	1	1	0	1	9	0	4	4	1	0	0	3	16	4	5	49
Say	1992	0	0	0	0	4	3	4	7	0	3	1	6	8	8	4	48
<i>Harpalus fuliginosus</i>	1991	0	0	5	2	0	0	0	1	2	4	0	0	11	3	2	30
Duftschmid	1992	4	2	1	2	5	0	1	3	0	2	0	2	9	16	4	51
<i>Harpalus laticeps</i>	1991	81	71	79	30	0	2	4	0	1	0	0	0	0	0	0	268
Leconte	1992	168	212	46	46	0	3	0	0	3	0	0	0	0	0	0	478

Table 5. Continued

CARABID SPECIES	YEAR	5 year old				15 year old				25 year old				40 year old				SUM
		Natural		Planted		Natural		Planted		Natural		Planted		Natural		Planted		
		B5A	B5B	PL89A	PL89B	B15A	PL76A	PL76B	B25A	B25B	PL67A	PL67B	B40A	B40B	PL52A	PL52B		
Harpalus lewisi	1991	32	225	33	42	0	1	0	0	1	1	0	0	0	0	1	336	
Leconte	1992	46	179	53	55	1	1	3	0	2	0	2	0	0	0	0	342	
Pterostichus adstrictus	1991	0	0	0	0	0	5	1	2	0	3	0	0	1	1	4	17	
Edstrictus	1992	5	0	0	0	0	0	0	1	1	0	0	6	1	7	0	21	
Pterostichus	1991	10	0	16	1	6	7	4	5	7	3	8	59	43	72	14	255	
pennsylvanicus Leconte	1992	2	0	40	2	15	5	2	20	6	3	22	175	41	57	166	556	
Synuchus impunctatus	1991	0	0	1	0	0	0	0	0	5	0	0	7	0	5	3	21	
Say	1992	4	0	0	1	1	9	0	0	5	0	1	2	2	47	30	102	
TOTAL		512	720	1043	349	84	66	251	85	75	45	195	284	168	301	262	4440	

Table 6. Wing characteristics of the most common wing dimorphic carabid species captured in Sandilands.

Carabid species	No. of dissections	Mean wing-length (mm)	Ratio (wing:elytra)	Percent rudimentary wings
Amara obesa Say	35	10.5	1.4	0
Agonum retractum Leconte	12	r/w	<0.5	75
Carabus serratus Say	12	r/w	<0.5	100
Synuchus impunctatus Say	83	r/w	<0.5	99

NOTE: r/w indicates rudimentary wing development (i.e wing:elytra <0.5).

Figure 1.

Location of the sites on a soil map of the Bedford Hill and Badger regions of the Sandilands Provincial Forest. Soil map was drawn and published by the Soil Research Institute, Research Branch, Canada Department of Agriculture, Ottawa, 1964 from base compiled by the Manitoba Soil Survey, Winnipeg, Manitoba (Smith et. al, 1964).

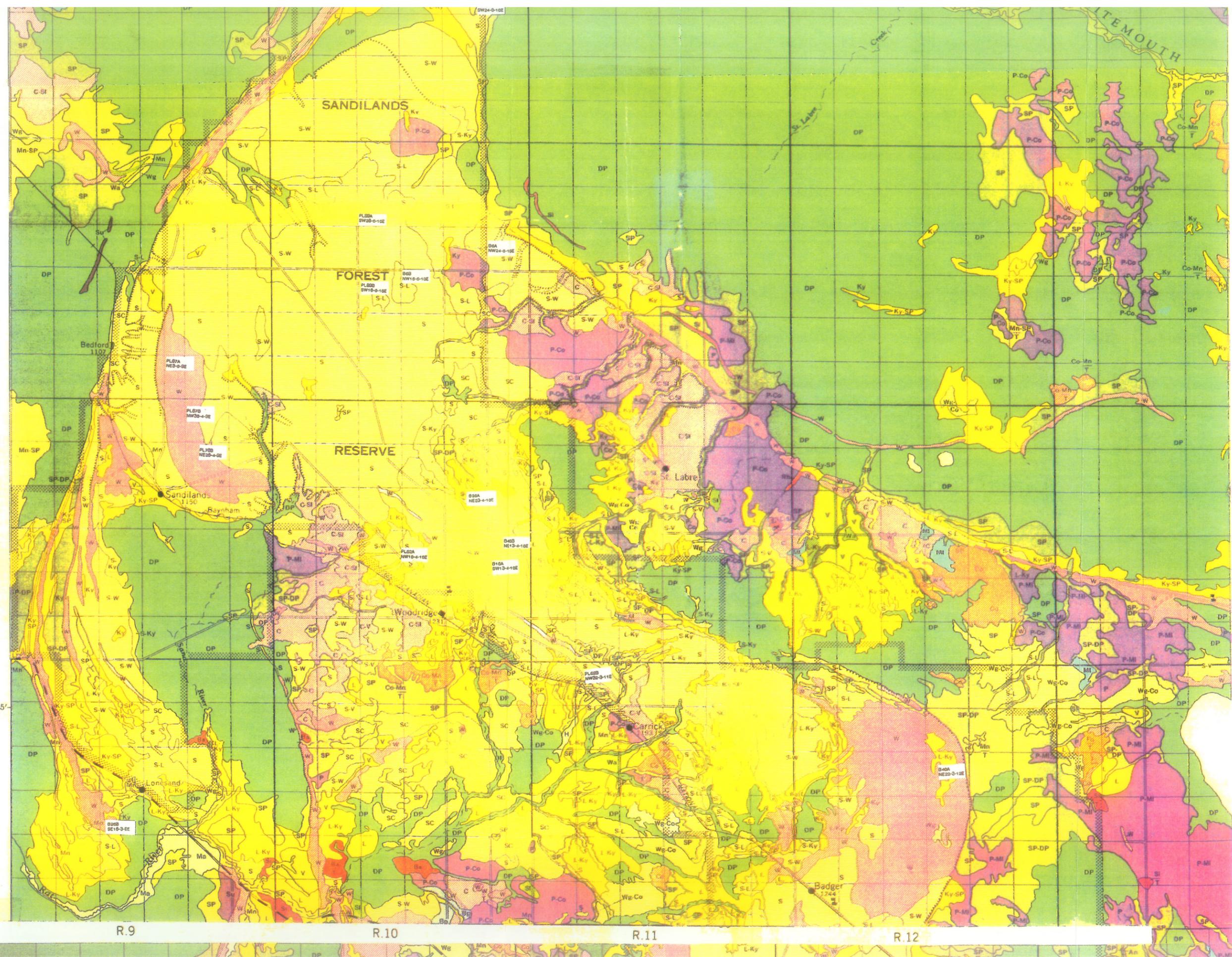
MAP SYMBOL	SOIL NAME AND DOMINANT TEXTURE	PROFILE TYPES	PARENT MATERIAL	NATURAL DRAINAGE	DOMINANT VEGETATION
Ky	KERRY Series (sand)	Peaty Gleysol	Sand deposits	Poor	Alder, willow, swamp birch, sedges, reeds
Ky-SP	KERRY-SHALLOW PEAT COMPLEX	Peaty Gleysol and Organic Soil	Sand deposits and 12-36" of peat over undifferentiated deposits	Poor and very poor	Alder, willow, swamp birch, sedges, reeds
L	LONESAND Series (sand)	Gleyed Podzol	Sand deposits	Imperfect	Aspen, balsam poplar, jack pine
LKy	LONESAND-KERRY COMPLEX	Gleyed Podzol and Peaty Gleysol	Aeolian and outwash sand deposits	Imperfect and poor	Aspen, balsam poplar, jack pine, willow, swamp birch, sedges
S	SANDILANDS Series (sand)	Minimal Podzol	Sand deposits	Excessive	Jack pine
SC	SANDILANDS CATENA (fine sand)	Minimal Podzol, Gleyed Podzol, Peaty Gleysol and Organic Soil	Aeolian sand and thin organic deposits over sand	Excessive to very poor	Jack pine, alder, willow, swamp birch, sedges
S Ky	SANDILANDS-KERRY COMPLEX	Minimal Podzol and Peaty Gleysol	Aeolian sand	Excessive and poor	Jack pine, alder, willow, swamp birch, sedges
S L	SANDILANDS-LONESAND COMPLEX	Minimal Podzol and Gleyed Podzol	Aeolian sand	Excessive and imperfect	Jack pine, alder, willow, aspen, balsam poplar
S V	SANDILANDS-VASSAR COMPLEX	Minimal Podzol and Bisequa Grey Wooded	Sand and 6-30" of fine sand over clay loam to clay lacustrine or till deposits	Excessive and good	Jack pine, aspen, birch
W	SANDILANDS WOODRIDGE COMPLEX	Minimal Podzol and Orthic Grey Wooded	Stratified sand and gravel deposits	Excessive	Jack pine, aspen
SP	SHALLOW PEAT	Organic Soil	Peat 12-36" thick over undifferentiated deposits	Poor to very poor	Black spruce, tamarack, cedar, swamp birch, sedges, reeds
W	WOODRIDGE Series (sand)	Orthic Grey Wooded	Calcareous, stratified sand and gravel deposits	Excessive	Jack pine
W T	WOODRIDGE till sub-stratified base (Sand)	Orthic Grey Wooded	6-30" of above sediments over calcareous till	Good	Jack pine, aspen, birch

Tp.6

Tp.5

Tp.4

Tp.3



R.9

R.10

R.11

R.12

15°

Map showing various land parcels, rivers, and geographical features. Labels include Sandilands, Forest Reserve, Woodridge, Carrick, Badger, and various township and range coordinates.

Figure 2. 5 year old planted site PL89A.

Figure 3. 5 year old natural site B5A.



Figure 4. 15 year old planted site PL76A.

Figure 5. 15 year old natural site B15A.



Figure 6. 25 year old planted site PL67A.

Figure 7. 25 year old natural site B25A.



Figure 8. 40 year old planted site PL52A.

Figure 9. 40 year old natural site B40A.



Figure 10. Ground vegetation, 1 m x 1 m quadrat sample.

Figure 11. Shrub vegetation, 2 m x 2 m quadrat sample.

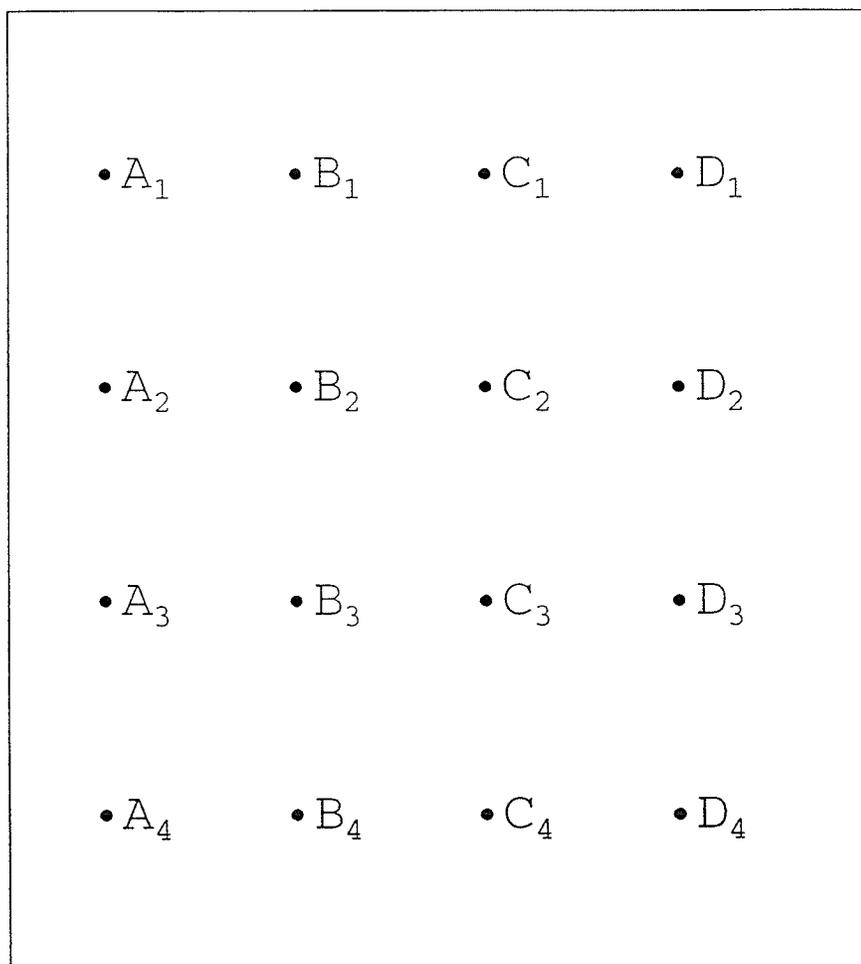


Figure 12. Tree vegetation, 10 m x 10 m quadrat sample.

Figure 13. Litter and soil temperature measurements.



Figure 14. Pitfall trap pattern within the site.



A line = wet

B line = dry

C line = wet

D line = dry

Figure 15. "Dry trap": Pitfall trap without preservative.

Figure 16. "Wet trap": Pitfall trap with preservative.

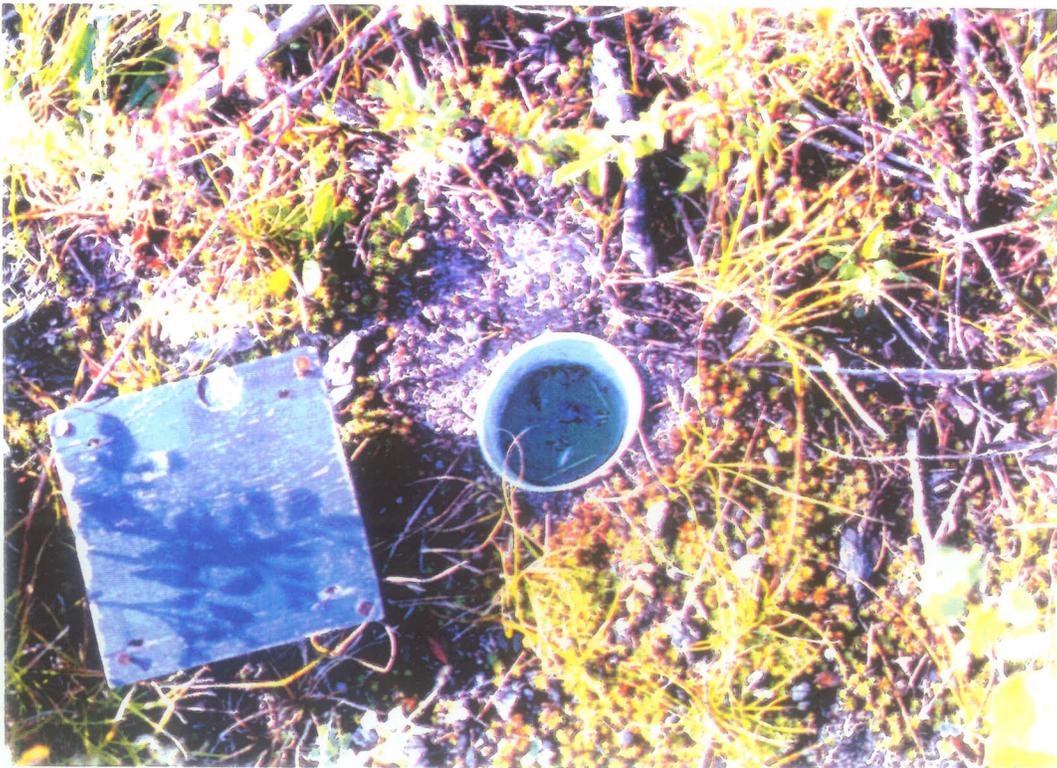
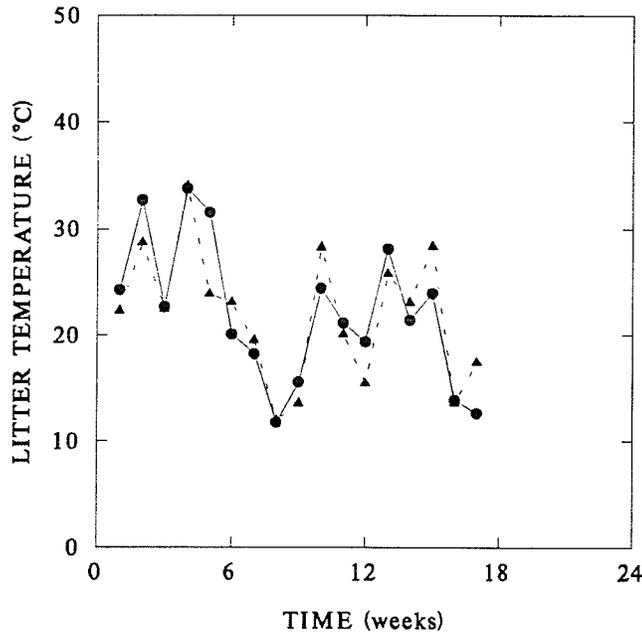
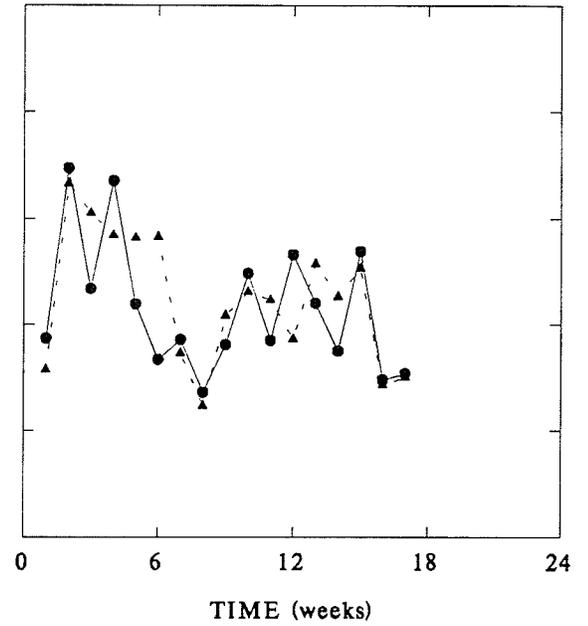


Figure 17. Seasonal patterns of litter temperature in the 1991 planted (\blacktriangle ---) and natural (\bullet —) sites of the four different age classes. Time is expressed in weeks starting with "week 1", which corresponds to the week of May 11.

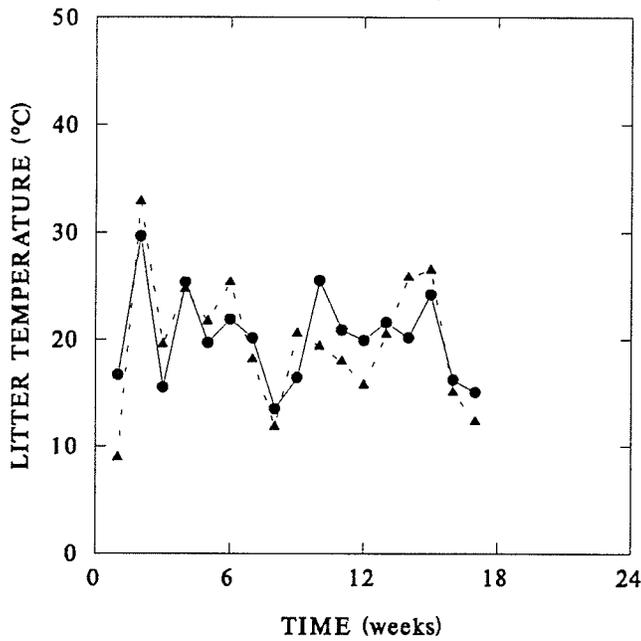
5 year old



15 year old



25 year old



40 year old

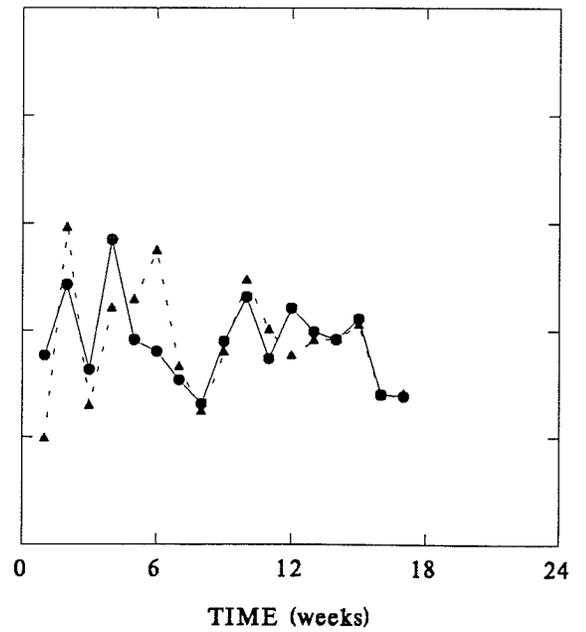
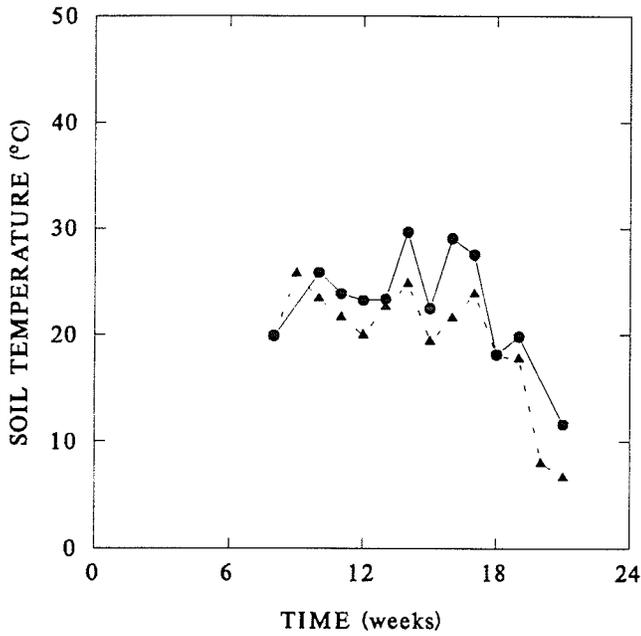
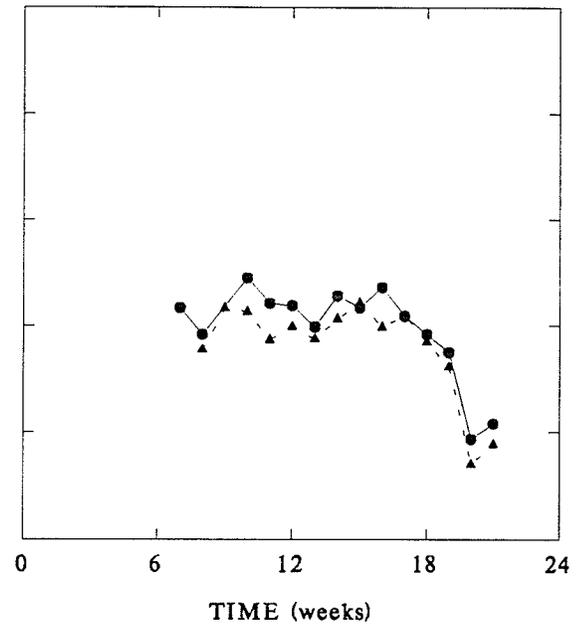


Figure 18. Seasonal patterns of soil temperature in the 1991 planted (\blacktriangle ---) and natural (\bullet —) sites of the four different age classes. Time is expressed in weeks starting with "week 1", which corresponds to the week of May 11.

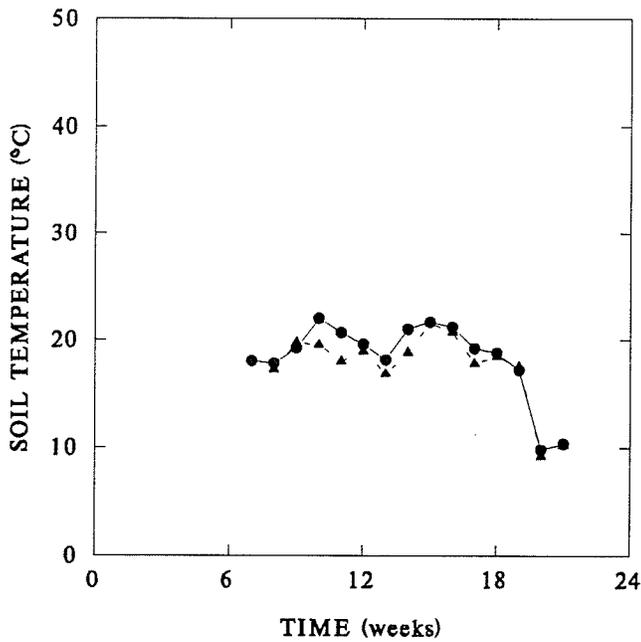
5 year old



15 year old



25 year old



40 year old

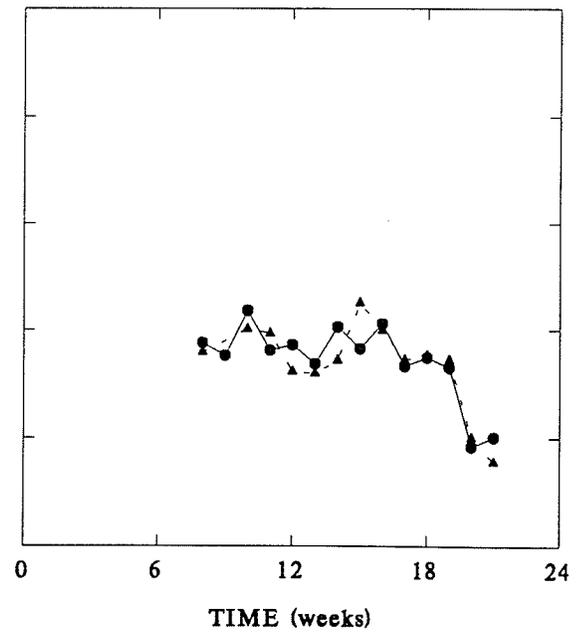
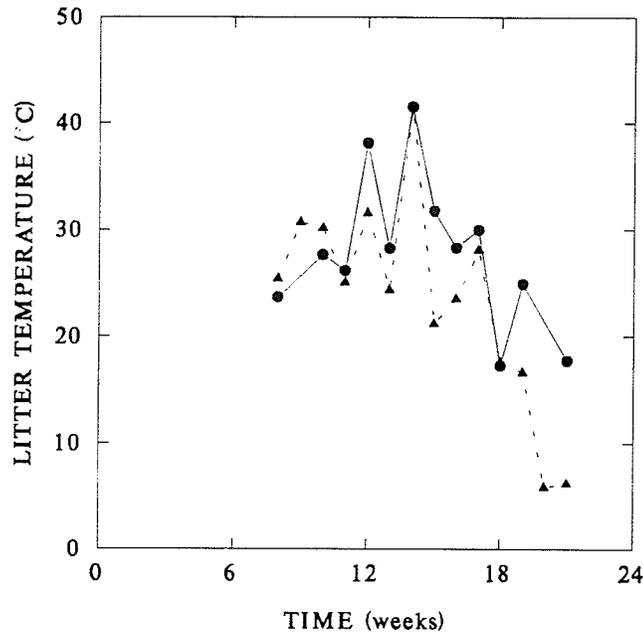
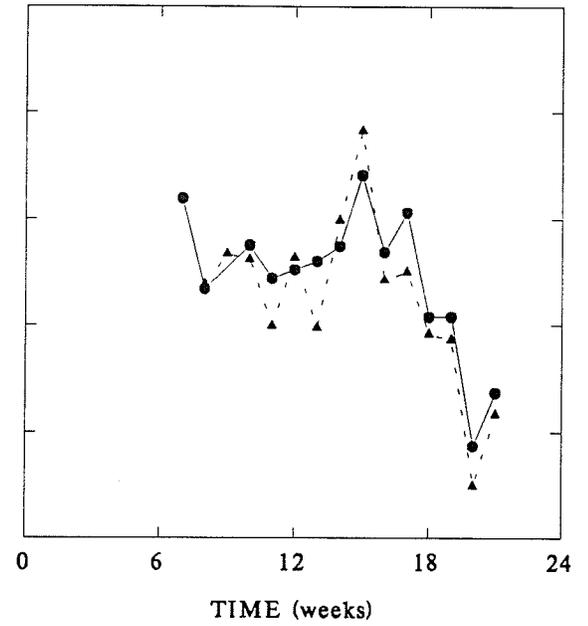


Figure 19. Seasonal patterns of litter temperature in the 1992 planted (\blacktriangle ---) and natural (\bullet —) sites of the four different age classes. Time is expressed in weeks, starting with "week 1", which corresponds to the week of May 11.

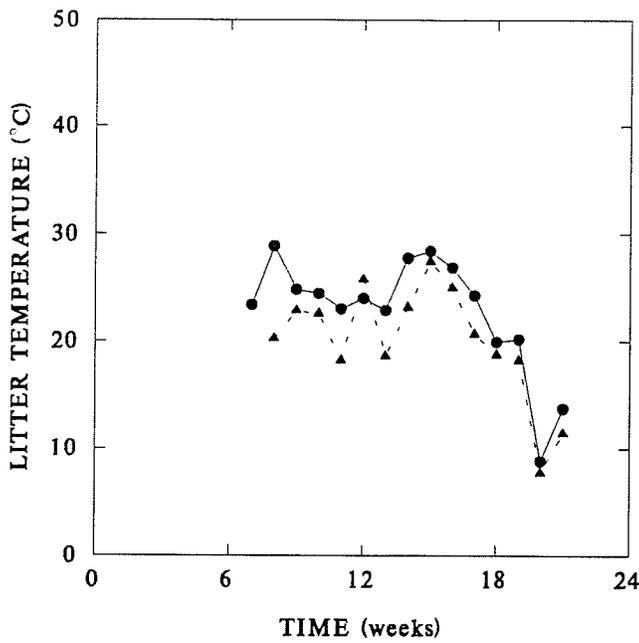
5 year old



15 year old



25 year old



40 year old

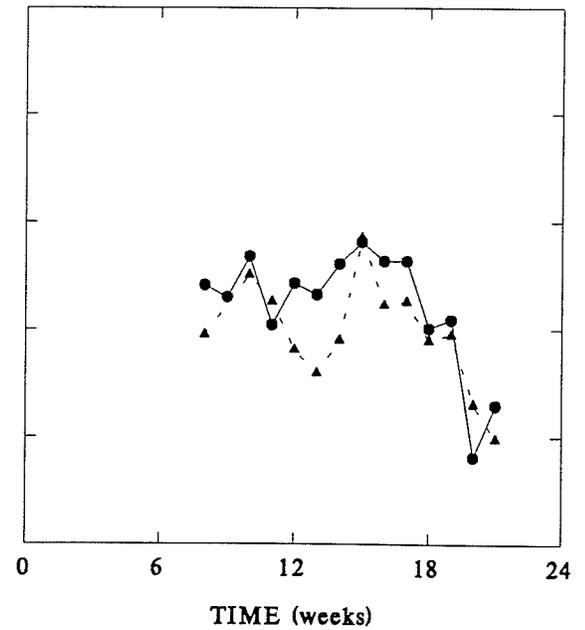
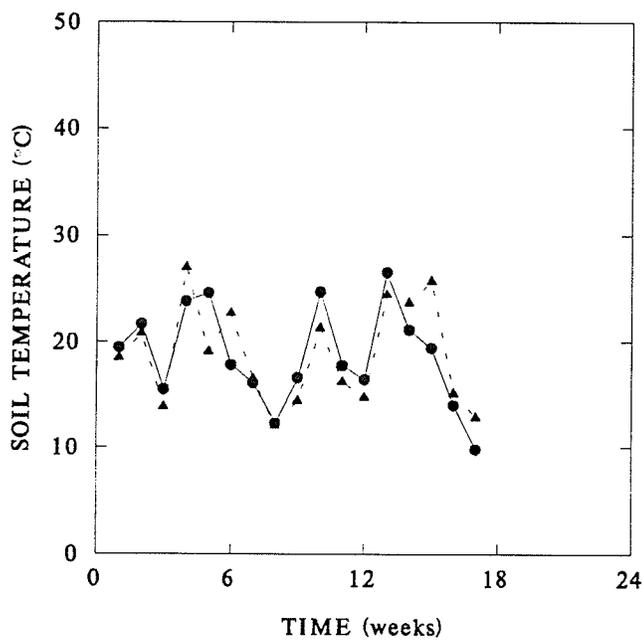
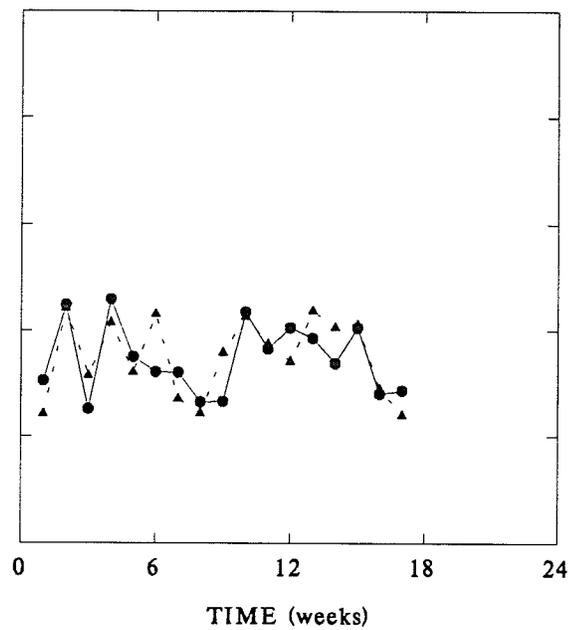


Figure 20. Seasonal patterns of soil temperature in the 1992 planted (▲ ---) and natural (● —) sites of the four different age classes over time. Time is expressed in weeks starting with "week 1", which corresponds to the week of May 11.

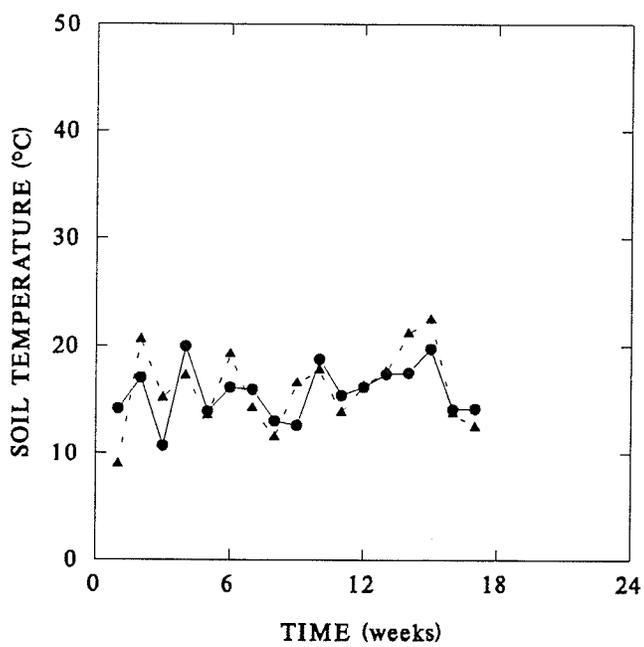
5 year old



15 year old



25 year old



40 year old

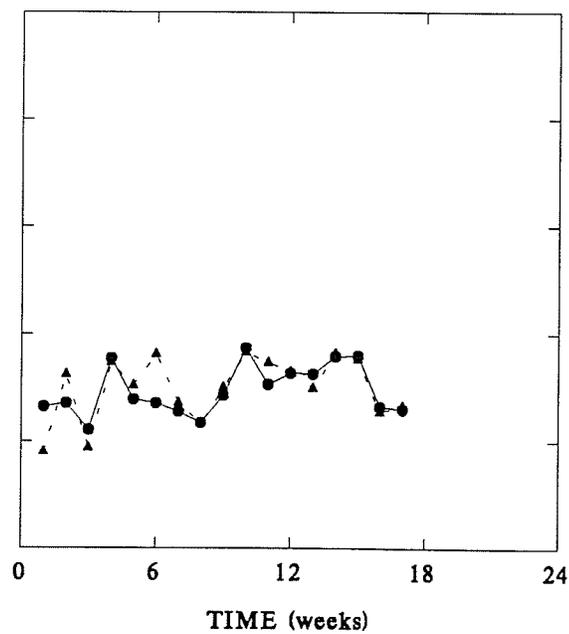


Figure 21. The effects of stand age on mean base line difference in soil temperatures in planted (Δ ---) and naturally regenerated (\bullet —) sites in 1991.

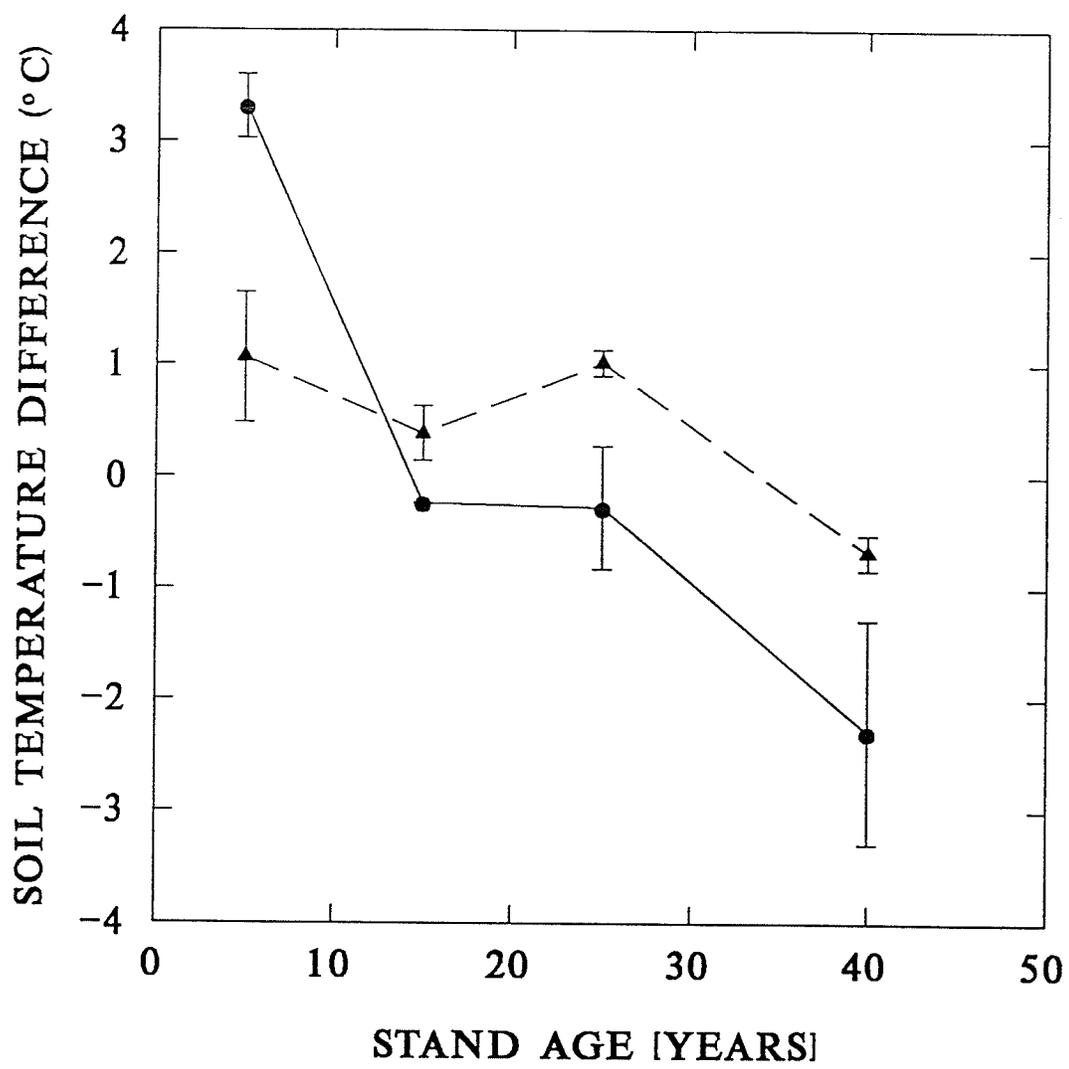


Figure 22. The effects of stand age on mean base line difference in soil temperatures in planted (▲ ---) and naturally regenerated (● —) sites in 1992.

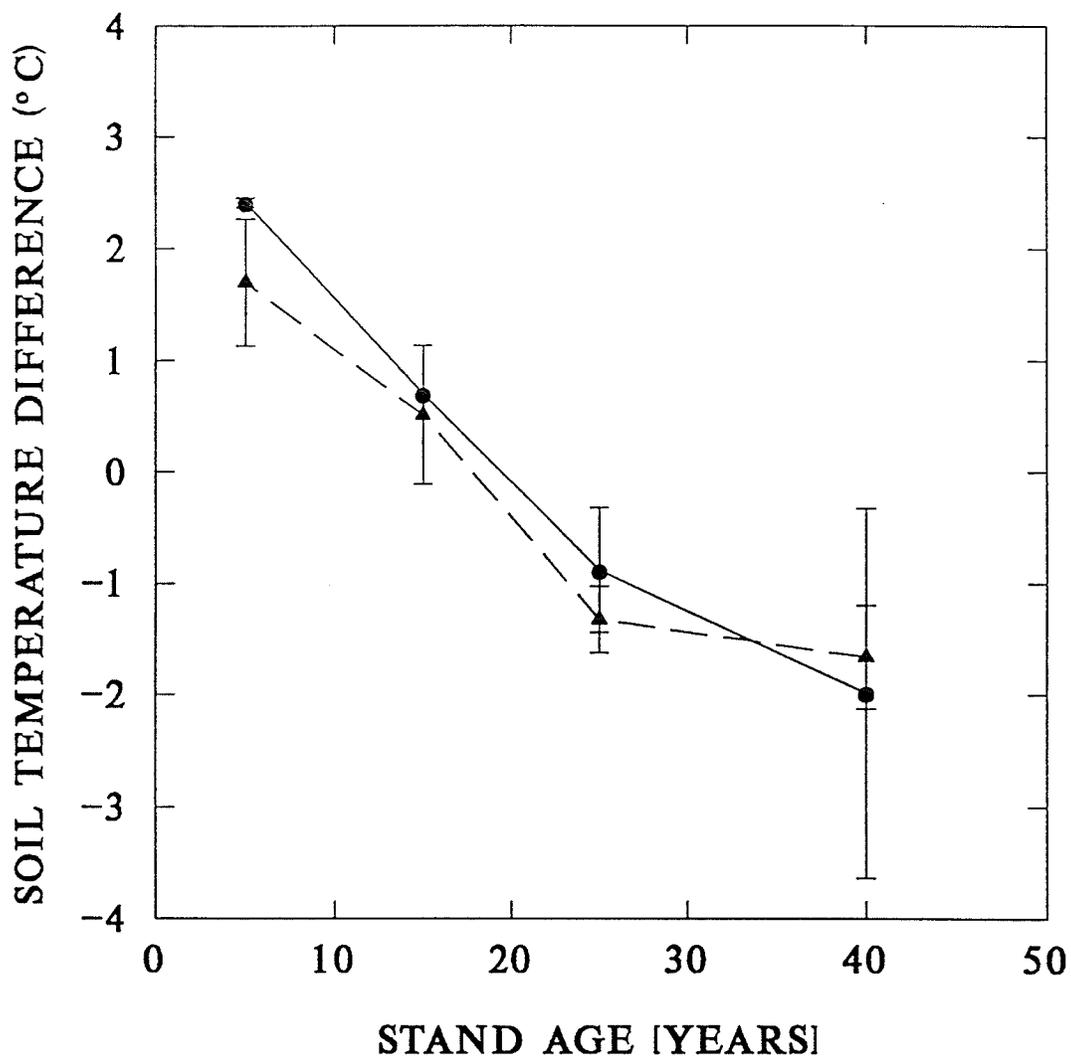


Figure 23. The effects of stand age on mean base line difference in litter temperatures in planted (Δ ---) and naturally regenerated (\bullet —) sites in 1991.

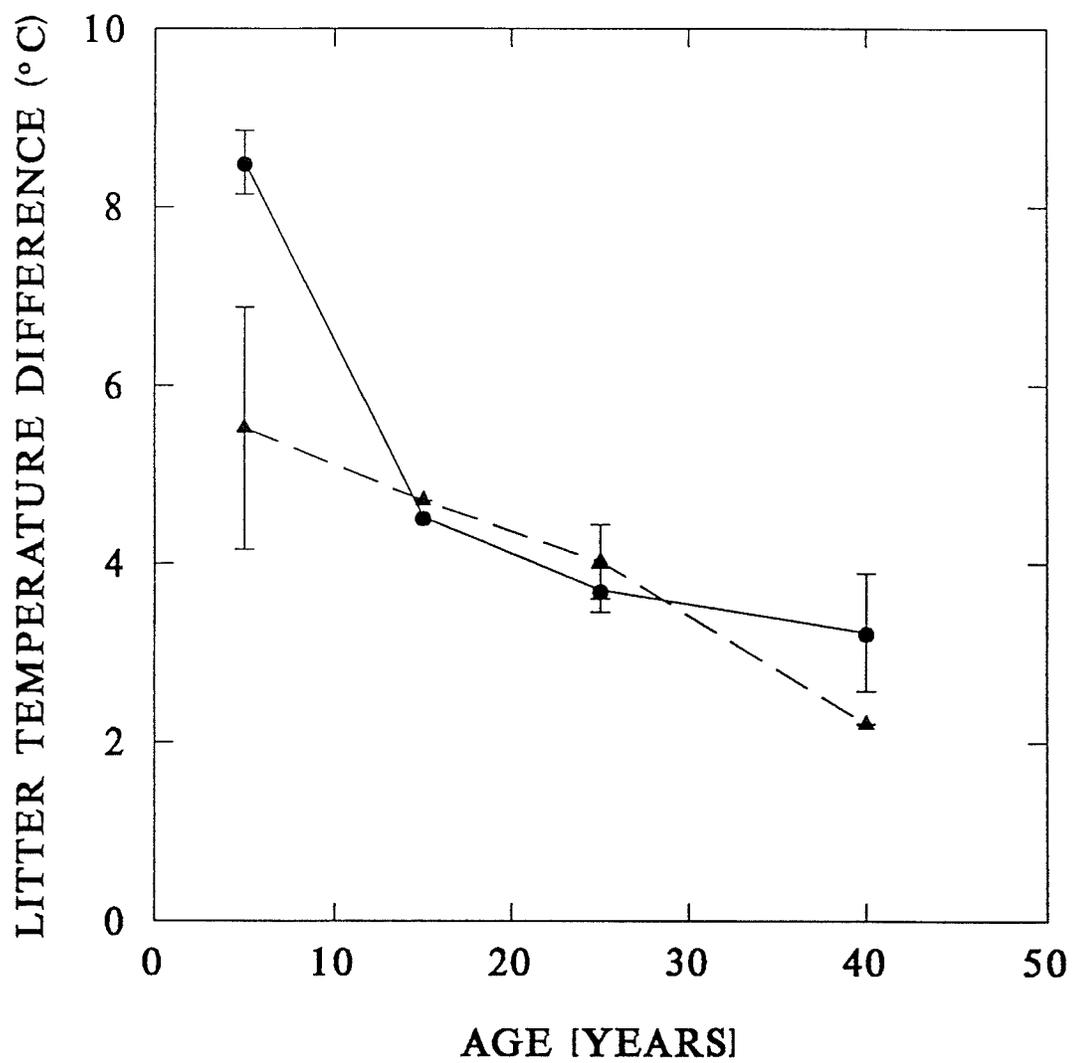


Figure 24. The effects of stand age on mean base line difference in litter temperatures in planted (Δ ---) and naturally regenerated (\bullet —) sites in 1992.

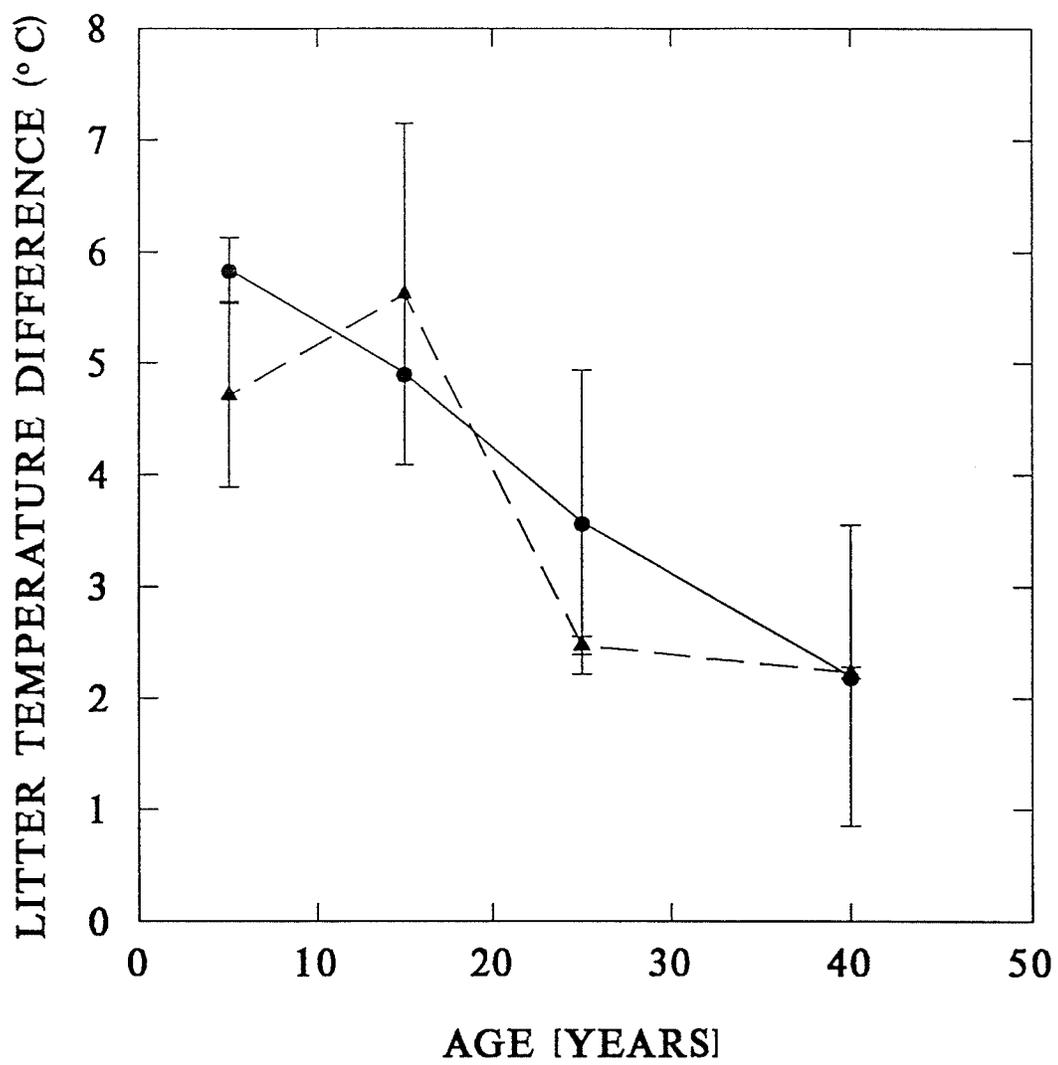


Figure 25. The effects of stand age on mean light intensity at ground level in planted (▲ ---) and naturally regenerated (● —) sites in 1992.

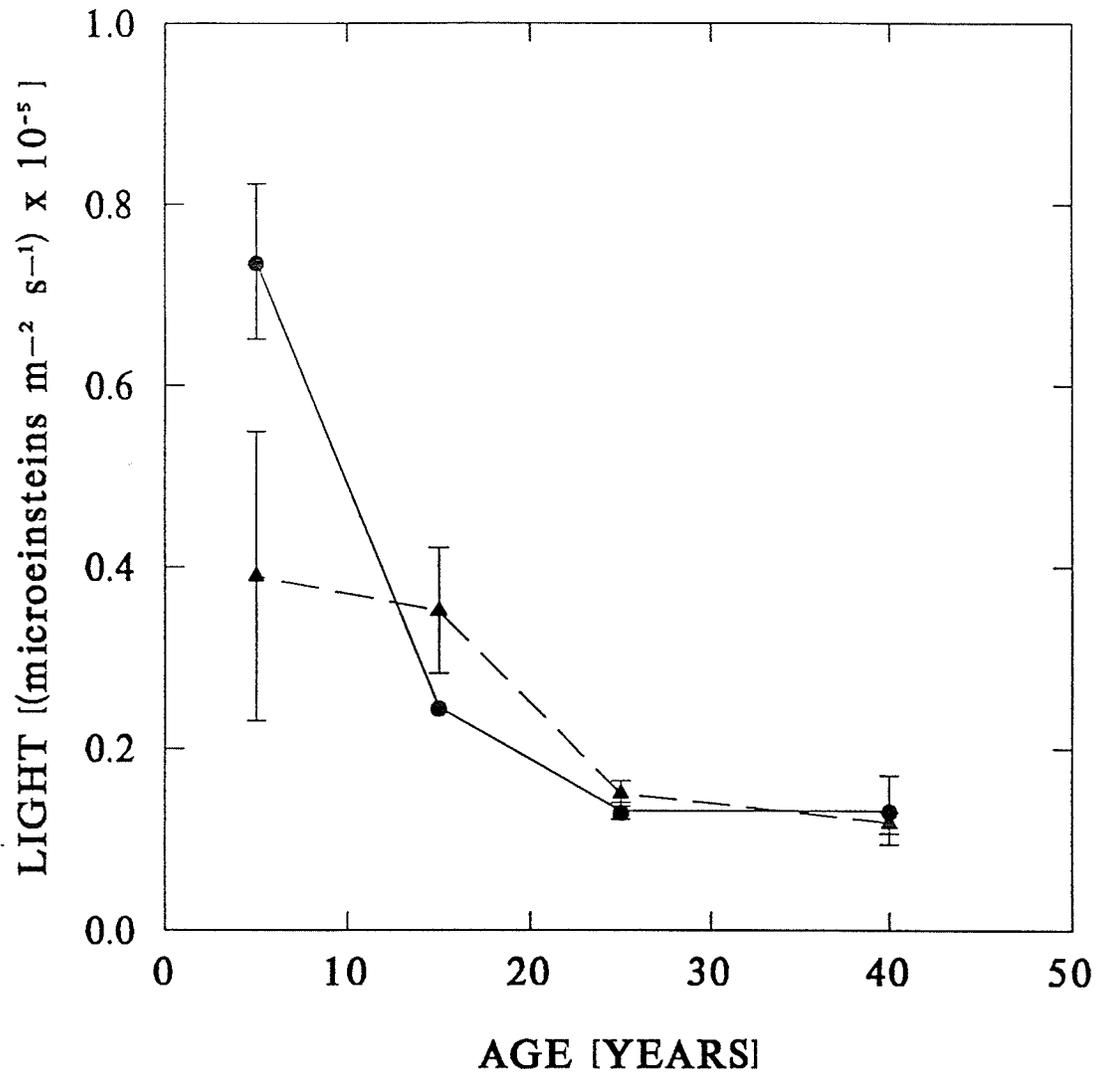


Figure 26. The effects of stand age on mean light intensity at 2 m above ground level in planted (Δ ---) and naturally regenerated (\bullet —) sites in 1992.

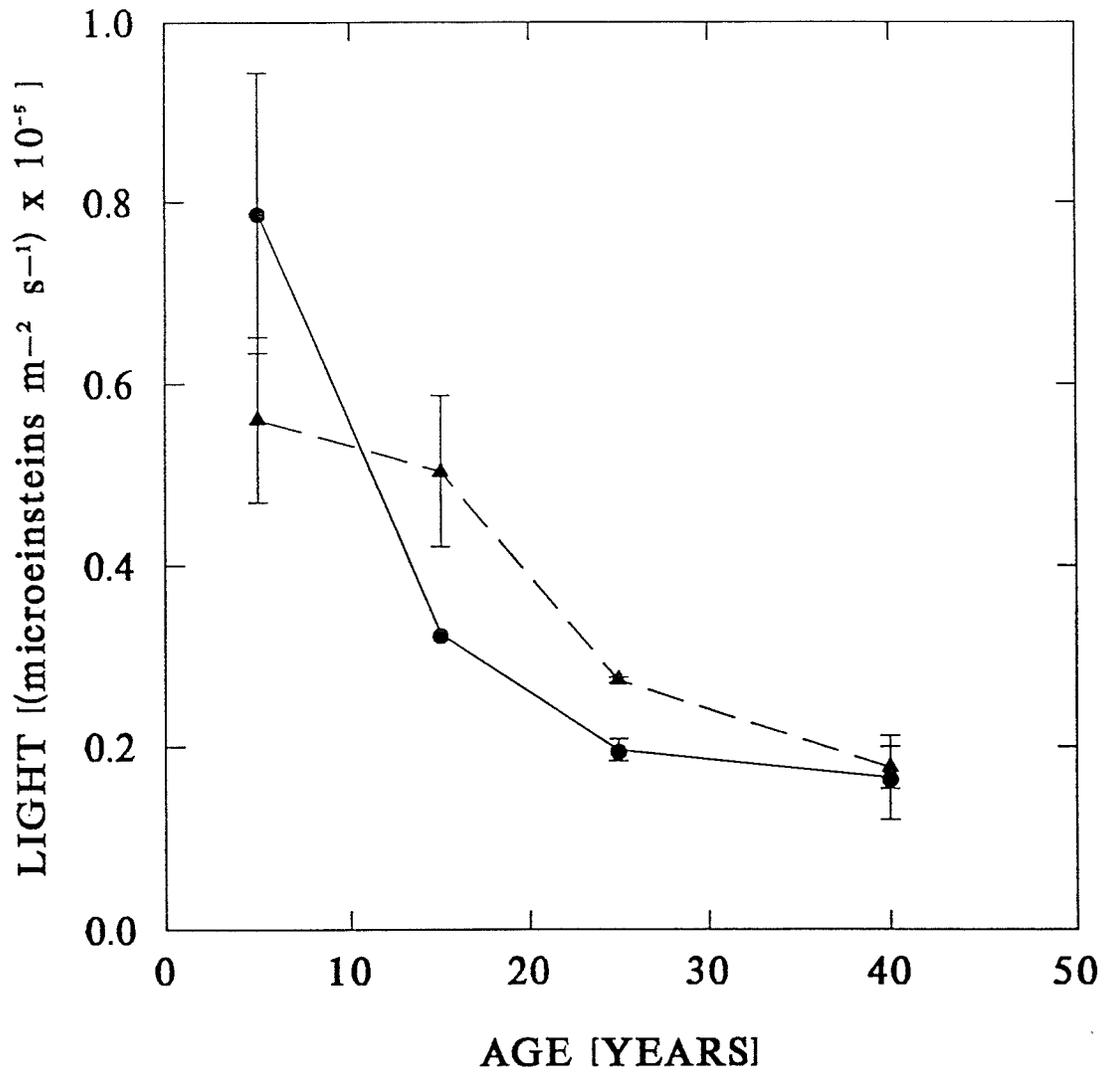


Figure 27. The effects of stand age on mean number of carabid beetles collected per site in planted (\blacktriangle ---) and naturally regenerated (\bullet —) sites in 1991.

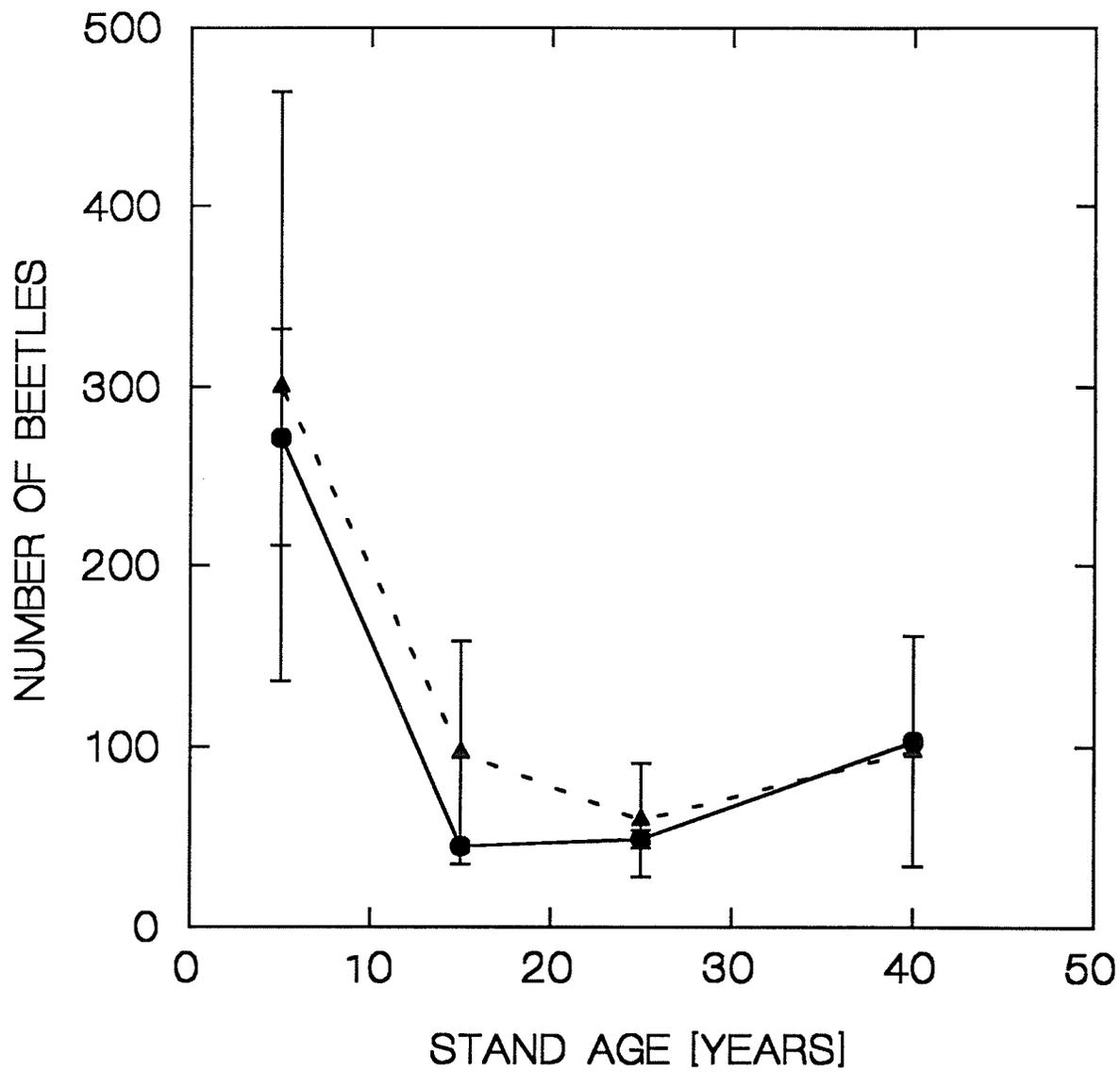


Figure 28. The effects of stand age on mean number of carabid beetles collected per site in planted (▲ ---) and naturally regenerated (● —) sites in 1992.

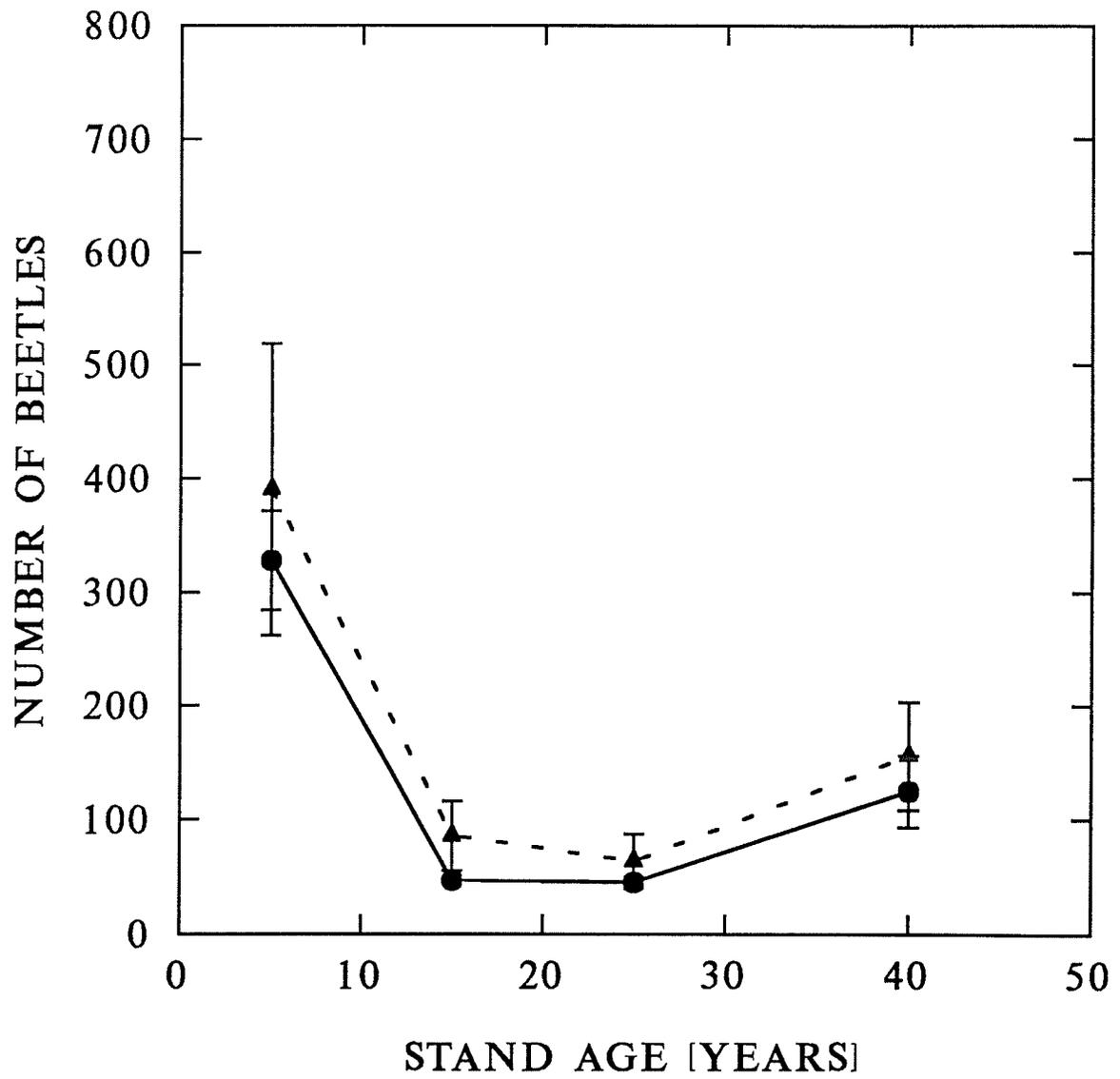


Figure 29. The effects of stand age on mean number of carabid beetles species collected per site in planted (▲ ---) and naturally regenerated (● —) sites in 1991.

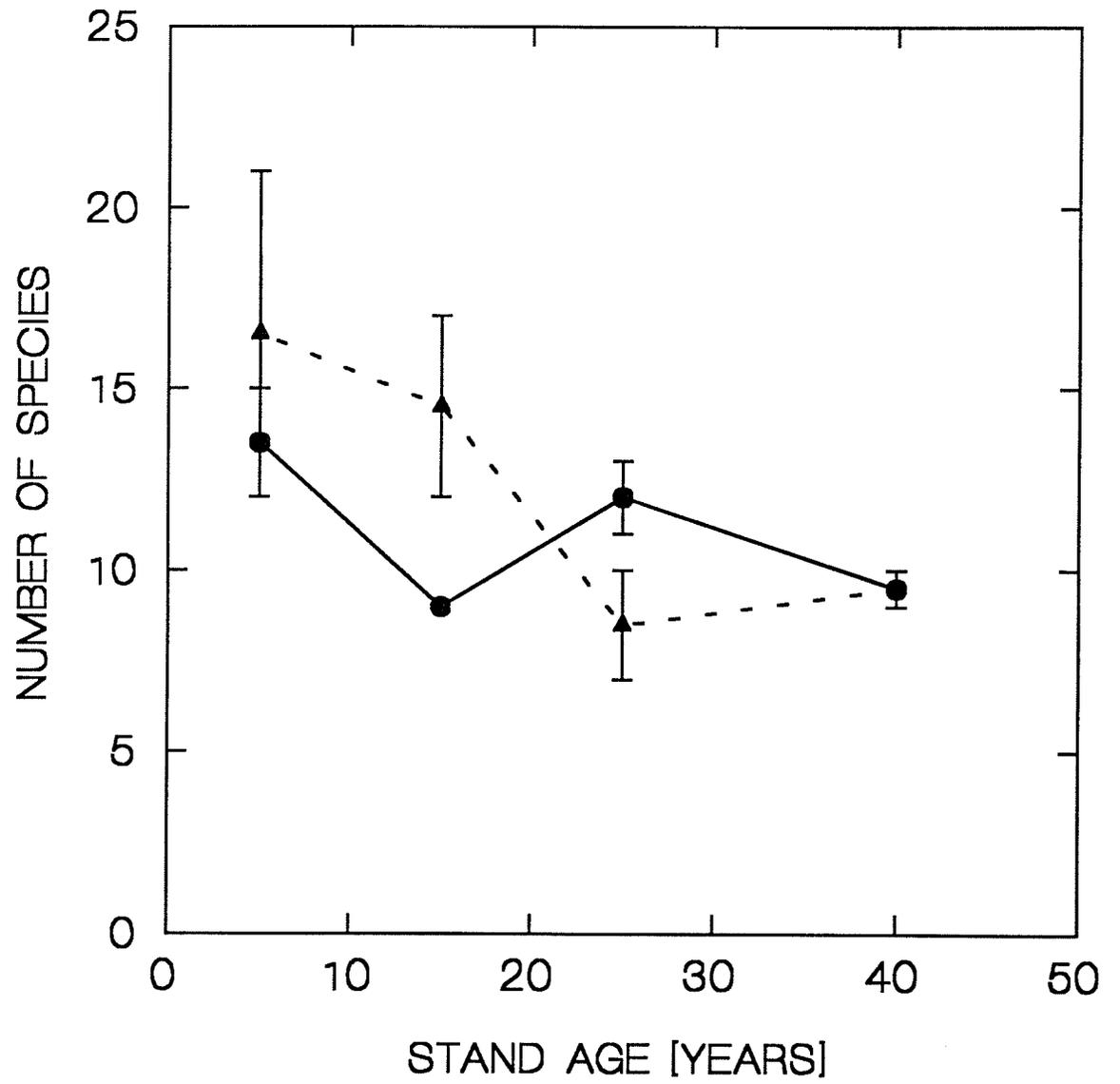


Figure 30. The effects of stand age on mean number of carabid beetle species collected per site in planted (▲ ---) and naturally regenerated (● —) sites in 1992.

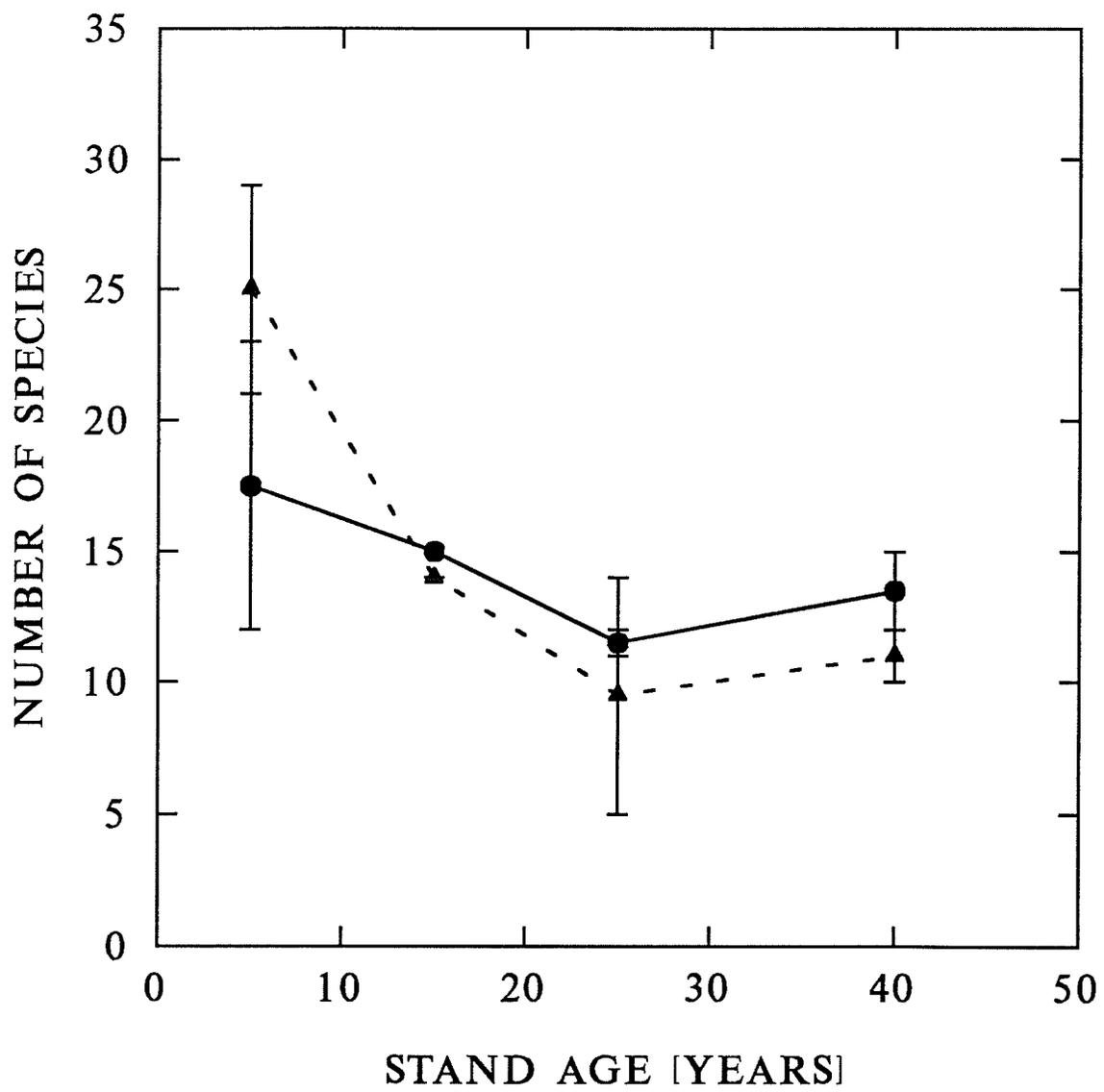


Figure 31. The effects of stand age on the Shannon Wiener index in planted (\blacktriangle ---) and naturally regenerated (\bullet —) sites in 1991.

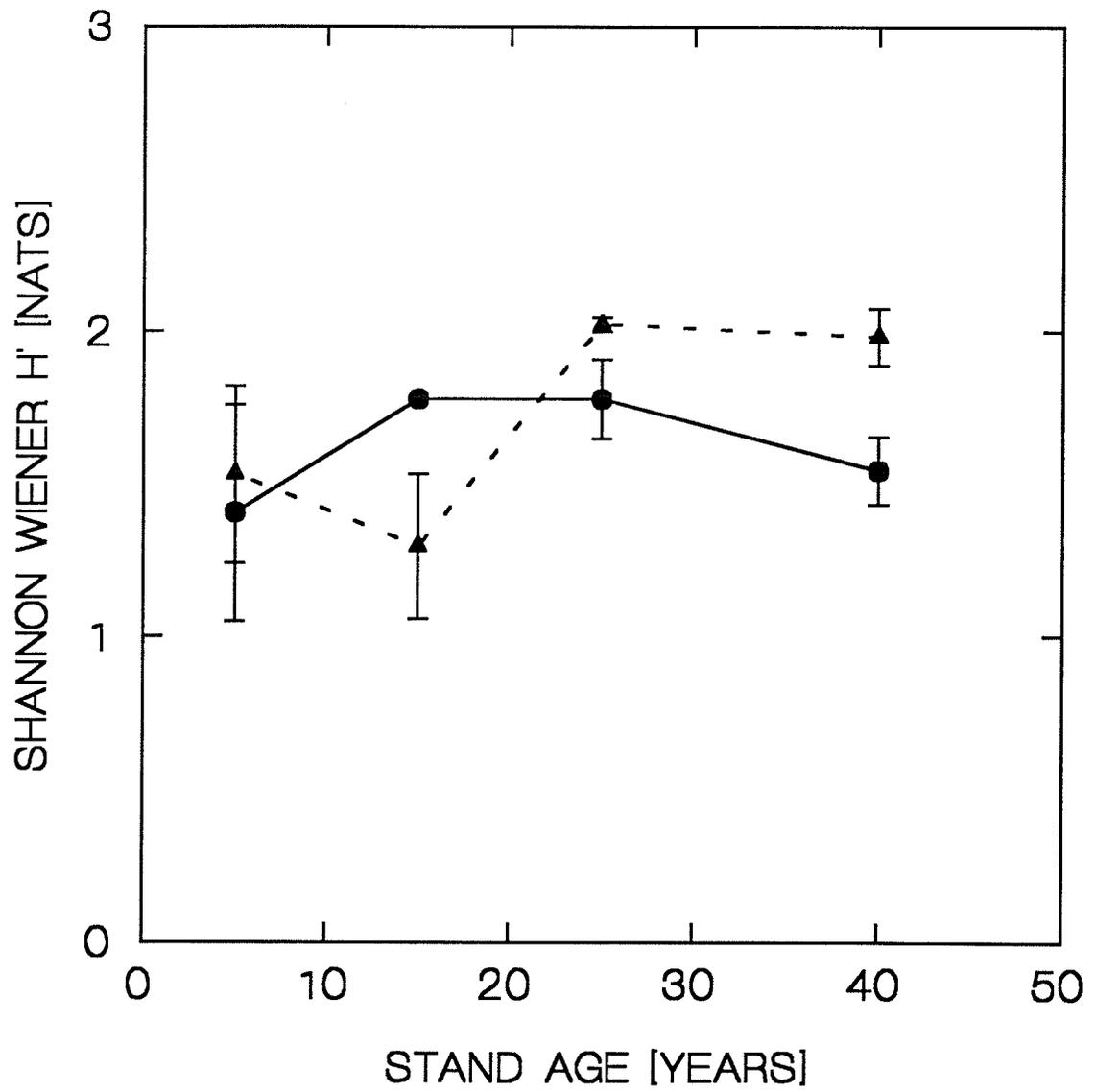


Figure 32. The effects of stand age on the Shannon Wiener index in planted (\blacktriangle ---) and naturally regenerated (\bullet —) sites in 1992.

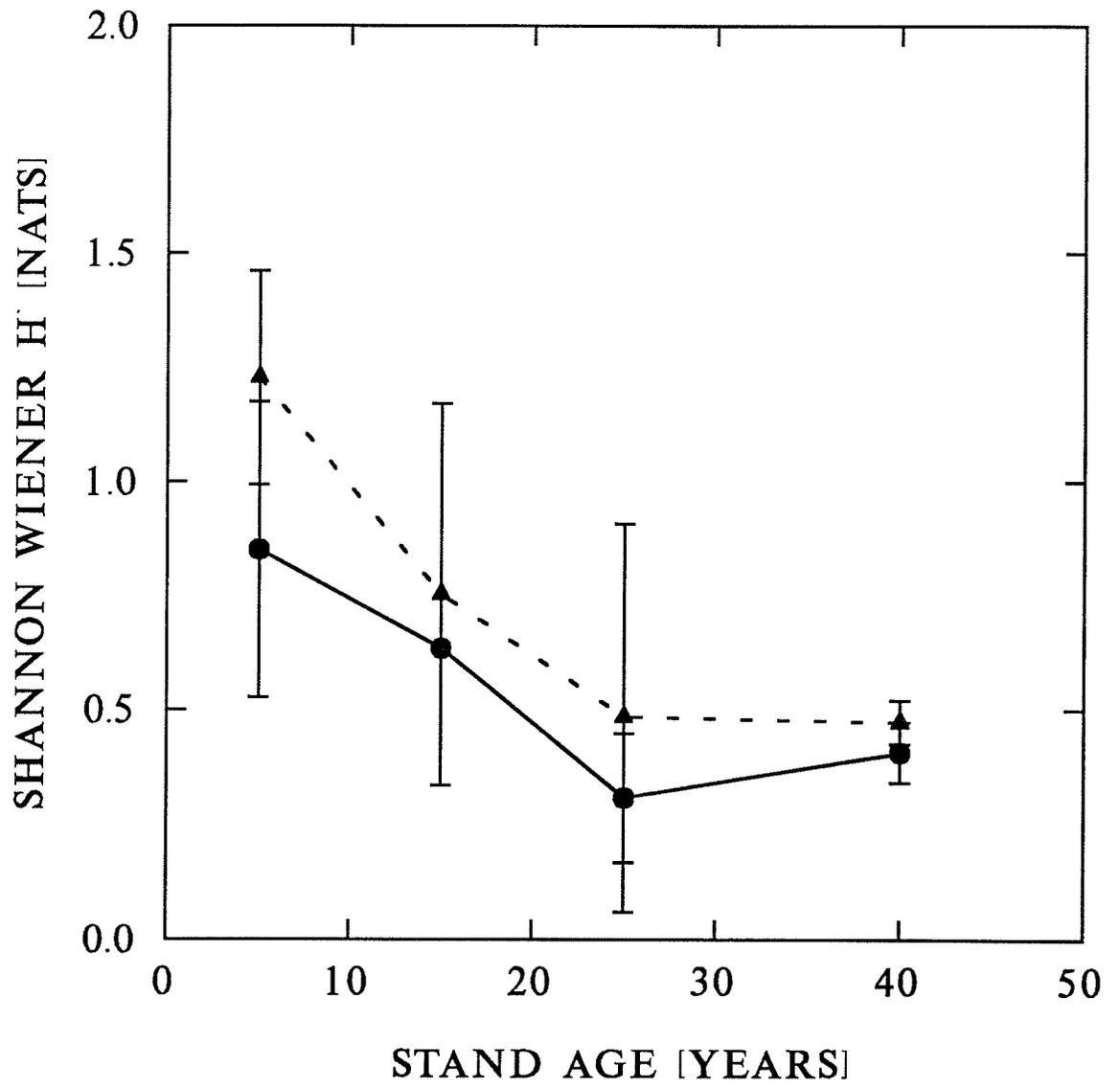


Figure 33. The effects of stand age on the Log series α index in planted (\blacktriangle ---) and naturally regenerated (\bullet —) sites in 1991.

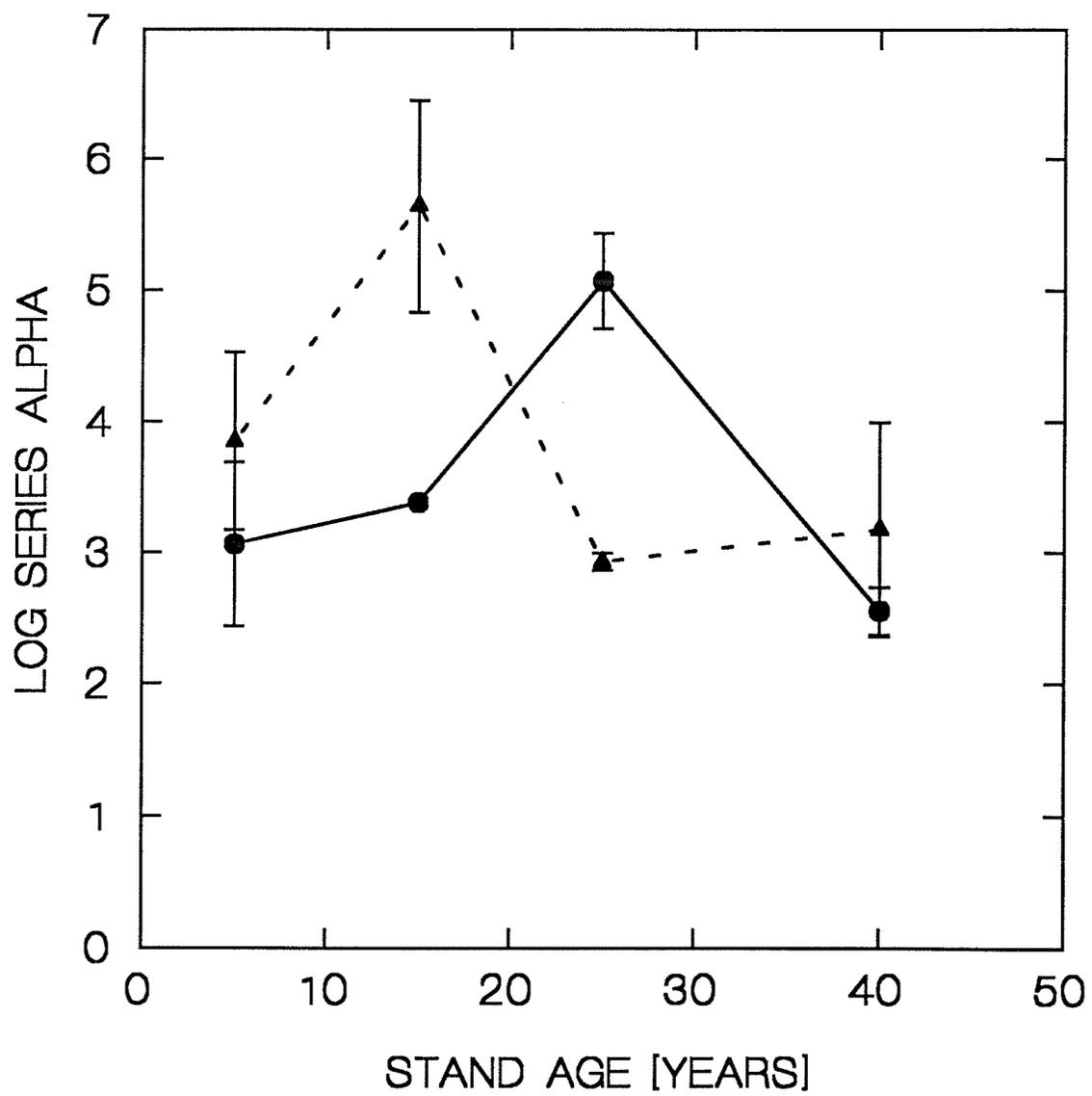


Figure 34. The effects of stand age on the Log series α index in planted (\blacktriangle ---) and naturally regenerated (\bullet —) sites in 1992.

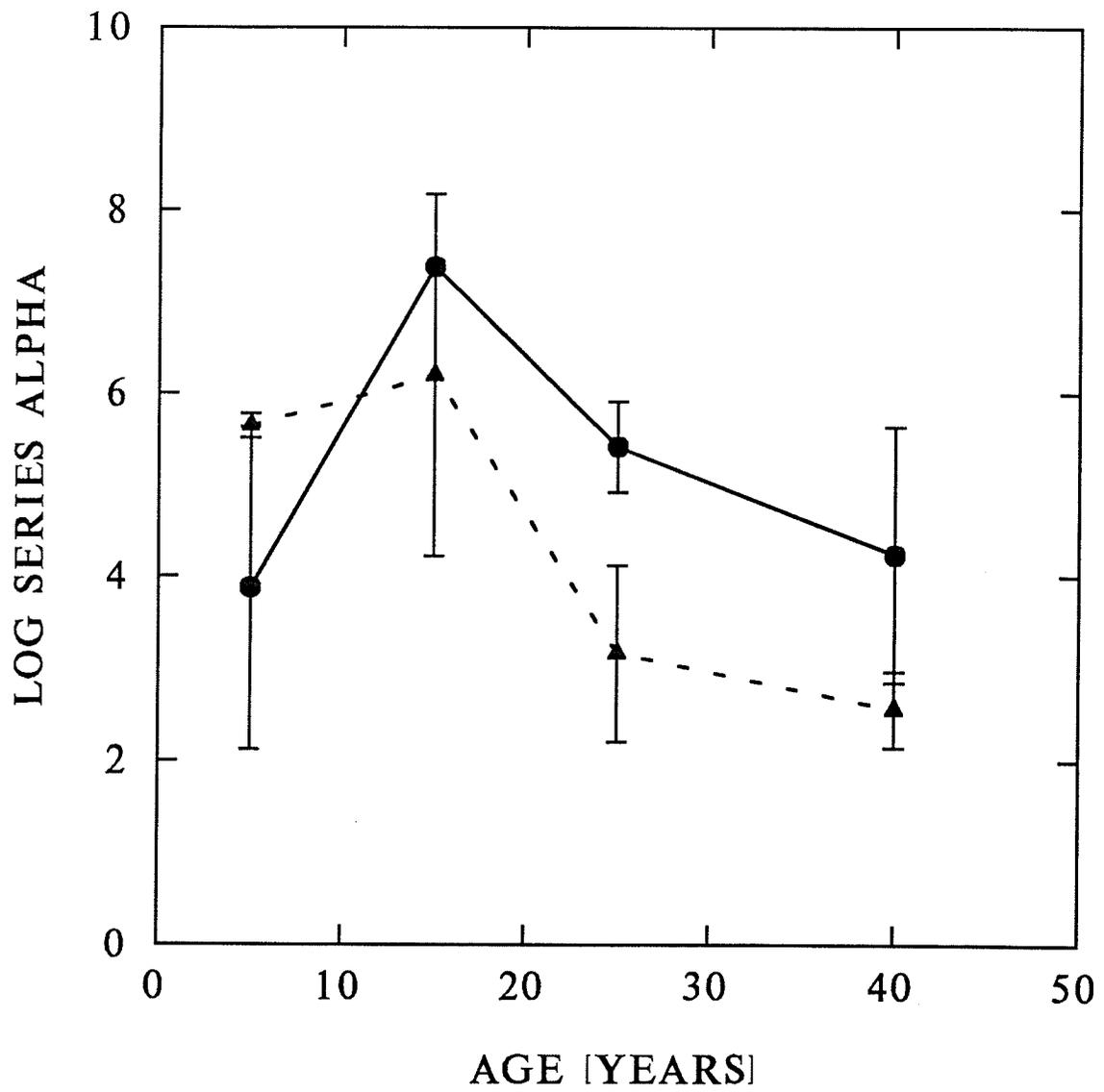


Figure 35. The effects of stand age on Jaccard's index of similarity in planted (Δ ---) and naturally regenerated (\bullet —) sites in 1991.

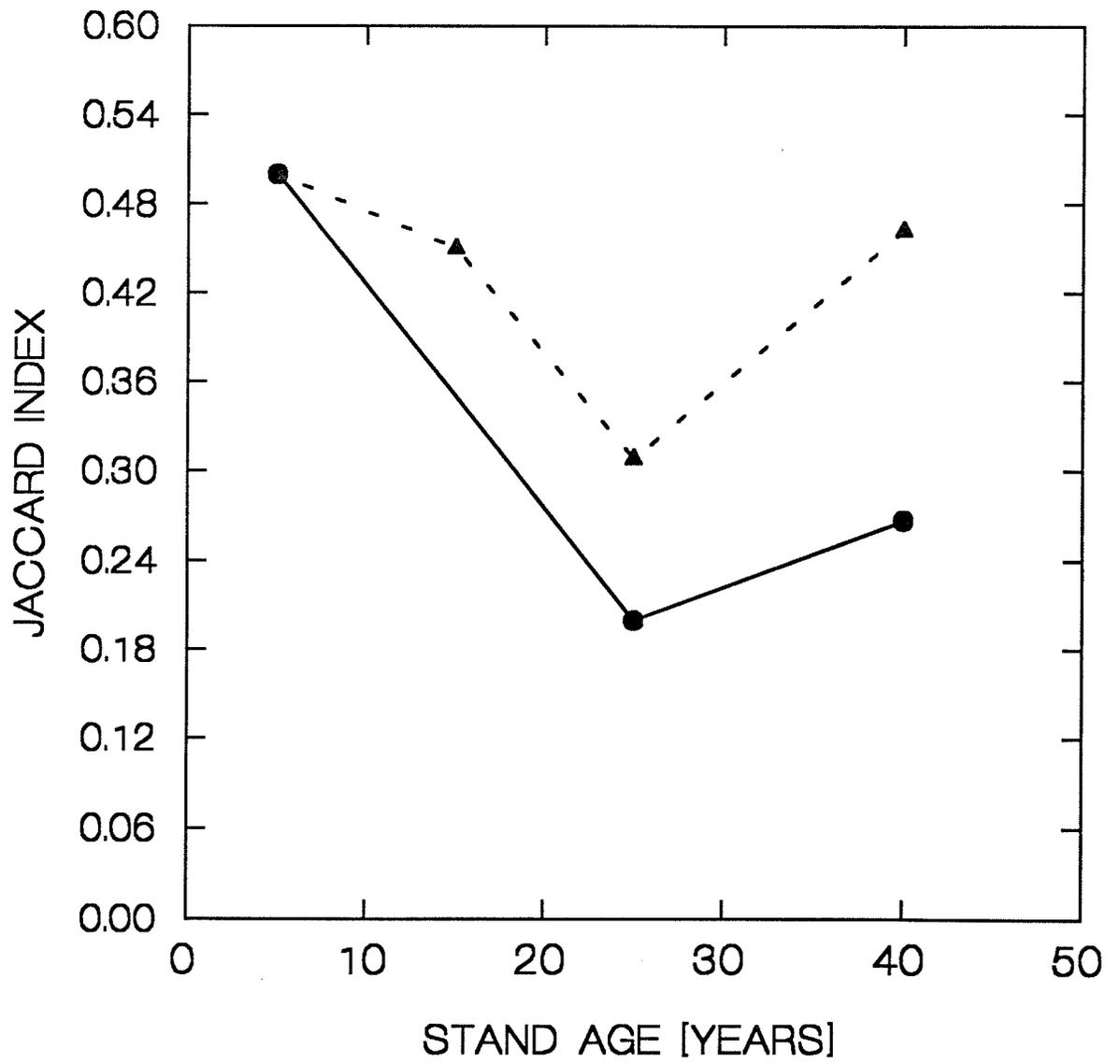


Figure 36. The effects of stand age on Jaccard's index of similarity in planted (Δ ---) and naturally regenerated (\bullet —) sites in 1992.

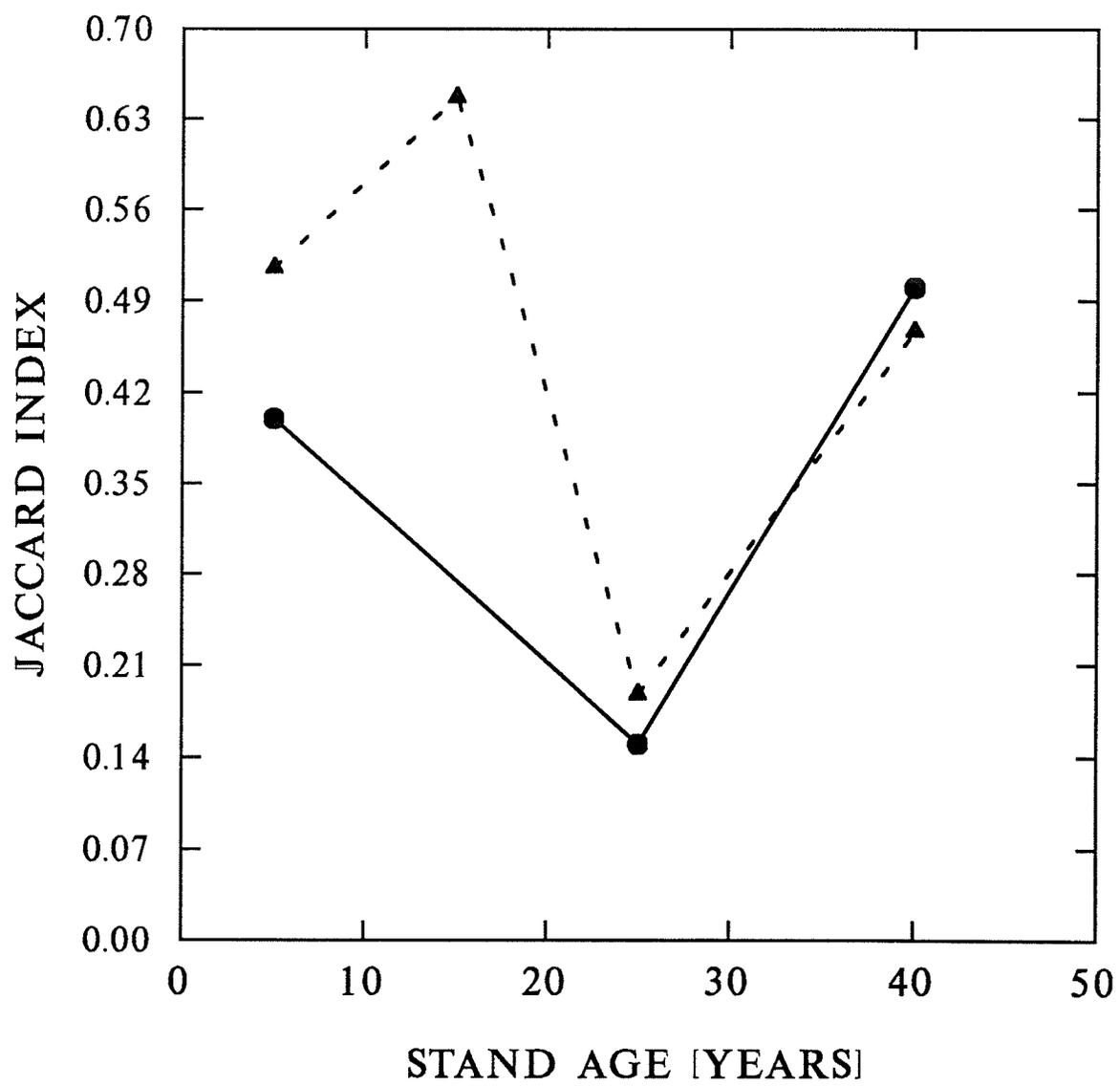


Figure 37. The effects of stand age on Kendall's τ index of similarity in planted (\blacktriangle ---) and naturally regenerated (\bullet —) sites in 1991.

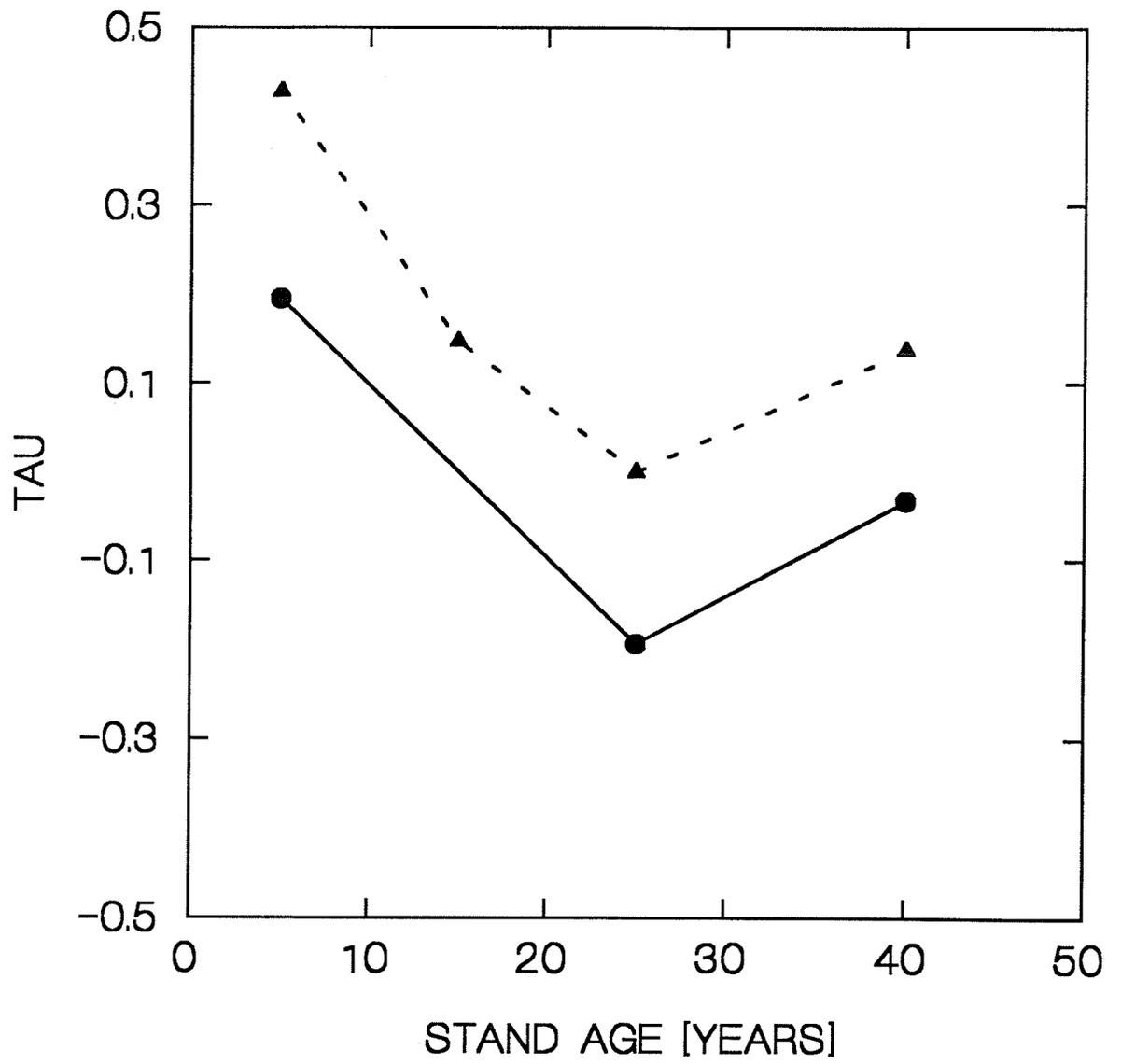


Figure 38. The effects of stand age on Kendall's τ index of similarity in planted (\blacktriangle ---) and naturally regenerated (\bullet —) sites in 1992.

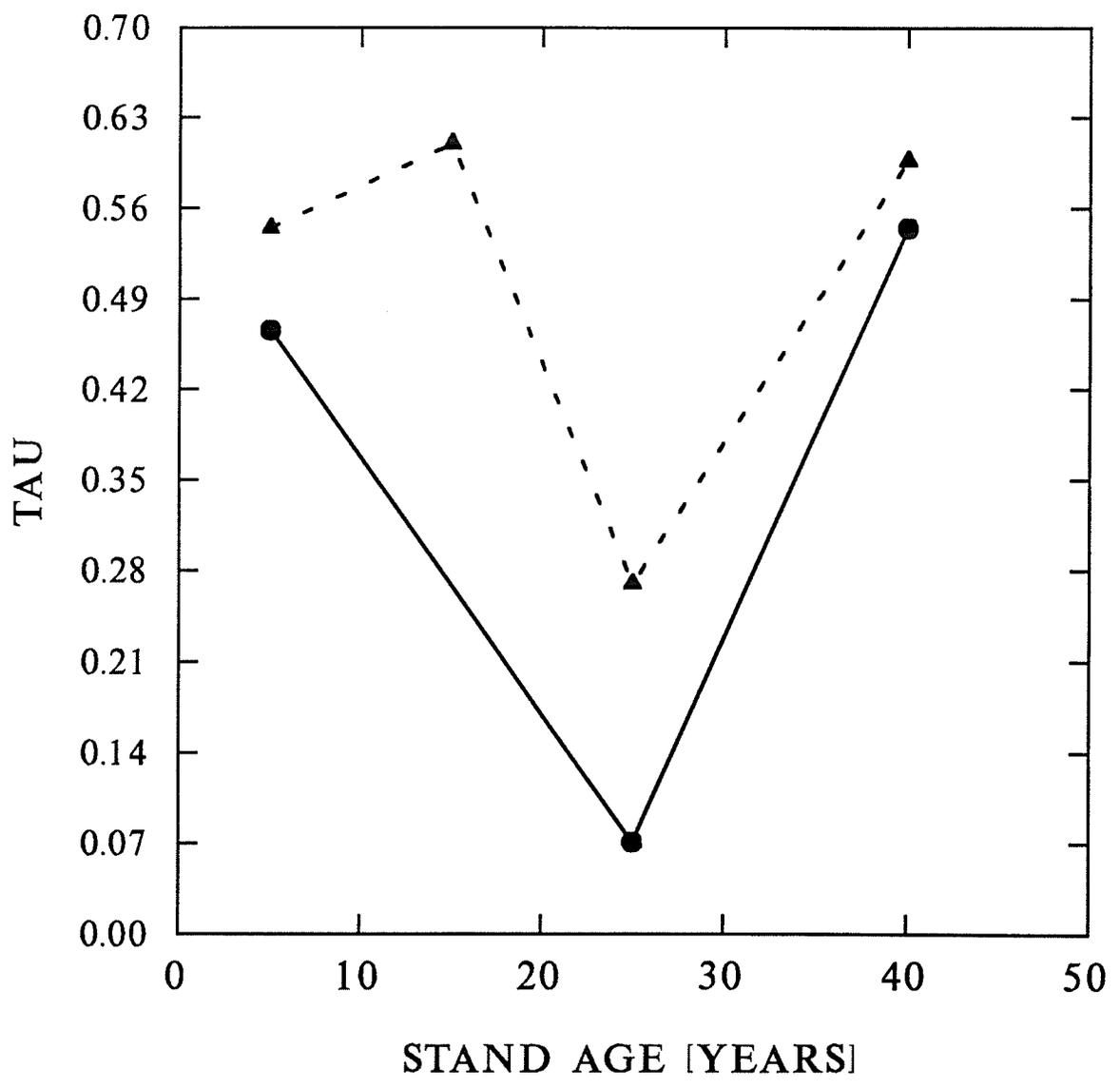


Figure 39.

1991 carabid data: CA ordination diagram with site scores (○) in which the size of the site symbols correspond to a rank of increasing light intensity and litter temperatures in the sites. Large symbols indicate high light intensity and litter temperatures. The carabid species scores (■). The first axis, (horizontal) has an eigenvalue of 0.474 = 42.1 % and the second axis, (vertical) has an eigenvalue of 0.198 = 17.6 %. The carabid species are: AP = *Agonum placidum*, ALAE = *Amara laevipennis*, ALAT = *Amara latior*, AO = *Amara obesa*, CA = *Calosoma calidum*, CI = *Calathus ingratus*, CS = *Carabus serratus*, CT = *Carabus taedatus*, DS = *Dicaelus sculptilis*, HF = *Harpalus fuliginosus*, HLA = *Harpalus laticeps*, HLE = *Harpalus lewisi*, PA = *Pterostichus adstrictus*, PP = *Pterostichus pensylvanicus*, SI = *Synuchus impunctatus*.

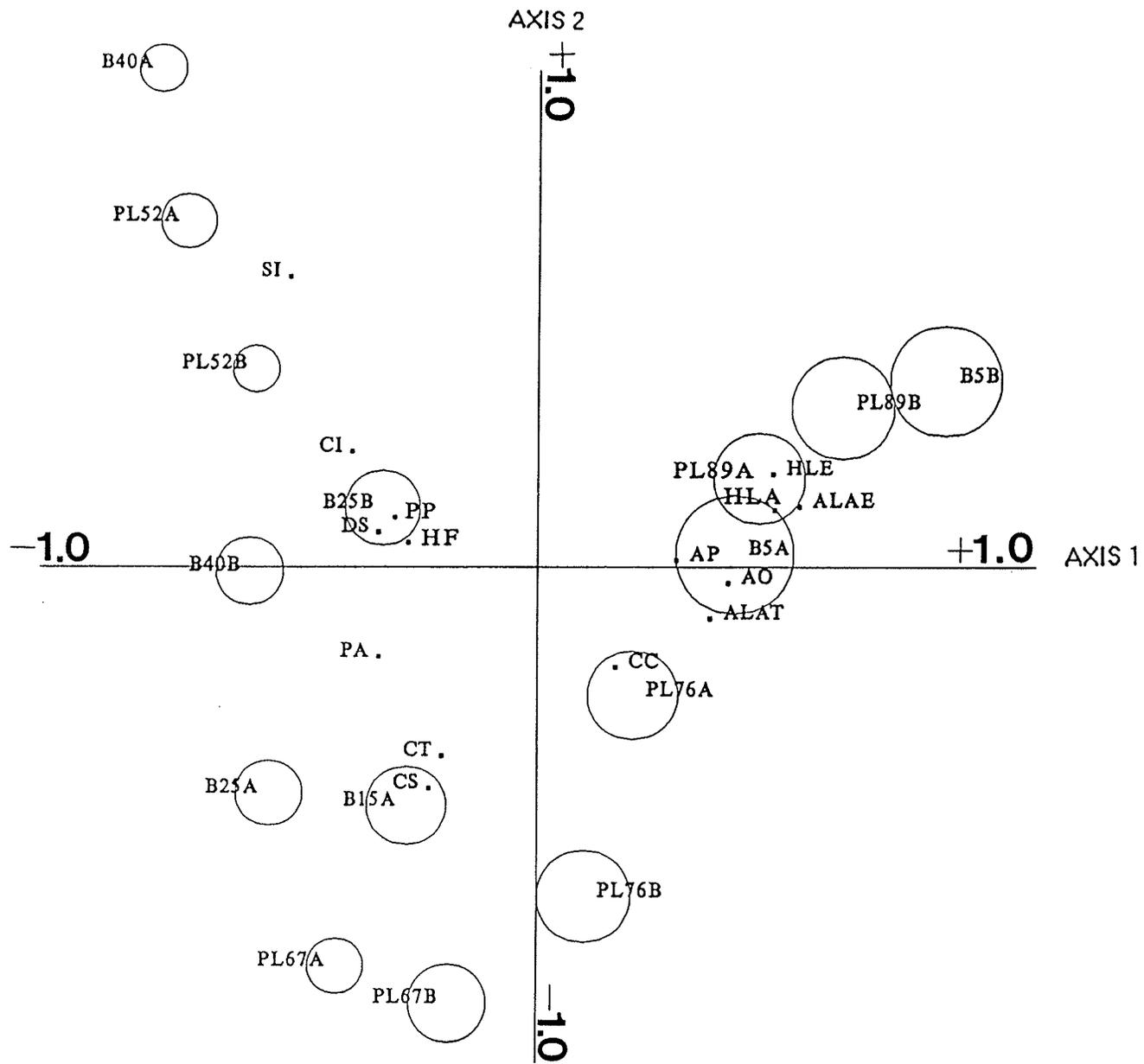


Figure 40. 1992 carabid data: CA ordination diagram with site scores (○) in which the size of the site symbols correspond to a rank of increasing light intensity and litter temperatures in the sites. Large symbols indicate high light intensity and litter temperatures. The carabid species scores (■). The first axis, (horizontal) has an eigenvalue of 0.469 = 52.5 % and the second axis, (vertical) has an eigenvalue of 0.155 = 17.2 %. The carabid species are: AP = *Agonum placidum*, ALAE = *Amara laevipennis*, ALAT = *Amara latior*, AO = *Amara obesa*, CA = *Calosoma calidum*, CI = *Calathus ingratus*, CS = *Carabus serratus*, CT = *Carabus taedatus*, DS = *Dicaelus sculptilis*, HF = *Harpalus fuliginosus*, HLA = *Harpalus laticeps*, HLE = *Harpalus lewisi*, PA = *Pterostichus adstrictus*, PP = *Pterostichus pensylvanicus*, SI = *Synuchus impunctatus*.

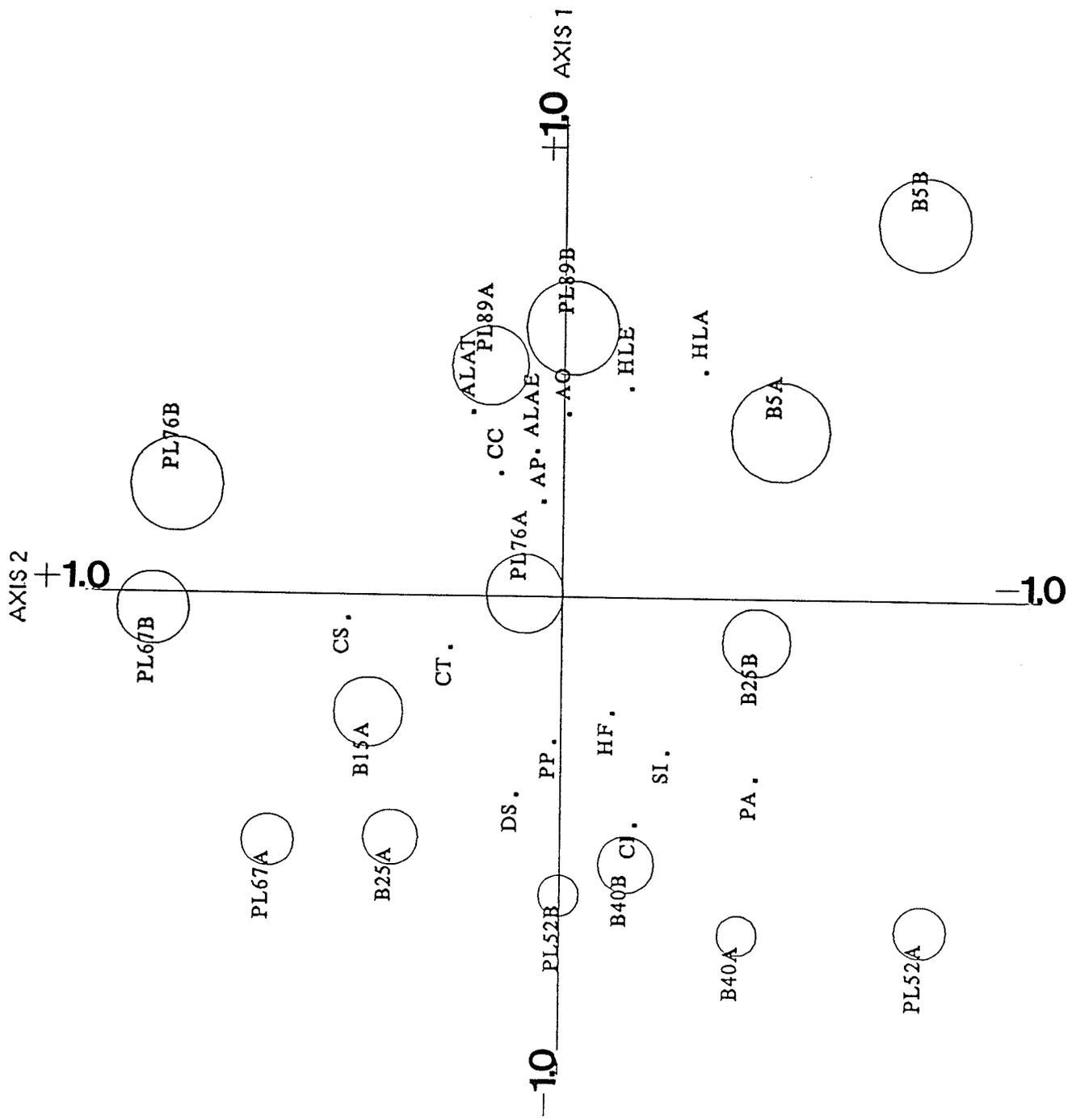


Figure 41.

1991 carabid and vegetation data: CCA ordination diagram with site scores (○), carabid species scores (■) and vegetation species (arrows). The size of the site symbols correspond to a rank of increasing light intensity and litter temperatures in the sites. Large symbols indicate high light intensity and litter temperatures. The first axis, (horizontal) has an eigenvalue of 0.420 = 37.3 % and the second axis, (vertical) has an eigenvalue of 0.152 = 13.5 %. The carabid species are: AP = *Agonum placidum*, ALAE = *Amara laevipennis*, ALAT = *Amara latior*, AO = *Amara obesa*, CA = *Calosoma calidum*, CI = *Calathus ingratus*, CS = *Carabus serratus*, CT = *Carabus taedatus*, DS = *Dicaelus sculptilis*, HF = *Harpalus fuliginosus*, HLA = *Harpalus laticeps*, HLE = *Harpalus lewisi*, PA = *Pterostichus adstrictus*, PP = *Pterostichus pensylvanicus*, SI = *Synuchus impunctatus*. The vegetation species are: CM = *Cladina mitis*, KG = *Koeleria gracilis*, and PS = *Pleurozium schreberi*.

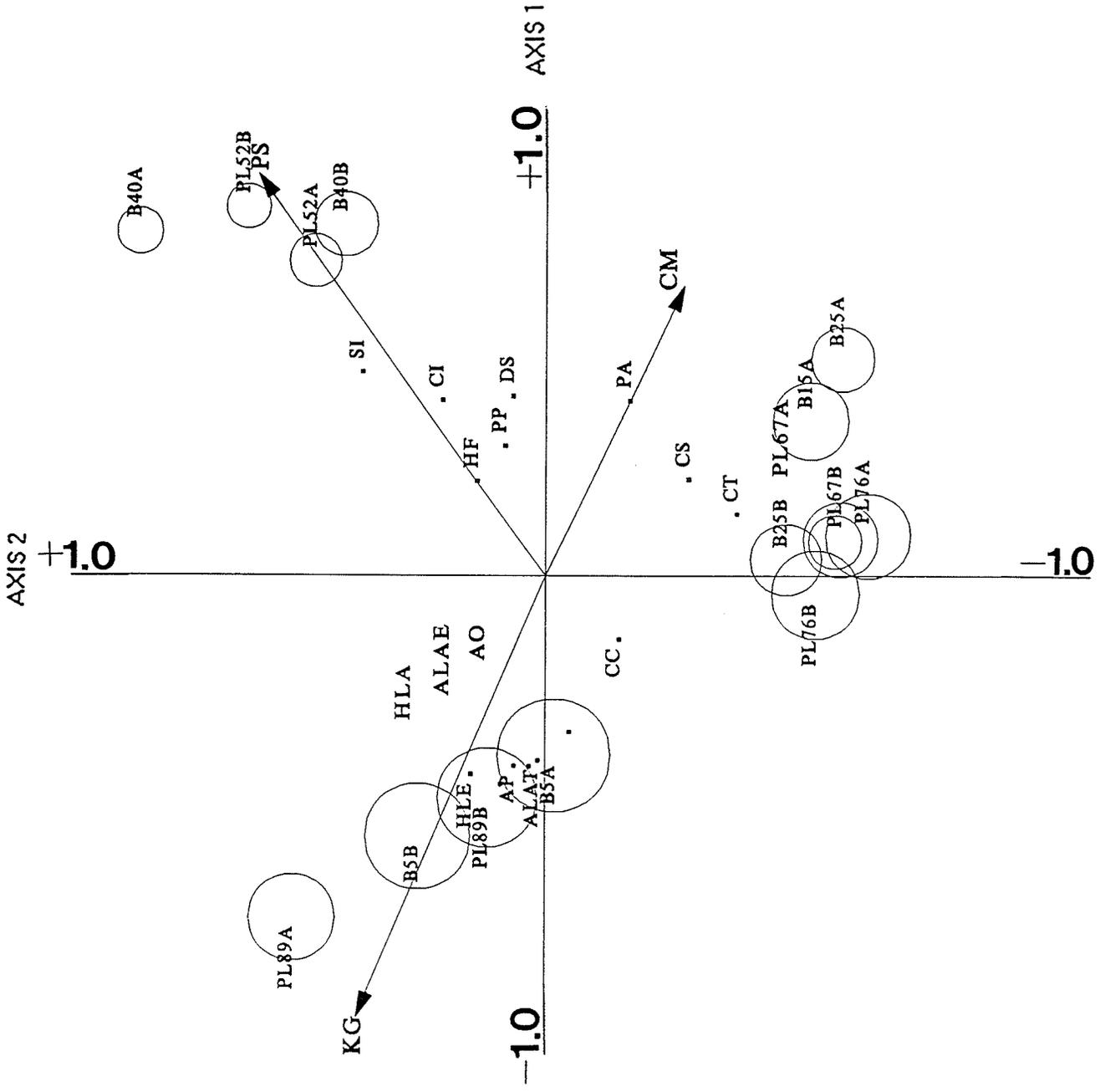


Figure 42.

1992 carabid and vegetation data: CCA ordination diagram with site scores (○), carabid species scores (■) and vegetation species (arrows). The size of the site symbols correspond to a rank of increasing light intensity and litter temperatures in the sites. Large symbols indicate high light intensity and litter temperatures. The first axis, (horizontal) with an eigenvalue of 0.431 = 48.0 %, second axis, (vertical) with an eigenvalue of 0.079 = 8.8 %. The carabid species are: AP = *Agonum placidum*, ALAE = *Amara laevipennis*, ALAT = *Amara latior*, AO = *Amara obesa*, CA = *Calosoma calidum*, CI = *Calathus ingratus*, CS = *Carabus serratus*, CT = *Carabus taedatus*, DS = *Dicaelus sculptilis*, HF = *Harpalus fuliginosus*, HLA = *Harpalus laticeps*, HLE = *Harpalus lewisi*, PA = *Pterostichus adstrictus*, PP = *Pterostichus pensylvanicus*, SI = *Synuchus impunctatus*. The vegetation species are: CM = *Cladina mitis*, KG = *Koeleria gracilis*, and PS = *Pleurozium schreberi*.

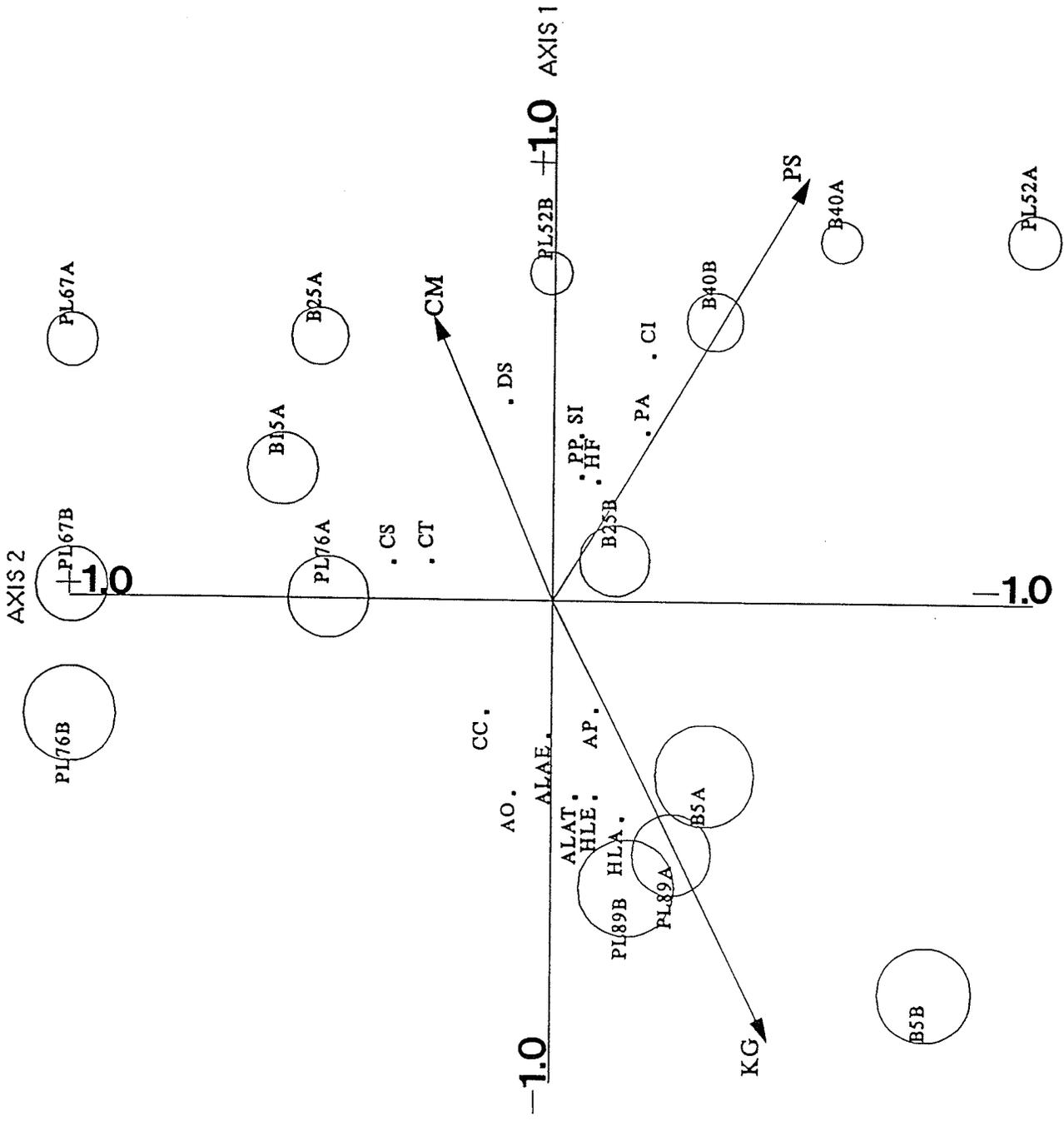


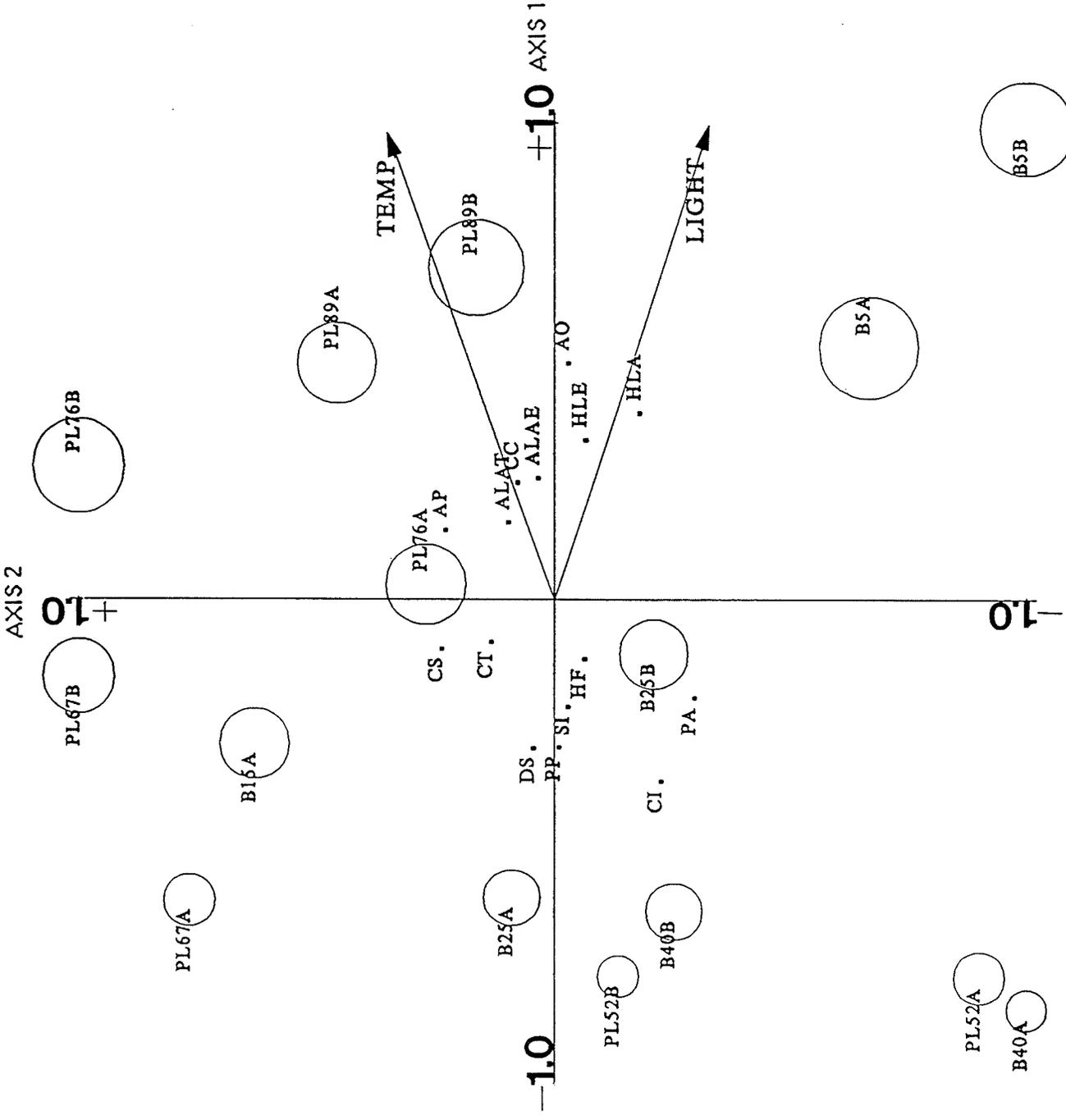
Figure 43.

1991 carabid and environmental data: CCA ordination diagram with site scores (○), carabid species scores (■) and environmental variables (arrows). The size of the site symbols correspond to a rank of increasing light intensity and litter temperatures in the sites. Large symbols indicate high light intensity and litter temperatures. The first axis, (horizontal) has an eigenvalue of 0.321 = 28.5 % and the second axis, (vertical) has an eigenvalue of 0.048 = 4.3 %. The carabid species are: AP = *Agonum placidum*, ALAE = *Amara laevipennis*, ALAT = *Amara latior*, AO = *Amara obesa*, CA = *Calosoma calidum*, CI = *Calathus ingratus*, CS = *Carabus serratus*, CT = *Carabus taedatus*, DS = *Dicaelus sculptilis*, HF = *Harpalus fuliginosus*, HLA = *Harpalus laticeps*, HLE = *Harpalus lewisi*, PA = *Pterostichus adstrictus*, PP = *Pterostichus pensylvanicus*, SI = *Synuchus impunctatus*. The environmental variables are: TEMP = litter base temperature difference and LIGHT = light intensity at ground level.

Figure 44.

1992 carabid and environmental data: CCA ordination diagram with site scores (○), carabid species scores (■) and environmental variables (arrows) in which the size of the site symbols correspond to a rank of increasing light intensity and litter temperatures in the sites. Large symbols indicate high light intensity and litter temperatures. The first axis, (horizontal) has an eigenvalue of 0.305 = 34.0 % and the second axis, (vertical) has an eigenvalue of 0.060 = 6.7 %. The carabid species are: AP = *Agonum placidum*, ALAE = *Amara laevipennis*, ALAT = *Amara latior*, AO = *Amara obesa*, CA = *Calosoma calidum*, CI = *Calathus ingratus*, CS = *Carabus serratus*, CT = *Carabus taedatus*, DS = *Dicaelus sculptilis*, HF = *Harpalus fuliginosus*, HLA = *Harpalus laticeps*, HLE = *Harpalus lewisi*, PA = *Pterostichus adstrictus*, PP = *Pterostichus pensylvanicus*, SI = *Synuchus impunctatus*. The environmental variables are: TEMP = litter base temperature difference and LIGHT = light intensity at ground level.

AXIS 2



CHAPTER V

Discussion

Section A - Planting and Age-Related Effects on Habitat Characteristics.

The habitat characteristics of the different regeneration types were very similar with respect to vegetation composition, light intensity, and soil and litter temperatures. It would appear that the younger sites exhibited greater vegetational differences between planted and naturally regenerated sites than the older sites. The greatest difference between the 5 year old planted sites and the 5 year old natural sites was the amount of tree debris (slash), remaining in the sites during the regeneration process. In the 5 year old natural sites, a large amount of slash was present and appeared likely to be a dominant component of the site structure composition for some time to come. In planted stands, a large proportion of the slash was removed prior to planting (David Ip, pers. commun.). The soil surface topography in the 5 year old planted sites also had a more uniform relief than the corresponding natural sites. Levelling often occurs during the scarification process prior to planting (Heliovaara and Varsonen, 1984; Burger and Pritchett, 1988).

The major differences in habitat characteristics were

between the different age classes. The abiotic environmental conditions in the sites, such as temperature and light intensity generally decreased with the age of the sites. As canopy develops in the older sites, the shade produced reduces daytime ground temperatures, which probably results in reduced evaporation and transpiration of the soil and plant water (Watterston, 1967). This in turn promotes the succession of plants better adapted to the cooler and moister conditions of forest habitats (Mueller-Dombois, 1964). Over time, a deep organic layer develops in the older sites which tends to boost further growth of cool-adapted species, which assist in the perpetuation and maintenance of a cool-moist habitat (Rowe, 1956).

The biotic environmental characteristics of the sites were also influenced by the age of the stands. In terms of the shrubs, only small changes in the overall abundance and composition were observed in the sites of the different age classes. The 5 year old sites were dominated by a single family, Rosaceae, while in the 15 year old sites, the same Rosaceae shrubs were present, but in addition, shrubs from the *Vaccinium* species were an important component. In the 25 and 40 year old sites, the final mixture of shrubs included all of the previous, plus species from the family Caprifoliaceae. It appears that the number of shrub species generally increased with the age of the sites until it reached a plateau between the 25 and 40 year old sites.

This is concordant with the successional theory that suggests a forest ecosystem species richness generally reaches a plateau during what is known as the shrub phase, 15-20 years after the initial disturbance (Whittaker, 1972). At ground level, the changes in dominant ground cover were more profound than at the shrub level. Species common in the younger sites did not occur or were noticeably less abundant in the older sites. The general trend was from:

- 1) Grass dominated habitat in the 5 year old sites.
- 2) Grass, ericaceous, and lichen dominated habitats in the 15 and 25 year old sites.
- 3) Moss, dominated habitat in the 40 year old sites.

Rowe (1956) found that the major trend in the vegetation succession of the Boreal forest is toward plants that prefer cool, moist habitats (Rowe, 1956). The ground vegetation and its microclimate, are affected by the maturation of the stand (Oksanen, 1986). Ultimately, surface dwelling organisms such as carabid beetles and phalangids that utilize the ground vegetation as habitat, may also be affected by such developments (Thiele, 1977; Heliovaara and Varsonen, 1984).

Section B - Planting and Age Related Effects on Carabid Species Composition.

The carabid species composition in the planted and naturally regenerated sites was very similar with the

exception of a significantly greater number of *H. laticeps* collected in the 5 year old natural sites than in the 5 year old plantations. The connection between *H. laticeps* and recently burned areas is not known. It would appear that this species is primarily attracted to the open habitats with sparse vegetation (Larochelle, 1975). A second factor influencing the distribution of *H. laticeps* may be the abundance of the charred and decaying woody debris which is typical of forest stands after a fire (Holliday, 1984). The advantage of inhabiting areas after a fire is that *H. laticeps* has the appearance of charred wood which would provide camouflage during daylight (Holliday, 1984; 1992). Decaying wood in the burn sites may also prove to be a direct or indirect food source for these carabid beetles. The greater numbers of *H. laticeps* collected in 1992 as opposed to 1991 be associated with increasing numbers of fallen trees. In the fall of 1991 over 50 % of the dead standing trees in B5A and B5B had fallen since the beginning of the study. There was therefore an increased amount of charred debris at ground level in the sites to attract greater numbers of *H. laticeps* in 1992.

The effect of age of the stand on the carabid species composition was evident. By extrapolation from the chronosequence sites to succession, it would appear that there was a species turn-over from macropterous carabid species that invade the early stages of succession when grasses dominated

(5 year old sites) to brachypterous carabid species that dominate the lichens phase of forest successional (15 and 25 year old sites). In many cases, some of the open habitat species, such as *A. latior*, *A. obesa*, and *C. calidum*, continued to be collected in relatively high numbers in the 15 year age class, especially in sites such as PL76B with a high percent cover of *K. gracilis*. These species were capable of co-existing with the *Carabus* species, which were collected in these sites at relatively high frequency. The pattern of catches does indicate that the two groups of species can occur together, with small changes in catching frequency. This would suggest that species turn-over is gradual and that as long as the area retains a significant proportion of suitable habitat conditions in close proximity, carabid species will occasionally be collected in areas which otherwise could be considered an atypical. (den Boer, 1986).

There was little turn-over in carabid species between the intermediate age class and the 40 year old sites. There was however a difference in the relative abundance of the species rather than a difference in species. For example, the number of *C. taedatus* decrease in the 40 year old sites compared to the 25 year old sites. Cool-adapted species such *P. pensylvanicus* (Lindroth, 1966) increased to the point where it was the dominant carabid species in the old forest sites (Table. 7). *C. taedatus* probably decreased in

the 40 year old sites due to a reduction of potential food sources. As a conifer stand matures, changes to the habitat occur, such as the dominance of bryophyte vegetation over forbs and grasses, in conjunction with the suppression of the deciduous shrub layer (Mueller-Dombois, 1964). This may cause a reduction in the number of Lepidoptera, which are eaten by *C. taedatus* (Lindroth, 1966; Goulet, 1974). In regard to *P. pensylvanicus*, this cool-adapted species' distribution is strongly influenced by climatic conditions (Lindroth, 1966). As the mean soil and litter temperature decreased with the age of the stand the number of *P. pensylvanicus* increased.

The typical successional sequence of carabid species turn-over in forested habitat after a disturbance (eg. fire) is from the open habitat, macropterous r-strategist to the flightless, mature forest k-strategist (Holliday, 1991). In this study the number of macropterous carabid species, such as *A. placidum*, *C. calidum*, the *Amara* and *Harpalus* species, with the exception of *H. fuliginosus*, have decreased with increasing age of the sites. *H. fuliginosus* is an open-habitat species which typically prefers to occupy sandy soil areas with sparse vegetation (Lindroth, 1968). *H. fuliginosus* tends to occupy all sites regardless of the dominant vegetation cover as long as the primary component in the soil make-up is sand (Szyszko, 1974). Thus, the behaviour of *H. fuliginosus* would appear to be similar to

that of *P. pensylvanicus*, in that despite desirable vegetative cover, it was more likely to select a habitat based on abiotic rather than biotic factors.

Section C - Controlling Factors Affecting Carabid Beetle α and β Diversity.

It would appear that, at the stand level, the carabid α diversity of planted and natural stands were not significantly different. Niemelä et. al. (1988) in Finland, and Sustek (1984) in Poland, found similar results when they compared α diversity of managed forest to old, natural pine forests. Carabid α diversity, using the log series α , was highest in the intermediate sites. Holliday (1992), in a study of post-fire regeneration of boreal forest and Niemelä et. al. (1992) in a study of climax natural taiga forest, have both indicated that carabid beetle α diversity is positively correlated to habitat heterogeneity. The dominant vegetation species in the intermediate sites was a mixture of grasses, ericaceous plants and lichens. These sites contained species of carabids that occurred in grassy habitats, such as *A. obesa* and *C. calidum* as well as species that typically occurred in open forest environments, such as *C. taedatus* and *C. serratus*. There were also some of the more common mature forest species, such as *P. pensylvanicus* and *D. sculptilis* (Fig. 33, 34; Table 2, 7). It does appear however that natural sites may maintain their peak in α

diversity longer than planted stands. Natural stands tend to have a greater number of open areas and dense clusters of trees than do uniform plantations (Cayford and Bickerstaff, 1968). They are therefore more likely to maintain a higher percentage of open habitat species and forest species longer than planted stands. By the time the sites were 40 years old, the difference between the two types of regeneration techniques reached a stage where they were, once again, very similar (Fig. 33, 34). Ahlgren (1974) in northeastern Minnesota, noted that jack pine and black spruce begin to show signs of natural thinning as early as 15 year after the fire. This is not surprising, because in a typical Boreal conifer succession, most of the major changes to the habitat occur in the first 40 years after the disturbance (Heinselman, 1981).

Carabid β diversity was also highest in the intermediate sites, with the 25 year old sites being the least similar in terms of their carabid species composition and abundance. The β diversity tended to be lower in planted stands, although this difference was not always significant. Again the uniformity of tree spacing and age within planted stands may result in greater habitat similarity in the planted sites (Cayford and Bickerstaff, 1968). This in turn may have caused a greater degree of similarity between the carabid beetle assemblages in planted stands. This could have a profound effect on the regional

or γ diversity of an area, in that an ecosystem consisting of many sites with lower β diversity, would be less diverse than the same ecosystem consisting of many sites with high β diversity.

CHAPTER VI

Synthesis

Carabid α and diversity in planted and natural sites were not significantly different, although it does appear that because of the greater degree of patchiness in the natural sites, the peak in carabid species diversity tended to be maintained longer. It would also appear that because of the lower habitat heterogeneity in planted stands, β diversity, in terms of carabid species relative abundance among site replicates was consistently lower in planted sites. In order to maintain high levels of ecological diversity in man-made forests it is important to preserve or create habitat heterogeneity in these areas (Haila, 1994). Planting a variety of species, leaving open areas and planting trees closer together would all contribute to habitat heterogeneity of an area, but may prove not to be practical or economical (Haila, 1994).

In a forest succession, carabid beetle species richness is most strongly influenced by the microclimatic conditions and plant ecology of the habitat. In this study, microclimatic conditions and vegetation succession were significantly influenced by stand age and not by the type of regeneration. Niemelä et. al. (1993), indicated that habitat heterogeneity represented by stands of differing

ages influences carabid species richness. Therefore, mixing small plantations of different age would contribute to the habitat heterogeneity in monoculture forested areas.

It is important to determine the specific relationship between the vegetation and the presence of certain carabid species. Do the plants simply function as shelter for the carabid beetles, were they acting as a direct food source, or both? It is most likely that the role of vegetation as a direct food source decreases with succession because of the decreasing occurrence of herbaceous carabid species in forest habitats (Thiele, 1977).

Little research has been devoted to understanding the feeding behaviour of forest carabid species and the research on agricultural carabids has been typically in the form of surveys of what carabid beetles would eat (Frank, 1971; Allen, 1979). These types of studies are often conducted in the laboratory and therefore may not be representative of natural conditions (Allen, 1979). More studies are needed on the feeding behaviour including studies of gut contents, and of general beetle ecology in order to understand the specific relationship between the carabids and their environment (Rushton et al., 1990; Maelfait and Desender, 1990).

More research is also needed on the understanding of carabid beetles species turnover in a forest succession. With the exception of Holliday (1992), the majority of the

studies record species turnover data for only a short period of time, typically less than five years. Holliday (1992) recorded carabid species composition in a black spruce forest succession over an 11 year period after a forest fire. Holliday found that the rate of species turnover is strongly influenced by habitat structure, which is assumed to be an index of niche space availability in the site. The question that still remains to be answered is what biotic and abiotic factors are involved in the formation of a niche space? Longterm studies which examine changes in carabid species composition over time are needed to identify the important and measurable factors influencing species turnover in a "true" as opposed to a chrono-sequence succession.

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Appendix I. Species list of vegetation in the sites with percent cover greater than one percent.

	5 year old		15 year old				25 year old				40 year old				SUM	
	Natural		Planted		Natural		Planted		Natural		Planted					
	B05A	B05B	PL89A	PL89B	B15A	PL76A	PL76B	B25A	B25B	PL67A	PL67B	B40A	B40B	PL52A		PL52B
GROUND VEGETATION																
<i>Amelanchier alnifolia</i>	0	0	<1	0	0	0	3	<1	0	0	0	0	0	0	<1	3
<i>Amorpha canescens</i>	0	0	0	0	0	0	9	0	<1	0	0	0	0	0	0	9
<i>Andropogon gerardi</i>	14	11	18	7	5	9	22	8	24	8	8	<1	3	6	5	148
<i>Anemone patens</i>	0	0	0	1	2	0	<1	1	1	<1	<1	0	1	<1	0	6
<i>Anemone quinquefolia</i>	0	0	0	0	2	<1	0	1	1	3	1	1	2	0	5	16
<i>Antennaria</i> spp.	0	0	0	0	0	<1	0	2	1	0	<1	<1	4	0	<1	7
<i>Apocynum androsaemifolium</i>	0	0	0	1	0	0	0	0	0	0	0	0	<1	0	0	1
<i>Aralia nudicaulis</i>	0	0	0	0	0	0	0	0	0	0	<1	2	0	0	0	2
<i>Arctostaphylos uva-ursi</i>	2	15	6	5	12	14	4	6	20	2	5	<1	11	5	4	111
<i>Aster laevis</i>	2	0	1	4	0	<1	2	1	0	0	<1	0	0	1	<1	11
<i>Carex</i> spp.	<1	1	2	0	0	0	<1	0	1	<1	<1	<1	1	0	<1	5
<i>Ceanothus ovatus</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
<i>Cladina mitis</i>	<1	0	0	0	7	3	<1	10	<1	<1	0	<1	4	2	3	29
<i>Cladina rangiferina</i>	0	0	0	0	7	15	1	10	2	<1	<1	<1	5	4	3	47
<i>Cornus canadensis</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
<i>Cyperus</i> spp.	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	6
<i>Dicranum polysetum</i>	1	0	0	0	<1	<1	<1	<1	1	1	0	<1	2	0	1	6

Appendix I. (continued)

	5 year old		15 year old				25 year old				40 year old				SUM	
	Natural		Planted		Natural		Planted		Natural		Planted					
	B05A	B05B	PL89A	PL89B	B15A	PL76A	PL76B	B25A	B25B	PL67A	PL67B	B40A	B40B	PL52A		PL52B
<i>Epilobium angustifolium</i>	0	0	0	0	0	0	0	0	0	0	0	2	0	0	<1	2
<i>Equisetum hyemale</i>	0	0	0	0	<1	3	0	0	0	0	0	0	1	0	<1	4
<i>Fragaria virginiana</i>	0	0	<1	0	0	<1	2	0	1	1	1	0	1	<1	<1	6
<i>Galium boreale</i>	2	0	2	0	3	2	0	2	0	3	0	2	0	0	1	17
<i>Gaultheria procumbens</i>	<1	<1	0	0	<1	0	0	2	0	0	0	<1	2	0	0	4
<i>Heuchera richardsonii</i>	2	0	0	0	<1	0	0	0	0	0	<1	<1	0	0	0	2
<i>Koeleria gracilis</i>	5	7	9	6	<1	<1	1	<1	<1	<1	0	0	<1	0	0	28
<i>Lathyrus</i> spp.	<1	0	<1	0	0	0	<1	<1	1	1	<1	1	0	0	1	4
<i>Linnaea borealis</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
<i>Lithospermum canescens</i>	3	<1	<1	0	1	0	<1	1	<1	<1	<1	<1	1	0	0	6
<i>Lonicera</i> spp.	0	0	0	<1	0	0	0	0	0	0	1	0	0	0	<1	1
<i>Maianthemum canadense</i>	1	<1	<1	<1	2	<1	<1	4	1	0	7	11	11	8	9	54
<i>Oryzopsis</i> spp.	0	0	0	0	5	3	<1	3	<1	2	2	7	3	5	2	32
<i>Pleurozium schreberi</i>	0	<1	0	0	2	0	0	2	<1	1	1	19	15	15	17	72
<i>Poa palustris</i>	0	0	0	1	0	0	1	0	<1	0	0	0	0	0	0	2
<i>Polygonum convolvulus</i>	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2
<i>Prunus pensylvanica</i>	0	1	0	0	<1	0	0	0	0	0	0	0	0	0	0	1
<i>Prunus pumila</i>	2	1	2	0	0	0	1	0	0	2	0	<1	1	<1	0	9

Appendix I. (continued)

	5 year old		15 year old				25 year old				40 year old				SUM	
	Natural		Planted		Natural		Planted		Natural		Planted					
	B05A	B05B	PL89A	PL89B	B15A	PL76A	PL76B	B25A	B25B	PL67A	PL67B	B40A	B40B	PL52A		PL52B
<i>Prunus virginiana</i>	0	0	2	<1	0	1	2	0	0	0	0	0	0	0	1	6
<i>Pteridium aquilinum</i>	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
<i>Rhus radicans</i>	0	0	0	0	0	0	0	0	<1	5	0	0	0	0	0	5
<i>Rosa</i> spp.	1	2	2	1	<1	1	1	0	<1	0	5	3	<1	<1	<1	16
<i>Selaginella rupestris</i>	0	0	0	0	<1	<1	1	0	0	0	0	0	0	0	0	1
<i>Smilacina trifolia</i>	0	0	2	0	<1	0	0	0	0	<1	0	0	1	0	0	3
<i>Solidago hispida</i>	0	2	<1	<1	0	1	0	0	0	0	0	0	0	0	0	3
<i>Spireae alba</i>	<1	2	4	0	0	2	0	0	0	0	0	<1	0	0	0	8
<i>Symphoricarpos</i> spp.	<1	0	0	0	1	0	4	0	0	11	0	0	0	<1	1	17
<i>Vaccinium</i> spp.	3	5	4	4	19	16	2	10	6	1	18	5	21	8	11	133
SITE TOTALS	384	272	200	135	1706	1294	1101	1467	1158	2957	2308	2197	1350	2088	1720	20337
SHRUB VEGETATION																
<i>Alnus rugosa</i>	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	7
<i>Amelanchier alnifolia</i>	1	0	<1	<1	1	2	2	<1	5	15	25	5	1	7	3	67
<i>Apocynum androsaemifolium</i>	0	<1	<1	<1	0	0	0	0	<1	<1	2	0	0	3	0	5
<i>Ceanothus ovatus</i>	<1	0	0	0	<1	0	4	4	0	4	5	2	1	1	<1	21

Appendix I. (continued)

	5 year old		15 year old				25 year old				40 year old				SUM	
	Natural		Planted		Natural		Planted		Natural		Planted					
	B05A	B05B	PL89A	PL89B	B15A	PL76A	PL76B	B25A	B25B	PL67A	PL67B	B40A	B40B	PL52A		PL52B
<i>Cornus stolonifera</i>	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	3
<i>Corylus cornuta</i>	0	0	0	0	0	0	0	0	0	0	3	7	0	0	0	10
<i>Lonicera</i> spp.	<1	0	0	0	0	0	0	0	0	14	2	0	0	12	0	28
<i>Populus tremuloides</i>	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
<i>Prunus pensylvanica</i>	5	1	0	0	0	0	0	3	0	4	5	2	1	1	<1	22
<i>Prunus virginiana</i>	0	0	<1	<1	1	3	12	0	5	2	8	1	2	10	3	47
<i>Rose</i> spp.	2	<1	0	1	1	<1	<1	1	<1	14	5	6	2	7	3	42
<i>Salix</i> spp.	3	4	0	0	0	0	0	0	0	2	0	0	0	<1	0	9
<i>Spirea alba</i>	0	2	2	2	0	<1	0	3	0	0	0	<1	0	<1	<1	9
<i>Symphoricarpos</i> spp.	0	0	0	0	0	0	2	0	0	24	5	<1	2	7	8	48
<i>Vaccinium</i> spp.	0	0	0	0	12	0	<1	0	0	3	0	0	5	0	<1	20
SITE TOTAL	17	7	2	3	15	5	20	11	10	82	60	33	14	48	17	344

Appendix I. (continued)

	5 year old		15 year old				25 year old				40 year old				SUM	
	Natural		Planted		Natural		Planted		Natural		Planted					
	B05A	B05B	PL89A	PL89B	B15A	PL76A	PL76B	B25A	B25B	PL67A	PL67B	B40A	B40B	PL52A		PL52B
TREE VEGETATION																
<i>Pinus banksiana</i>	0	0	0	0	66	49	34	62	48	74	52	75	45	61	69	635
<i>Populus tremuloides</i>	0	0	0	0	0	4	0	0	0	0	<1	7	0	0	0	11
<i>Quercus macrocarpa</i>	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	2
SITE TOTAL	0	0	0	0	66	53	34	62	48	74	54	82	45	61	69	648

Appendix II. Species list of carabid beetles collected in 1991.

	5 year old		15 year old				25 year old				40 year old		SUM			
	Natural		Planted		Natural		Planted		Natural		Planted					
	B05A	B05B	PL89A	PL89B	B15A	PL76A	PL76B	B25A	B25B	PL67A	PL67B	B40A		B40B	PL52A	PL52B
CARABID SPECIES																
Agonum cupreum Dejean	0	0	2	0	0	1	0	0	1	0	0	0	0	0	0	4
Agonum decentis Say	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Agonum placidum Say	0	3	10	0	0	0	0	0	2	0	2	0	0	0	0	17
Agonum retractum Leconte	0	0	0	0	0	0	0	0	0	0	3	9	0	4	0	16
Agonum trigeminum Lindroth	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Amara carinata Leconte	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2
Amara laevipennis Kirby	1	4	1	8	0	1	1	0	0	0	0	0	0	0	0	16
Amara latior Kirby	0	1	171	17	0	1	21	0	0	0	3	0	0	0	0	214

Appendix II. (continued)

	5 year old		15 year old			25 year old			40 year old			SUM				
	Natural		Planted		Natural		Planted		Natural		Planted					
	B05A	B05B	PL89A	PL89B	B15A	PL76A	PL76B	B25A	B25B	PL67A	PL67B		B40A	B40B	PL52A	PL52B
<i>Amara obesa</i>	54	11	47	22	2	11	25	0	0	0	0	0	0	0	0	172
Say																
<i>Badister neopulchellus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
Lindroth																
<i>Calosoma calidum</i>	8	3	7	1	7	1	8	1	0	0	2	0	1	0	0	39
Fabricius																
<i>Calathus ingratus</i>	2	0	2	2	1	0	1	8	0	0	1	12	21	68	0	118
Dejean																
<i>Calosoma lepidum</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Leconte																
<i>Carabus serratus</i>	1	0	0	0	0	0	9	2	0	2	2	0	2	0	1	19
Say																
<i>Carabus taedatus</i>	7	0	1	0	16	3	64	17	30	14	68	0	5	2	0	227
Fabricius																
<i>Chlaenius sericeus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Forster																

Appendix II. (continued)

	5 year old		15 year old				25 year old				40 year old				SUM	
	Natural		Planted		Natural		Planted		Natural		Planted					
	B05A	B05B	PL89A	PL89B	B15A	PL76A	PL76B	B25A	B25B	PL67A	PL67B	B40A	B40B	PL52A		PL52B
<i>Cymindis borealis</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Leconte																
<i>Cymindis cribricollis</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Dejean																
<i>Dicaelus sculptilis</i>	1	1	0	1	9	0	4	4	1	0	0	3	16	4	5	49
Say																
<i>Euryderus grossus</i>	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	3
Say																
<i>Harpalus erraticus</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Say																
<i>Harpalus fuliginosus</i>	0	0	5	2	0	0	0	1	2	4	0	0	11	3	2	30
Duftschmid																
<i>Harpalus funerarius</i>	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	3
Csiki																
<i>Harpalus herbivigous</i>	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	4
Say																

Appendix II. (continued)

	5 year old		15 year old				25 year old				40 year old				SUM	
	Natural		Planted		Natural		Planted		Natural		Planted					
	B05A	B05B	PL89A	PL89B	B15A	PL76A	PL76B	B25A	B25B	PL67A	PL67B	B40A	B40B	PL52A		PL52B
Harpalus laticeps Leconte	81	71	79	30	0	2	4	0	1	0	0	0	0	0	0	268
Harpalus lewisi Leconte	32	225	33	42	0	1	0	0	1	1	0	0	0	0	1	336
Harpalus ochropus Kirby	0	0	1	0	1	0	0	0	1	0	0	0	2	0	0	5
Harpalus opacipennis Haldeman	0	0	16	6	0	0	7	0	0	0	0	0	0	0	0	29
Harpalus pensylvanicus DeGeer	9	8	12	0	2	1	3	2	0	1	1	1	1	1	2	44
Harpalus uteanus Casey	0	0	45	0	0	0	1	0	0	0	0	0	0	0	0	46
Notiophilus semistriatus Say	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Pasimachus elongatus Leconte	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	4

Appendix II. (continued)

	5 year old		15 year old				25 year old				40 year old		SUM			
	Natural		Planted		Natural		Planted		Natural		Planted					
	B05A	B05B	PL89A	PL89B	B15A	PL76A	PL76B	B25A	B25B	PL67A	PL67B	B40A		B40B	PL52A	PL52B
<i>Patrobus foveocollis</i> Eschscholtz	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
<i>Pterostichus adstrictus</i> Edstrictus	0	0	0	0	0	5	1	2	0	3	0	0	1	1	4	17
<i>Pterostichus caudicalis</i> Say	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Pterostichus lucublandus</i> Say	2	0	11	4	0	0	1	0	0	0	0	0	0	0	0	18
<i>Pterostichus pensylvanicus</i> Leconte	10	0	16	1	6	7	4	5	7	3	8	59	43	72	14	255
<i>Sphaeroderus lecontei</i> Dejean	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	10
<i>Synuchus impunctatus</i> Say	0	0	1	0	0	0	0	0	5	0	0	7	0	5	3	21
TOTAL	211	332	463	136	45	35	158	44	54	28	91	103	103	161	34	1998

Appendix III. Species list of carabid beetles collected in 1992.

	5 year old		15 year old				25 year old				40 year old				SUM	
	Natural		Planted		Natural		Planted		Natural		Planted					
	B05A	B05B	PL89A	PL89B	B15A	PL76A	PL76B	B25A	B25B	PL67A	PL67B	B40A	B40B	PL52A		PL52B
CARABID SPECIES																
Agonum cupripenne Say	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	3
Agonum cupreum Dejean	3	1	5	0	0	0	1	0	0	0	0	0	1	0	0	11
Agonum decentis Say	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2
Agonum placidum Say	2	0	15	5	1	0	3	0	1	0	0	0	1	1	0	29
Agonum retractum Leconte	0	0	0	0	0	0	0	0	0	0	1	7	0	2	2	12
Agonum trigeminum Lindroth	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	2
Amara laevipennis Kirby	5	1	6	25	1	2	2	0	0	0	1	0	1	0	0	44
Amara latior Kirby	4	3	502	60	0	1	15	0	0	0	14	0	0	0	0	599

Appendix III. (continued)

	5 year old		15 year old			25 year old			40 year old			SUM				
	Natural		Planted		Natural		Planted		Natural		Planted					
	B05A	B05B	PL89A	PL89B	B15A	PL76A	PL76B	B25A	B25B	PL67A	PL67B		B40A	B40B	PL52A	PL52B
<i>Amara obesa</i>	46	1	2	17	0	2	10	0	0	0	0	0	0	0	0	78
Say																
<i>Amara quenseli</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Schonher																
<i>Amara</i> spp.	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	2
<i>Anisodactylus merula</i>	0	14	6	1	0	0	0	0	0	0	0	0	0	0	0	21
Germar																
<i>Badister neopulchellus</i>	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	3
Lindroth																
<i>Calosoma calidum</i>	14	6	9	6	5	1	14	2	0	0	3	0	0	0	0	60
Fabricius																
<i>Calosoma frigidum</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Kirby																
<i>Calathus ingratus</i>	2	0	0	0	1	0	0	3	0	0	1	8	2	10	12	39
Dejean																
<i>Calosoma lepidum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2
Leconte																

Appendix III. (continued)

	5 year old		15 year old				25 year old				40 year old				SUM	
	Natural		Planted		Natural		Planted		Natural		Planted					
	B05A	B05B	PL89A	PL89B	B15A	PL76A	PL76B	B25A	B25B	PL67A	PL67B	B40A	B40B	PL52A		PL52B
Carabus serratus	0	0	1	1	2	1	5	2	0	0	6	0	0	0	2	20
Say																
Carabus taedatus	13	0	5	3	7	6	50	7	10	10	60	4	3	0	14	192
Fabricius																
Chlaenius tomentosus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Say																
Cymindis cribricollis	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	2
Dejean																
Dicaelus sculptilis	0	0	0	0	4	3	4	7	0	3	1	6	8	8	4	48
Say																
Euryderus grossus	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2
Say																
Harpalus egregius	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Casey																
Harpalus ellipsis	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Leconte																
Harpalus erraticus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Say																

Appendix III. (continued)

	5 year old		15 year old				25 year old				40 year old				SUM	
	Natural		Planted		Natural		Planted		Natural		Planted					
	B05A	B05B	PL89A	PL89B	B15A	PL76A	PL76B	B25A	B25B	PL67A	PL67B	B40A	B40B	PL52A		PL52B
Harpalus fuliginosus Duftschmid	4	2	1	2	5	0	1	3	0	2	0	2	9	16	4	51
Harpalus funerarius Csiki	3	0	1	1	0	0	0	0	0	0	0	0	0	0	0	5
Harpalus herbivigous Say	4	1	2	7	0	0	0	0	1	0	0	0	0	0	0	15
Harpalus indigens Casey	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Harpalus laticeps Leconte	168	212	46	46	0	3	0	0	3	0	0	0	0	0	0	478
Harpalus lewisi Leconte	46	179	53	55	1	1	3	0	2	0	2	0	0	0	0	342
Harpalus ochropus Kirby	0	0	3	1	0	0	0	0	1	0	0	1	1	0	0	7
Harpalus opacipennis Haldeman	2	0	4	6	0	0	0	0	0	0	0	0	0	0	0	12
Harpalus pensylvanicus DeGeer	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	4

Appendix III. (continued)

	5 year old		15 year old				25 year old				40 year old				SUM	
	Natural		Planted		Natural		Planted		Natural		Planted					
	B05A	B05B	PL89A	PL89B	B15A	PL76A	PL76B	B25A	B25B	PL67A	PL67B	B40A	B40B	PL52A		PL52B
Harpalus uteanus Casey	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Lebla pumila Dejean	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	2
Notiophilus semistriatus Say	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	2
Pasimachus elongatus Leconte	4	1	1	0	3	0	0	0	1	1	0	0	0	0	0	11
Pterostichus adstrictus Edstrictus	5	0	0	0	0	0	0	1	1	0	0	6	1	7	0	21
Pterostichus caudicalls Say	8	0	1	0	0	0	0	3	0	0	3	0	3	10	28	56
Pterostichus corvus Leconte	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pterostichus lucublandus Say	4	0	3	0	1	1	2	0	0	0	0	0	0	0	4	15
Pterostichus pensylvanicus Leconte	2	0	40	2	15	5	2	20	6	3	22	175	41	57	166	556

Appendix III. (continued)

	5 year old		15 year old				25 year old				40 year old				SUM	
	Natural		Planted		Natural		Planted		Natural		Planted					
	B05A	B05B	PL89A	PL89B	B15A	PL76A	PL76B	B25A	B25B	PL67A	PL67B	B40A	B40B	PL52A		PL52B
Sphaeroderus lecontei Dejean	0	0	0	0	0	1	0	0	0	0	0	2	0	1	0	4
Synuchus impunctatus Say	4	0	0	1	1	9	0	0	5	0	1	2	2	47	30	102
TOTAL	346	422	714	243	49	37	113	51	32	19	117	216	76	162	266	2863