ABIES LASIOCARPA ESTABLISHMENT OF SUBALPINE MEADOWS IN GLACIER NATIONAL PARK, MONTANA

A Dissertation

by

DIANNA ALSUP GIELSTRA

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2009

Major Subject: Geography

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Approved by:

Chair of Committee,	David M.Cairns
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ABSTRACT

Abies Lasiocarpa Establishment of Subalpine Meadows in Glacier National Park,
Montana. (May 2009)

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Chair of Advisory Committee: Dr. David M. Cairns

Studies on subalpine meadow invasions by *Abies lasiocarpa* (subalpine fir) in the Sierra Nevada and the Rocky Mountain Front Range are abundant, yet little is understood about this important process in the subalpine zone of Glacier National Park (GNP), Montana. This study evaluates spatiotemporal influences of climate on conifer invasions into subalpine meadows. Seedling establishment of *A. lasiocarpa* show both time and site dependent relationships to interannual variation in climate. Annual and seasonal climate models were constructed for temperature data, and these data were plotted against establishment. Regression analyses between climate data and conifer establishment were performed, and residual statistics show strong positive relationship between fall temperatures, Pacific Decadal Oscillation, and establishment. Correlations between climate and establishment showed significant positive trend between mean maximum temperature in fall, mean minimum temperature in fall and mean temperature in fall, and forest establishment. Both forest and meadow categories showed significant inverse trends in Pacific Decadal Oscillation and establishment. These data indicate warmer fall temperatures and alteration in snowpack lengthen the growing season and provide more moisture for meadows, a limiting resource, over the course of the growing season. The spatial pattern of tree invasion age and size structure were examined by drawing age class maps based on mapped and aged trees and by drawing size class maps based on mapped tree diameter. A multi-distance spatial analysis was used at tree scale to describe and understand these patterns. The tree age and size structure of *A. lasiocarpa* invasion showed differences over distance across meadow-forest boundaries attributed to strategies in competition and facilitation and variations in soil depth and topography. One of the small meadows in the study area was distributed in random patterns of tree spatial associations over the extent of the neighborhood. All other meadows showed clumped spatial associations for seedling establishment over the extent of the neighborhood. These meadows showed clustered spatial patterns of tree establishment, with larger trees and seedlings having strong spatial associations over range of the neighborhood at different scales indicating contagious dispersion. Observed spatial differences of conifer invasion in subalpine meadows shows instability in meadow/forest boundaries, and this instability is pronounced along the elevation gradient in erosional and depositional meadows. These results indicate a vegetation dynamic which may result in increased expansion of forests into meadows over time in periods of favorable climate.

DEDICATION

This manuscript is dedicated to all my family and friends. Your love, support, and companionship are what sustained me in this endeavor.

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NOMENCLATURE

AHCCD – Adjusted Historical Canadian Climate Data

AMLI –Anselin Local Morans I

ANCOVA – Analysis of Covariance

BBCI – Batcheler Bell Closest Individual

BD – Basal Diameter

CI-Closest Individual

DBH – Diameter at Breast Height

D- Depression

DEM – Digital Elevation Model

F – Flat

GIS – Geographic Information System

GPS – Global Positioning System

GNP – Glacier National Park

IPCC – Intergovernmental Panel on Climate Change

LF – Lower Forest

LM – Lower Meadow

PDO – Pacific Decadal Oscillation

MM – Mid Meadow

NCDC – National Climate Data Center

NN – Nearest Neighbor

NOAA – National Oceanic Atmospheric Administration

NPS – National Park Service

R – Rise

RNG - Random Number Generator

MMNT – Mean Minimum Temperature

MNMT – Mean Temperature

MMXT – Mean Maximum Temperature

UF – Upper Forest

UM – Upper Meadow

US-DOI – United States Department of Interior

USGS – United States Geological Survey

T_{avg} – Average Temperature

T_{min} – Minimum Temperature

T_{max} – Maximum Temperature

TPCP – Total Precipitation

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1. INTRODUCTION

1.1 Problem Statement

There is a need for scientists to understand the relationship between climate change and its impacts on ecological systems. Climate trends indicate a 2° to 5º C increase in global temperatures within the next century, and plant species may shift in their response to this alteration of climate (IPCC 1992, IPCC 2007). Changes in vegetation patterns in montane regions may be responding to these changes in climate. An example of vegetation response to climate is seedling incursions into treeline ecotones, such as subalpine forest-meadows (Laroque et al. 2000). As plant species change on a landscape, so does landscape structure and function (Malanson 1995).

Montane regions are sensitive systems to changes in climate (Peterson 1994). Subalpine meadows are maintained through a variety of factors, but are predominantly maintained via climate or through interactions of climate and fire (Agee and Smith 1984, Butler 1986, Lepofsky et al. 2003, Taylor 1990). Changes in subalpine meadow size and distribution may be influenced by changes in temperature, snowpack, fire, grazing and other factors (Fonda and Canaday 1974). Studies have shown an increase in the recruitment, growth, and distributions of subalpine conifer species in western North America. (Hessl and Baker 1997, Little et al. 1994, Innes 1991, Rochefort et al. 1994). In this research project, I will investigate conifer invasions in the subalpine forest-meadow ecotone and their relationship to climate change in Glacier National Park, Montana.

This dissertation follows the style of the *Journal of Vegetation Science.*

1.2 Observed Changes in Establishment Patterns-The Subalpine Forest-Meadow Ecotone

The tree invasion patterns observed in the subalpine forest-meadow ecotone show a pattern of restructuring at broad, regional scales. Though regional climates vary, a general increase in temperature could cause a common growth response throughout the American West. Studies confirm that increases in tree establishment have been in response to mechanisms of climate change (Butler 1986, Franklin et al. 1971, Graumlich 1991, Heikkinen 1984, Innes 1991, Kearney 1982, Laroque et al. 2000, Leemans and Vliet 2004, Lepofsky et al. 2003, Mckenzie et al. 2001, Peterson 1994).

Research has examined areas in the American West for vegetation changes in the subalpine forest-meadow ecotone. Studies examined showed all subalpine meadows experiencing invasion. Studies also found disturbance factors, in addition to climate, that attribute to subalpine meadow recruitment, such as fire and grazing (Callaway and Walker 1997, Taylor 1990, Taylor 1995). Though climate for these regions vary from continental to Mediterranean, there are general trends and timelines for tree establishment in the subalpine forest-meadow ecotones. The Rocky Mountains have a Continental cold and dry climate, and show a vegetation response to climate as follows:

Research in the Cascades show an increase in tree establishment in subalpine meadows occurred after the warming of the Little Ice Age (Franklin et al. 1971). An increase in temperature showed an increase of growth and productivity for *Abies amabilis* and *Tsuga mertensia* in this area (Graumlich et al. 1989). Studies show increased invasions and tree establishment in the Rocky Mountains during a warmer, wetter period in the 1940s and 1950s (Butler 1986, Dunwiddie 1977, Koterba and Habeck 1971, Vale 1981).

The Sierra Nevada, a Mediterranean climate, shows forest margin expansion after 1890 (Hessl and Baker 1997, Innes 1991, Little et al. 1994, Rochefort et al. 1994). Increases in tree radial growth occurred from the 1850s to 1900 (Mckenzie et al. 2001, Peterson et al. 1990, Peterson and Peterson 2001). Tree invasions were recorded in the Pacific Northwest from 1917-1938. Tree establishment in subalpine meadows of the Northwest shows peaks from 1920-1950 (Woodward et al. 1995, Rochefort et al. 1994, Rochefort and Peterson 1996). Studies on the timing and pattern of conifer invasion in the subalpine forest meadow ecotone are lacking in Glacier National Park, Montana (Fig. 1.1).

The locations of meadow invasion studies are representative of general location, and not the specific study site.

Fig. 1.1. Locations of meadow invasion study sites in Western North America. 1. Rocky Mountain National Park; 2. Yellowstone National Park; 3. Lemhi Mountains; 4. Bitteroot Mountains; 5. North Cascades National Park; 6. North Cascades National Park; 7. Mount Ranier.

1.3 Significance of Study

Wilderness areas provide a unique perspective in assessing impacts of climate change. These more “pristine”, or less intensely managed, areas are minimally influenced by humans and may illustrate the difference between natural versus human change on ecosystems (Graumlich 2000). Glacier National Park is a wilderness area with a vast repository of climate change data found in the tree rings of subalpine meadow-forest ecotones.

Few studies of seedling recruitment in subalpine meadow ecotones have been performed on the east side of the Continental Divide. My research seeks to fill this knowledge gap to better understand the mechanisms facilitating seedling invasion into meadows. The recent encroachment of trees is threatening to enclose Glacier National Park's subalpine meadows. Encroachment by trees into meadows may alter meadow structure and composition important for foraging wildlife requirements (Lepofsky et al. 2003). Because data for tree invasions in the American Northwest are sparse, more studies are needed to determine the impact of climate change at a broader, regional scale (Peterson 1990).

Also, without further studies of the timing and pattern of tree encroachment, resource managers operate on out-moded models of wildlife conservation. Subalpine meadows contain high plant diversity and support foraging wildlife. They are an important constituent of ecosystem structure and function (Moore et al. 2000). Loss of these areas may have high ecological consequences for wildlife under severe environmental constraints for a large part of the year. Subalpine meadows are integral to ecosystem function and because they are an important aesthetic attraction of Rocky Mountain parks, a better understanding of how climate change serves to initiate conifer invasion is necessary to preserve these ecotone communities.

1.4 Research Objectives and Hypotheses

The goals of this research are to analyze and characterize spatial patterns of conifer invasions into the subalpine meadows of Glacier National Park and to evaluate processes that may contribute to their invasions. Few studies have been done in this park to demonstrate how conifer invasion of subalpine meadows may be related to climate patterns over time. Such a study would be useful in determining how regional climate phenomena may impact subalpine meadow conifer invasion. I will be specifically testing the following hypotheses:

- Changes in both temperature and precipitation are contributing to tree species invasion into subalpine meadows.
- Patterns of meadow invasion exhibit a lag response relative to climate changes.
- The spatial pattern of invasion is controlled by site specific environmental and resource variables many of which vary with elevation.
- Competition by and facilitation of neighboring vegetation contribute to the pattern of conifer invasion.

2. CONCEPTUAL OVERVIEW

2.1 Biogeography and Geoecology Concepts

This study combines the merits of two disciplines: biogeography and geoecology with emphasis placed on the former science. Biogeography requires the study of the organism and its patterns in the context of its ecosystem. A working definition of biogeography is the examination of organism spatial patterns and distributions as well as the ecosystem processes that influence these spatial patterns and distributions over time (Frosberg 1976, Huggett 1995). Biogeographical studies can vary in their scale, which is useful for geographical ecology in examining plant communities or associations (Kent et al. 1997, Kent et al. 2006, Pielou 1979). Geoecology requires the study of the ecosystem in its entirety with special emphasis placed on the organism of interest. Geoecology may be defined as the examination of ecosystems within a geographic space recognizing that the organism and its spatial environment are inseparable (Rowe and Barnes 1994, Stallins 2006). When using the geoecological approach, it is important to study ecosystems in the context of their physical environment to understand how processes operate to create biotic patterns, e.g. plant communities. The plant community scale and size are dependent on the constructs of the terrain and are influenced by the surrounding climate (Drury and Nisbet 1973, Kent et al. 1997, Ponge et al. 1998, Watt 1947). Thus it is important to understand the changes in biotic patterns based on changes in topography and associated environmental variables.

Scale is an important concept for plant biogeography, especially when considering the effects of climate pattern and disturbance on the landscape. Climate patterns operate at several different scales and are moderated by both biota and abiotic processes (Delcourt et al. 1983, Loehle 1998). Climate is a controlling variable in ecosystems, and as climate changes the effects of change on plant pattern is dependent on the spatiotemporal influences of this change. These patterns are complex, and though temperatures are predicted to rise 1.5 to 4.5 degrees C in this century, models predict warmer winters and summers-especially at higher latitudes (Dullinger et al. 2003, IPCC 2007, Romme and Turner 1991). An increase in winter precipitation is predicted at higher latitudes, but a decrease in summer precipitation and soil moisture is a consequence of global warming (Daniels and Veblen 2004, Holtmeier 1994, IPCC 2007, Romme and Turner 1991). These predictions all show variations at global, regional and local scales, and the magnitude and rate of spatiotemporal effects on temperature and precipitation are not as well understood (Dullinger et al. 2003, Graumlich 1993, Graumlich 2000, Lloyd and Graumlich 1997, Turner and Romme 1990). The scale of disturbance operates similarly to climate in that as the extent of frequency and magnitude of disturbance are also determining factor of plant biogeographic patterns (Delcourt and Delcourt 1988).

2.2 Meadow Invasion

Many studies examining tree regeneration in the subalpine zone are available because of the openness of the site and destabilization of meadow – forest boundaries and its location nearer to extreme climate thresholds (Brubaker 1986, Graumlich 2000, Hessel and Baker 1997, Little et al. 1994, Peterson and Peterson 2001, Vellaba and Veblen 1997). Low temperatures and short growing seasons are the determining factors constraining the trees in the subalpine and alpine zones (Daubenmire 1954). Bartlein (1997) modeled future conifer distributions based on warmer climate and enriched CO_2 levels in Yellowstone National Park (YNP) and projected a continuance of warmer and drier climate favor tree establishment.

Studies have shown an increase in tree establishment within subalpine meadows over the last century and these invasions are temporally associated with warming climate (Agee and Smith 1984, Dunwiddie 1977, Franklin 1971, Jakubos and Romme 1993, Lepofsky 2003, Rochefort and Peterson 1996). Specifically, this pattern of meadow loss coincides with a significant, increased warming trend in temperature (Millar et al. 2004, Millar and Woolfenden 1999). However, Vellaba and Veblen (1997) found limited establishment with more drought-like conditions after 1980, but from 1900 to the 1970s an increase in establishment occurred with a warmer spring and fall temperatures in combination with wetter growing seasons. Modeling species growth response to climatic variability predicted if current climate trends continue, then areas with decreased snowpack distribution and elongated growth seasons will have progressive meadow enclosure (Dullinger et al. 2003, Peterson and Peterson 2001). Romme and Turner (1991) modeled the effects of anthropogenic climate change, or the increases in greenhouse gases- specifically elevated atmospheric CO_2 levels, on lower and upper timberline biogeographic pattern, and found increased invasion upslope at higher elevations and tree mortality at lower elevations.

As greenhouse gases increase, whether due to human caused or naturally caused sources and sinks, temperature increases as well; but tree life cycles respond more slowly to these conditions which would favor fast growing species as long as climate conditions remain suitable for forest growth and maintenance (Loehle 1998, Solomon and Kirilenko 1997). As immigration of trees into meadows closes the forest canopy, then climate conditions would favor a shade tolerant, fast growing species as the light resource becomes diminished (Solomon and Kirilenko 1997). For example, Romme and Turner (1991) found a warmer, drier climate would shift species in the Yellowstone area conservatively upward 460 meters. As forest move upward in elevation, species that competed well at cooler temperatures, such as *Pinus albicaulis*, will stabilize or retreat, and species that are better competitors in drier and variable shade conditions will become more dominant, i.e. *Abies lasiocarpa*. Unfortunately, the high mountain environment has limited area for subalpine and alpine plant community migration, and on lower mountains subalpine meadows and alpine tundra may disappear as they become out-competed by lower elevation forest moving upslope (Dullinger et al. 2003, Loehle 1998). Loss of these ecosystems may mean a loss in biodiversity and species richness of plants adapted to past climate regimes for the subalpine environments.

Other factors that may contribute to meadow invasion from forested landscapes outside of the subalpine zone are disturbances. Processes that contribute to meadow invasions from forested boundaries include unnatural fire regimes and grazing of domestic livestock; however, these factors are also considered as part and parcel of meadow maintenance (Arno and Gruell 1986, Taylor 1990, Vale 1981). Subalpine meadows are thought to be specifically maintained by climate or via interactions of climate and fire (Agee and Smith 1984, Butler 1986, Dyer and Moffett 1999, Lepofsky 2003, Taylor 1990, Vale 1981). As climate changes, then climate producing drier summers may create conditions more favorable to large fires (Swetnam and Betancourt 1990). Mega-fires remove large tracts of forested stands. In response to this disturbance the forest-meadow plant species composition may shift in favor of pioneer, herbaceous species that out-compete tree seedlings. However, an increase in spring, summer and annual precipitation characteristic of climate change favors woody species in lieu of herb or grass species (Daniels and Veblen 2004, Neilson et al. 1989, Taylor 1990, Taylor 1995). For example, subalpine fir seedling germination favors a moist humus layer, and these seedlings experience increased mortality with drought (Burns and Honkala 1990).

2.3 Subalpine Meadows and Ribbon Forests

The subalpine zone ranges between lower subalpine (1,292 m in elevation) and upper subalpine (above 1,981 m in elevation). The meadows are situated lower topographically than the higher elevation ribbon forests and below the alpine zone of 2,134 meters. In GNP the subalpine zone can be divided into lower subalpine located from 1,219 meters to 1,676 meters and upper subalpine located from 1,676 meters to 1,981 meters extending to the treeline (Rockwell 1995). Woodland and forests alternate with open meadows that contain scattered conifers.

The effects of snow-pack and wind can affect the creation of subalpine meadows and ribbon forest. Graumlich (1991) found lingering snow-pack presence shortened the growing season for subalpine forest. Fonda and Canaday (1974) found snowpack, combined with fire, limited seedling establishment. Billings (1969) studied ribbon forests of the Medicine Bow Mountains of SE Wyoming, USA and indicated that in areas where snowdrift does not melt until July wet meadow vegetation is favored over seedlings. He viewed ribbon forest creation as a process whereby once seedlings established on windward edges, the forest expand in the windbreak north to south, perpendicular to westerly winds. Snow builds up on the lee side of this forested area. As snow melts it creates suitable soil moisture presence to increase seedling establishment and growth. As trees die, they change the pattern of these lateral forests, which may explain the unusual irregular bends present in ribbon forest patterns. Butler et al. (2003a) found similar processes stated above combined with strong geomorphic controls influencing the ribbon forest pattern in Preston Park. Possible reasons these meadows seemed to have such a strong foothold on the landscape are varied. Butler et al. (2003b) determined site topography, lithology, and stratigraphy precluded tree invasion patterns in these meadows, and found trees in higher, parallel to subparallel, well-drained sites. Higher sites have an earlier timing of snowmelt and greater organic material. As climate changes the amount and duration of snow-pack, the warmer, drier environment reduces snowpack prevalence in meadows providing an earlier and longer growing season which favors tree invasions into subalpine meadows.

Changes in subalpine meadow vegetation patterns have been recorded worldwide. Examples of changes or shifts in subalpine meadow vegetation patterns are occurring at a global level include Motta and Nola (2001), who found *Larix decidua* and *Pinus cembra* are more abundant with individuals ages 100 years or younger. Shifts in tree and shrub distribution of subalpine meadows were found in Austria (Dullinger et al. 2003). In Sweden *Pinus sylvestris* populations invaded subalpine meadows over a 400 year time period (Kullman 1987, Kullman 2002). New Zealand has also seen alteration in subalpine tree dynamics (Cullen et al. 2001). Growth increases in subalpine conifer species have been documented (Innes 1991). McKenzie et al. (2001) noted an increase in tree radial growth in many subalpine meadows and forests of the American Northwest since 1850. LaMarche et al. (1984) noted increases in *Pinus longaeva* (bristlecone pine) and *P. flexilis* (limber pine) growth rates in California and Nevada. Conifers in the Sierra Nevada, California invaded subalpine meadows in pulses with the strongest periods occurring between 1945 and 1976 (Millar et al. 2004). Subalpine meadows are experiencing tree incursions since the mid- 1800s in Colorado (Elliot and Baker 2004), Yellowstone National Park, Wyoming (Dunwiddie 1977, Jakubos and Romme 1993, Patten 1963), Montana (Arno and Gruell 1986, Koterba and Habeck 1971, Patten 1963), and Oregon (Vale 1981). Subalpine invasions are also documented for the Pacific Northwest (Agee and Smith 1984, Brink 1959, Fonda and Bliss 1969, Franklin et al. 1971).

2.4 Climate Change Effects on Meadow Invasion

High elevation forest ecosystems are useful to assess the direct effects of climate change ranging in scale from decadal to centurial (Graumlich 2000, Hessel and Baker 1997, Körner 1998, Körner 1999, Stevens and Fox 1991). These areas are more protected from disturbance events found at the lower elevation forests (Anderson and Smith 1997). Specifically, subalpine forest communities are recognized as sensitive indicators of climate change (Anderson and Smith 1997, Graumlich 1993, Lloyd and Graumlich 1997). Millar (2004) found that there is inadequate research demonstrating the effects of century-long interdecadal climate variability on subalpine forest dynamics, with emphasis on reversible directional shifts in invasion. However, there is research in central Colorado on expansion of the subalpine forest in both the upslope and downslope directions in the middle Holocene, which was a warmer and wetter climate than present (Hessel and Baker 1997, Jakkubos and Romme 1993, Romme and Turner 1991).

Upper elevation forest-meadow boundaries may be responsive to climate change, and this response may be dependent upon the rate and magnitude of environmental change and on the tolerances of the species (Risser 1995). As climate changes with time, so may the patterns of the plant communities in the ecotone and how the ecotone functions as a whole. Climate is thought to activate directional shifts between the meadow-forest boundaries over thousands of years (Taylor 1990, Taylor 1995). Biogeographical models also show directional shifts resulting from climate change, but these models do not account for abrupt changes due to interactions of species with climate (Lenihan and Neilson 1995, Sykes et al. 1996).

Conditions that favor tree invasion show strong climate component. Increased temperature and lower precipitation levels have been associated with increases in tree establishment in subalpine meadows (Butler 1986, Taylor 1990, Taylor 1995). Specifically, warmer and drier conditions between the late 1800s to the 1940s have been associated with forest margin expansion into meadows in the Cascades and the Olympic Mountains (Brink 1959, Fonda and Bliss 1969). These warmer and drier conditions are thought to increase growing season length in meadows (Daniels and Veblen 2004, Pelfini et al. 2006, Peterson and Peterson 2001). Invasion patterns tend to coincide with these changes in spring and summer temperatures. One example is tree establishment of *Tsuga neretensiana* (mountain hemlock) increased during years with above normal annual temperatures with seasonal trends of above normal summer temperatures and above normal precipitation (Taylor 1995). Another example of a strong climate component is snowpack influence on length of growing season for a site. Snowpack is important for determining position of forest and meadow boundaries in the subalpine zone (Brink 1959, Fonda and Bliss 1969, Franklin et al. 1971). A warmer spring changes duration of snow cover with an earlier timed snowmelt, and a warmer fall extends the growing season that would favor conifer invasion (Brink 1959). More recent studies show climate conditions favoring tree invasion, for example *Populus tremuloides* (quaking aspen) expansion into meadows involves a combination of decreased mean spring precipitation and an increased mean summer maximum temperature (Elliott and Baker 2004). Conifers in the Sierra Nevada showed distinct multi-decadal pulses from 1940s to 1970s and had significant correlations with minimum temperature and precipitation (Millar et al. 2004). *Abies lasiocarpa* showed distinct decadal pulses and significant responses to warmer drier springs and cooler, wetter summers (Agee and Smith 1984, Brink 1959, Little et al. 1994, Kearney 1982).

Other factors that may contribute to changes in the meadow-forest boundary include atmospheric and oceanic effects. The effects of ocean currents play an important part in influencing the climate and the environment of the American Northwest. The

Pacific Decadal Oscillation (PDO) is an anomaly in sea surface temperature variability. It causes changes in air pressure patterns, and as the air pressure patterns become altered, winds shift eastward, thus further increasing sea surface temperatures. PDO influences decadal to multi-decadal drought variability in the American west thus influencing moisture and fire regimes in these areas (Pederson et al. 2004). PDO occurs in cycles, and these range on average between 20 to 30 year periods (Mantua et. al. 1997, Zhang et al. 1997). The key dates associated with PDO studies have found that a cooler period of climate prevailed from 1890 to 1924 and again from 1947 to 1976. The warmer PDO periods of climate were found between 1925 to 1946 and 1977 to approximately 1994 or 1995 (Mantua et al. 1997, Minobe 1997). Millar et al. (2004) found that invasion responses from the 1920s to 1970s were significantly correlated with positive and negative PDO cycles. Pederson et al. (2004) found the U.S. Northern Rockies' snowpack is strongly associated with PDO with negative PDO resulting in higher snowpack and Snow Water Equivalent (SNE). In this study it found a greater than 50 year period of summer drought and decreased snowpack with peaks in 1919 and 1941.

2.5 Topography and Edaphic Factors

It is predicted that with increased warming trends in climate, the distribution of mountain plant species will shift to higher altitudes (Woodward 1998). Plant diversity in mountain environments is tied to topography. Variation in topography creates variability in environmental gradients (Douglas and Bliss 1977). The effects of climate on tree growth may be mediated by topography, which in turn may alter resource availability, such as soil and air temperature, irradiance levels, and soil fertility

(Oberhuber and Kofler 2000). Kuramoto and Bliss (1970) found subalpine meadows responded to topographical factors such as aspect and exposure, soil instability gradients, and to disturbance.

Soil properties affect plant distribution and may be affected by climate change. Meetemeyer (1984) found geographical patterns of litter decomposition rates and soil organic matter (SOM) accumulation in major ecosystem types are related to climate. In northern temperate, boreal systems, an increase in temperatures may change the balance between plant production and decomposition and net mineralization of carbon pools in SOM (Anderson 1991). Climate change may affect soil properties such as soil temperature, moisture, and resource quality, and in turn environmental constraints affect how trees respond to temperature (Moore 1981). A change in key soil properties may trigger changes in forest community composition. When climate alters these key soil properties, then it may also alter soil fertility by altering the dynamics of nutrient cycling and how nutrients are recycled through the soil system. For example, the alteration of snow depth could likewise affect soil moisture and temperature and alter the length of growing season for the plant situated at that specific site. Alterations of the above and belowground biomass and litter, their chemical composition, and the SOM dynamics are affected when climate alters the soil dynamics (Anderson 1991). Increased soil temperatures may limit soil decomposition, and this is greater than the influence of air temperatures on primary production (Anderson 1991). If soil moisture resource quality and temperature constraints are removed, then soil microbial activity and carbon availability decline with the age of decomposing litter (Jansson and Berg 1985). The resource quality of litter is a function of both the mineral nutrient content and carbon availability and may be altered in the presence of modifiers, such as tannins (Austin and Vitousek 2001, Swift et al. 1979). Bonan et al. (1990) predicted that in climatically favorable areas, a delay in seedling colonization and establishment may occur due to the time required for soil development.

Aspect can influence plant distribution patterns in mountain environments. Especially influenced by the role of aspect are trees located on the north versus south facing aspects. Aspect determines the amount of solar irradiance received in an area, the dryness of soils, and influences prevailing winds in mountainous areas with leeward slopes found in the rain shadow (Huggett 1995). Billings (1990) provides an example of the aspect effect with trees found in the Northern Cascades. In this area the eastern, leeward slopes are drier than the westward facing, windward slopes, thus tree species change from firs (*Abies lasiocarpa and Abies amabilis*) to western larch (*Larix occidentalis*) and Ponderosa Pine (*Pinus ponderosa*) when moving east to west.

Slope properties, including slope gradient, length, curvature, and position, have an affect on soil properties (Gerrard 1988, Huggett 1995). Anderson and Furley (1975) determined that downslope gradients were diminished of the quality of SOM, such as the content of nitrogen, carbon and phosphorus as well as soil moisture. The amounts these factors were diminished were dependent on the steepness of the slope and the soil makeup and texture. Relationships between slope and soils are difficult to assess in mountainous areas because these soils are extremely variable over short distances. Phillips (1993) suggested that abrupt changes in the spatial variance structure found in soil may result from chaos dynamics in the soil landscape. Gerrard (1988) found a relationship between the soils and their position on the slope were tempered by their position within a drainage basin in Dartmoor, England. Swanson et al. (1988) found geomorphology affects slope and soil properties which affect plant distribution and pattern on a landscape in the Rocky Mountains. Thus, there is an interaction among landform, geomorphic processes and the ecosystem.

The montane mesoclimate during the summer is affected by topography which influences the following factors: temperature, atmospheric moisture, solar radiation, precipitation and wind. These environmental factors vary greatly across a region, especially those regions found in mountainous environments, and are profoundly affected by changes in topographical features, such as aspect, slope, and elevation of the surrounding forest cover associated with the topography.

Studies of the ameliorating effects of microtopography include Douglass and Bliss (1977), who found that microenvironmental variables, such as air temperature, soil profile temperatures, and soil moisture regimes of both vegetated and non-vegetated sites varied considerably along a transect in the plant communities of the western North Cascades. These studies specifically focused on subsurface soil temperature and moisture regimes which showed a sharp vertical gradient between the surface soils and approximately 10 cm of soil levels over short transect distances. Holtmeier and Broll (1992) studied forest-tundra ecotone and found that microtopography may affect microclimates and ameliorate site conditions affecting snow depth and duration of snow cover. Tessier et al. (1997) found microsites influence tree response to environmental stress and tree ring formation. Species may benefit from being located on microtopographic features that serve to protect individuals from disturbances, such as fire or browsing, or from climate extremes, such as in areas that experience an earlier snowmelt and elongated the growing season. However, these microsite features, when accompanied by longer snow-free seasons, may create conditions that are amenable for tree species establishment (Agee and Smith 1984, Woodward et al. 1995).

2.6 Seed and Resource Availability

Topographical factors are not the sole influence on establishment patterns of seedlings. Seedling establishment patterns that invade into meadow interiors may vary spatially dependent on both seed availability and resource availability. The balance between biotic controls of the individual mature tree and the abiotic controls, or rather abiotic restrictions, of the environment determine the overall shifts in meadow-forest boundaries. In the high elevation, alpine environments, seed production may at times be limited due to extreme climatic conditions, and sole reproduction may occur from vegetative propagation (Archibold 1981, Grimes 1979, Molau and Larsson 2000).

Seed availability is dependent upon seed rain and dispersal, and the subsequent deposit and storage of seeds in the seed bank, seeds deposited in the soil strata. Seed availability is determined by dispersal of seeds from the forest margin into the meadow interior, and the density of these seeds in seed banks (Molau and Larsson 2000). Under ideal conditions subalpine fir will produce seed crops every three to six years, and high mountain winds may disperse seeds further than projected dispersal distances via seed rain (Morin and Payette 1988).

Once the seed rain becomes deposited in soils, and if the seeds persist in the soils and are viable, then these deposits allow populations to respond to propitious conditions in climate and site over time or respond quickly to disturbances that may remove above ground individuals (McGraw et al. 1991). Seed bank composition and density are dependent on factors, such as above ground species composition, disturbance regimes of soils (Chambers 1995). Also, seed rain often has greater species richness than the diversity of species found in the seed bank (Molau and Larsson 2000). Seed banks are also determined by the species, which determine the dormancy and the longevity of the seed. These factors contribute to seed bank spatial variability over time.

Seed banks characteristics are often dependent on the geomorphology of the environment. In alpine environments Morin and Payette (1988) found approximately 81 percent of seed banks were composed of above ground vegetation, and the most viable seeds were found in the first 3 cm of soil. In more bottomland-hardwood communities Schneider and Sharitz (1986) found shorter seed dormancy creates a seed bank similar to the above ground species composition. The shorter dormancy would make a species more competitive for capturing safe sites on the landscape more rapidly, but climatic conditions would need to be favorable and the environment free of perturbance for the seedling to successfully germinate and establish. In the Rocky Mountains, subalpine fir viability and chances of germination are only fair with 30 to 34% success rates (Burns and Honakala 1990). Most likely recent seed production the year before combined with a shorter dormancy and warmer spring and summer seasons contributes to individuals germinating successfully in Rocky Mountain subalpine meadows (Molau 1993).

Once dispersed, the presence of additional seedlings or shrubs may influence spatial pattern of invasion by “catching” the seed rain falling into meadows from forest margins, as well as ameliorating the effects of potentially lethal environmental factors on seeds (i.e. extreme temperature, high winds, and direct solar radiation) (Woodward et al. 1995). Other factors may be species-specific, for example in subalpine fir, seeds are produce when the tree reaches 1.5 meters tall and is 20 years of age with maximum seed production produces at 150 to 200 years of age (Burns and Honakala 1990). Subalpine fir also produces heavy seed crops every 3 years under ideal conditions, such as pure stands of subalpine fir with few Engelmann spruce associates. Additionally, subalpine fir individuals may establish via layering, which increases their reproductive success.

2.7 Intraspecific Competition

Spatial relationships of plants and their neighbors shape the patterns of conifer invasion in subalpine meadows. Intraspecific competition affects population dynamics and monotypic stands become varied in size and age with increased pressures stemming from competition. In asymmetrical size relationships the competitive effects vary with size, and create size hierarchies as light and space resources become pre-empted. If the neighboring plant is larger and exhibits a strong competitive influence on the smaller plant, then this relationship is “one-sided”. Effects from neighboring plants may have a positive or negative effect on an individual depending on the nature of the environment (Wilson and Agnew 1992). Examples used earlier in this section involve resource availability: soils moisture, soil nutrients and light. For younger tree seedlings high light environments may have a deleterious effect on the seedling. Yet if the seedling grows in the shadow of a mature individual, then the seedling benefits from the shading and its chances for survival increase. In drought conditions additional neighboring vegetation may reduce both soil moisture and soil nutrient availability, and can enhance negative impacts from plant competition (Callaway and Walker 1997).

2.8 Competition-Density Effects

Plant density, the number of plants per unit area, and plant pattern are important measures when studying plant interactions. As plants increase in age and size, which is not always the case with subalpine fir seedlings, they begin to compete for space and resources. If overcrowding in a plant community occurs, a density-dependent relationship is reached, and these plants will begin to die over time as a result of a process known as self-thinning (Silvertown and Doust 1993). When grown in the presence of competitors, such as other firs or mountain hemlock, subalpine fir becomes crowded out and reduced in number. Though almost monotypic subalpine fir stands are found on commercial land located on southern slopes in the Pacific Northwest (Burns and Honakala 1990).

3. STUDY AREA

This section describes the study area, Glacier National Park (GNP), Montana in terms of its physiography, climate, and biota with emphasis on vegetation. GNP is a United Nations-designated International Biosphere-Geosphere Reserve. This section examines disturbances found within the boundaries of GNP. Preston Park is the specific location within GNP that serves as the focus of this study.   The final section of this section describes Preston Park and its environment in greater detail.

3.1 Location and Physiography of GNP

Located in the northwestern United States in the Rocky Mountains, Glacier National Park was established in 1910 and encompasses a total of 410,000 ha (Fig. 3.1). GNP is bounded to the north by Waterton Lakes National Park in Alberta, Canada. The Continental Divide bisects central GNP northwest to southeast with the Livingston Range to the northwest and the Lewis Range to the southeast (Fig. 3.1). Glacier National Park combined with Waterton Lakes National Park forms Waterton-Glacier International Peace Park.

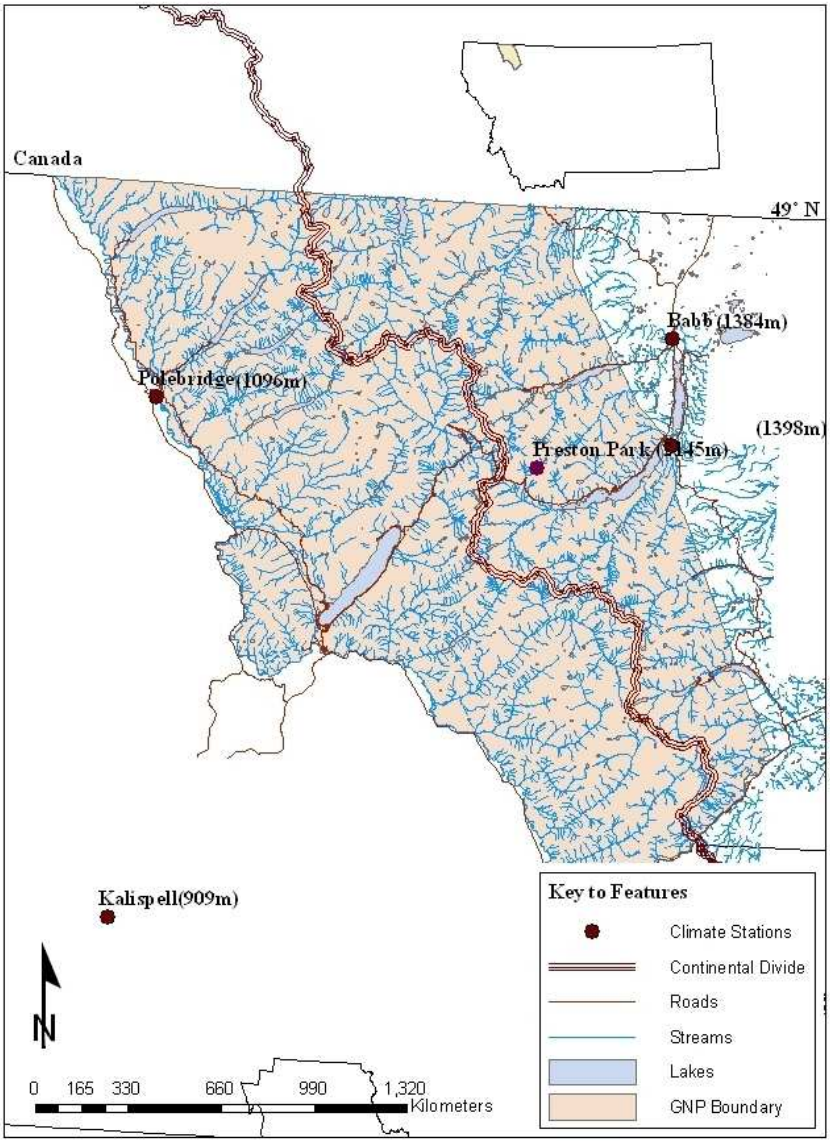


Fig. 3.1. Map of Glacier National Park, Montana and associated climatological stations.

3.2 Climate of GNP

The climate in western Montana is a highland complex contained in a continental, semiarid zone. These characteristics result in great climatic variability over small spatial scales of a few kilometers (Bamberg and Major 1968). The Continental Divide exerts a continental influence on the eastern side, while maritime air masses transport moisture to both sides of the Continental Divide. The east side of the park is slightly drier relative to the western side (Rockwell 1995). Pacific maritime air masses result in a wetter climate on the western side of the Continental Divide (Finklin 1986, McGregor 1998).

On average the maximum temperature ranges from -1.9 degrees C in January to 26.2 degrees C in July (Table 3.1). Average minimum temperature ranges from -9.5 degrees C in January to -8.4 degrees C in July (Table 3.1). Maximum high to low temperature ranges between 10 degrees C and -37.2 degrees C in January (Table 3.1). Maximum high to low temperature ranges between 37.2 degrees C and -0.6 degrees C in July (Table 3.1).

Table 3.1. Average temperatures for GNP as reported by the NPS (2008).

Temp.	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**July**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
Average Maximum Temp.	-1.9	1.5	5.5	11.6	17.8	21.8	26.2	25.6	19.3	11.5	2.9	-1.1
Average Minimum Temp.	-9.5	-7.3	-5.1	-1.3	2.8	6.5	8.4	7.9	3.8	-0.1	-3.9	-7.6
Maximum High Temp.	10.0	14.4	18.9	28.3	32.2	32.8	37.2	37.2	35.0	25.0	18.3	11.1
Maximum Low Temp.	-37.2	-35.6	-34.4	-16.1	-10.6	-4.4	-0.6	-3.3	-7.8	-19.4	-33.9	-37.8

Glacier National Park has experienced climatic variability over the last century, and this variability is impacting mountain ecosystem structure and function (Fagre et al. 2003). Climatic data is limited for GNP, and available data were collected from multiple non contiguous stations during variable time spans (NOAA 2006). The earliest climatological data for the region was collected in 1886 and 1899 from Lethbridge, Canada and from Kalispell, Montana respectively. Limitations regarding climate data for GNP exist both spatially and temporally. Finklin (1986) found increases in winter and summer temperatures of 1.1°C in GNP from 1910 through the 1970s. Other studies have suggested a recent warming trend in climate in Glacier National Park of a 1°C increase in temperature since 1899 (NCDC 2001, Walsh et al. 1993). The climate in GNP is also influenced by regional climate phenomena, such as Pacific Decadal Oscillation, and the climate is influenced by the Pacific Basin (Pederson et al. 2004).

St. Mary and East Glacier receive in the range between 66 cm and 76 cm of precipitation respectively. Historically, rainfall accounts for an insignificant portion of the annual precipitation total. St. Mary and Kalispell receive only a fraction of rain annually as compared to snowfall. The St. Mary data are limited to the twenty year period from 1982 to present.

Prevailing winds are from west to southwest with monthly average speeds recorded on topographic highs of 32 km per hour in the western part of the park and 24 km per hour in eastern part of GNP. The wind speed is variable within the topography of the divide (Finklin 1986, Vogler 1998). Warm Chinook winds occur periodically on the eastern side of the park.

3.3 Soils of GNP Subalpine Areas

Soil survey data available for Glacier County is limited. Subalpine forest and meadow soils for GNP grade from cold, moist soils Cryoboralfs and Cryoborolls, characterized as being saturated by winter snows (Anon 1980, Butler and Malanson 1989, Vogler 1998). These are well drained soils with a depth to bedrock that is deep to very deep (Vogler 1998). The soils of GNP are reflective of the parent materials. Soils have been analyzed in a few accessible regions of the park. For example, the Ptarmigan soil series was identified at Siyeh Pass in GNP, and the parent material is described as having characteristics of metamorphic rocks, and these include quartzite and argillite. Associated landforms with this soil series have long, uniform slopes (15 to 45 % grade) and a horizon sequence of A_o, A_1, B_{ir}, and C.

3.4 Biota of GNP-Vegetation

Coniferous forests dominate the park with some intermingled deciduous species, shrubs and grass communities reflecting gradients of soils, moisture, and fire history (White et al. 1998). The east versus west sides of the park experience different climatic regimes; these different moisture regimes favor different vegetation associations (Finklin 1986). Lowland forests with drier soils are composed of conifers, such as *Psuedotsuga menziesii* var. *glauca* (Douglas Fir) and *Pinus contorta* (lodgepole pine). Wetter soils are composed of *Thuja plicata* (western red cedar) and *Tsuga heterophylla* (western hemlock). Park areas prone to disturbance or more open areas are characterized by broadleaved species, such as *Betula papyrifera* (paper birch) and *Populus trichocarpa* (black cottonwood) (White et al. 1998). The eastern boundary of the park is densely populated with *Populus tremuloides* (aspen). The lower and upper subalpine zones are dominated by *Abies lasiocarpa*. Subalpine zones more centrally located parts within Glacier National Park include *Picea engelmanii* and *Pinus contorta*. Upper-treeline on both sides of the park is comprised of *A lasiocarpa*, *Pinus albicaulis,* and *P. engelmannii*.

Abies lasiocarpa is a tree that dominates cool, temperate forested zones on both sides of the Continental Divide. It grows within a narrow range of mean temperatures that varies from -3.9 ° C to 4.4 ° C with a July mean temperature of 7.2 ° C to 15.6 ° C (Burns and Honkala 1990). A*bies lasiocarpa* seedlings are particularly sensitive to moisture and temperature gradients. Woodard *et al.* (1995) found *A. lasiocarpa* tends to establish at the dry end of the precipitation gradient because it is outcompeted by other species, such as *Larix occidentalis* (western larch) at the wet end. Wetter years in dry sites or drier years in wet sites increases *A. lasiocarpa*'s competitive advantage and chances of establishment.

Pinus albicaulis is found in the westernmost United States and Canada at higher elevations. This species requires growing season temperatures with a minimum of 5.5 ° C maintained for at least 90 days, but it can tolerate intermittent frosts and snow (Baker 1944). *Pinus albicaulis* is a slow grower, taking approximately 250 years or more to reach optimum height in the presence of favorable conditions and establishment and growth is optimal in cool growing seasons (Baker 1944). *Pinus albicaulis* is a common pioneer species, and *A. lasiocarpa* often establishes in its presence. Franklin and Dryness (1973) observed a successional trend of *P. albicaulis* pioneers on open sites later surrounded or replaced by hemlock and fir communities. Due to the low tolerance to shading and competition of *P. albicaulis*, this species becomes replaced by other species that are better at forming a closed, forested stand. Seed production for *P. albicaulis* does not occur as regularly as *A. lasiocarpa* and has smaller seed crops. The seeds for this species are large, heavy, wingless, and are harvested frequently by animals such as *Tamiasciurus hudsonicus* (red squirrels), *Ursus arctos horribilis* (grizzly bears), and *Nucifraga columbiana* (Clark's Nutcracker). *Pinus albicaulis* regenerates effectively on open sites that have been burned and that are free of additional seed sources in the seed bank (Hutchings and Lanner 1982, Lanner and VanderWall 1980). *P. albicaulis* can reach a maximum height of 20 meters and persist for up to 500 or more years, and is often found where soils are shallow (Burns and Honkala 1990). With the advent of the fire suppression programs around 1910, older whitebark pines have become susceptible to pests and disease.

Herbaceous species found in the subalpine meadows and ribbon forests are also important for local wildlife feeding source. The *Erythronium grandiflorum* (glacier lily), a flower abundant in subalpine meadows and ribbon forests during snowmelt, are edible bulbs to grizzly bears who often forage for them via digging. Other species include *Aquilegia flavescens* (yellow columbine), *Castilleja miniata* (Indian paintbrush), *Castilleja rhexifolia* (Rhexia-leaved Paintbrush) and Allium schoenoprasum (purple onion) that bloom from June until September. *Xerophyllum tenax* (Common beargrass) are found in thick cover on open slopes as well as *Veratrum viride* (false hellebore) and *Epilobium angustifolium* (fireweed). In wetter meadows *Sisyrinchium idahoense* (common blue-eyed grass) is present along with woody species, such as *Salix arctica* (Arctic willow), a favorite food source for ptarmigan, and *Dryas octopetula* (white dryas).

Woody and herbaceous species both favor seasonal moisture regimes in the subalpine zone. Due to the increase of precipitation with higher elevation, forested and woodland stands of tall trees, such as *A. lasiocarpa* or *P. engelmannii*, and low shrubs, such as *Vaccinium scoparium* (grouseberry), *Sambucus racemosa* (black elderberry) capture a significant amount of snowpack. The intense shade provided by these stands reduce snow-pack melt rate, thus allowing snow-pack presence to remain into late spring creating wet meadows (Kershaw et. al. 1998). Thus many herbaceous species in the subalpine zone are moisture-loving. Meadow species that favor growth in moist meadows include *Aquilegia flavescens* (yellow columbine), *Anemone multifida* (cut-leaf anemone), *E. grandiflorum* (glacier lily), and *Heracleum lanatum* (cow parsnip).

In the relationship of dominant tree species P. albicaulis and A. lasiocarpa, P. albicaulis is considered the minor associate of subalpine fir-spruce forests of the Rocky Mountains. P. albicaulis is a long-lived, seral component in the Northern Rocky subalpine forest that makes up the Abies lasiocarpa-Pinus albicaulis habitat type (Pfister et al. 1977), and is considered a climax species (Weaver and Dale 1974). It is frequently a component of climax communities under cold, climatic extremes, such as those found at the treeline, or where sites are dry (Baker 1944, Weaver and Dale 1974).

Though climatic and topographic interactions are considered the primary controls for vegetation placement on a landscape, the continued maintenance of subalpine meadows plant distributions are also impacted by animal interactions within the meadows. Plant and animal interactions maintain and promote meadow herbaceous species (Tardiff and Stanton 1998). Frank and Groffman (1998) focused on the effects of ungulates on soil nitrogen and carbon in Yellowstone prairies and found ungulates substantially increased nitrogen mineralization and overall soil organic matter in grazed plots. Consumer pressure placed upon plants at particular sizes, densities, and life histories structure plant communities via both positive and negative interactions (Callaway and Walker 1997). Once an individual is removed from the plant population, site resources such as light, nutrients and soil moisture, become more abundant for neighboring individuals. The thinning of members of a population can have an overall positive affect if remaining individuals are hardy enough to withstand the pressures of the physical environment (intense solar radiation, exposure to winds, and exposure to heavy snow-packs). Mazancourt et al. (1998) found two caveats were required for "grazing optimization" via increased primary production and palatability to occur: 1) the proportion of nutrient lost to herbivory needs to be significantly less than the nutrient found in the overall ecosystem; and 2) the input of the nutrient must be greater than a threshold value for the system. These inputs to the ecosystem are dependent on plant uptake of the nutrient. Subalpine sites are located in shallow and infertile soils, thus a small load of nitrogen into the system might encourage tree incursions (Stohlgren 1998).

3.5 Disturbances within GNP

Disturbance can be generated by both natural and anthropogenic means. This process can be beneficial to natural environments, specifically plant communities, resulting in a more sustainable ecosystem by freeing trapped nutrient resources and growth of fire dependent species. Outside factors may include fire, avalanches, and herbivory, and human induced disturbance events such as trampling of vegetation by hikers and packhorse grazing.

3.5.1 Biotic Disturbance

3.5.1.1 Herbivory

The presence of animals that use subalpine meadows heavily may reinforce meadow presence by removing the recruitment of individuals through herbivory (Dunwiddie 1977, Vale 1981). Grazing disturbance alters subalpine vegetation zonation (Butler 1986, Moore et al. 2000). The high elevation subalpine meadows are generally small and are not considered accessible to pre-park grazing herds. Lower elevation meadows on alluvial fans are considered more suitable for grazing. Indigenous browsers are present in small number in the higher elevation meadows of GNP, but their impact is considerably smaller compared to the booming populations of browsers present in other National Parks, such as Yellowstone National Park's large herds of elk (GNP-NPS Park Archives, Moore et al. 2000). The National Park Service (NPS) in Glacier National Park has restricted grazing to outside the park boundaries since the early 20th century. Prior to the GNP herding and grazing restrictions feeding of deer and elk was restricted to Apgar, Polebridge and Kintla areas (Klasner, personal communication).

Though browsing may promote some conifer invasion by removing competitive herbaceous species, wildlife surveys over the past decades show browsing in this area is minimal. Observations in daily fieldwork indicated the browsing disturbance in this study area is minimal and it is not a primary facilitator of conifer invasion. There was greater evidence of digging by grizzly bear(s) and ground squirrels in this area. The lower meadows were well vegetated and showed little evidence of recent diggings, but ribbon forests just above the study area did show recent disturbance (Fig. 3.2).


a. b.

Fig. 3.2(a-b). Pictures of 2001 grizzly bear diggings near Piegan Pass.

3.5.1.2 Human Disturbance – Trail Blazers and Horse Concessions

Because the montane environment is sensitive and has a short growing season, anthropogenic impacts, even when minimal, contribute to a disturbance pattern that may linger for centuries. Prior to 1910 there were few visitors to the park, the presence of structures and activities since that period have been well-documented (Park Pub. "Science in Glacier National Park" 1993). The remote location of GNP makes it an excellent place to study natural and/or physical processes. Trails cut through the study area and horse concessions have traversed these trails historically, a brief history of this disturbance is warranted.

In GNP horse concessions are conducted with a limited number of animals. Historically, prior to the construction of The Going to the Sun Road, horse concessions were the only way to traverse the wilderness to chalets constructed in the area. Some 10,000 people annually ventured to the park from 1910 to the early 1930s with 1,000 horses being stocked (Fig. 3.3) (Fodors 2004). These concessions were reduced after the opening of the road and the introduction of motorized vehicle traffic. The horse concession stops were concentrated in one or two key meadow communities considered scenic stops and animals were restricted to these key areas, for example Piegan Pass. The current policies require that stock must remain on well-established trails and must be hitched to designated hitching areas, none of which are in the study area. Supplementary feed must be provided for stock and free grazing is prohibited (NPS 2006).

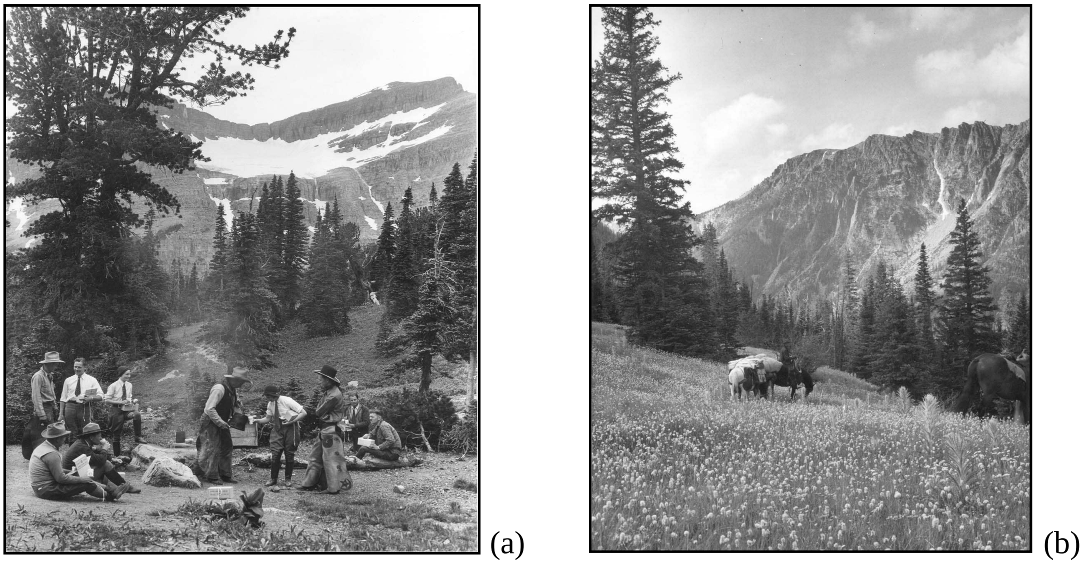
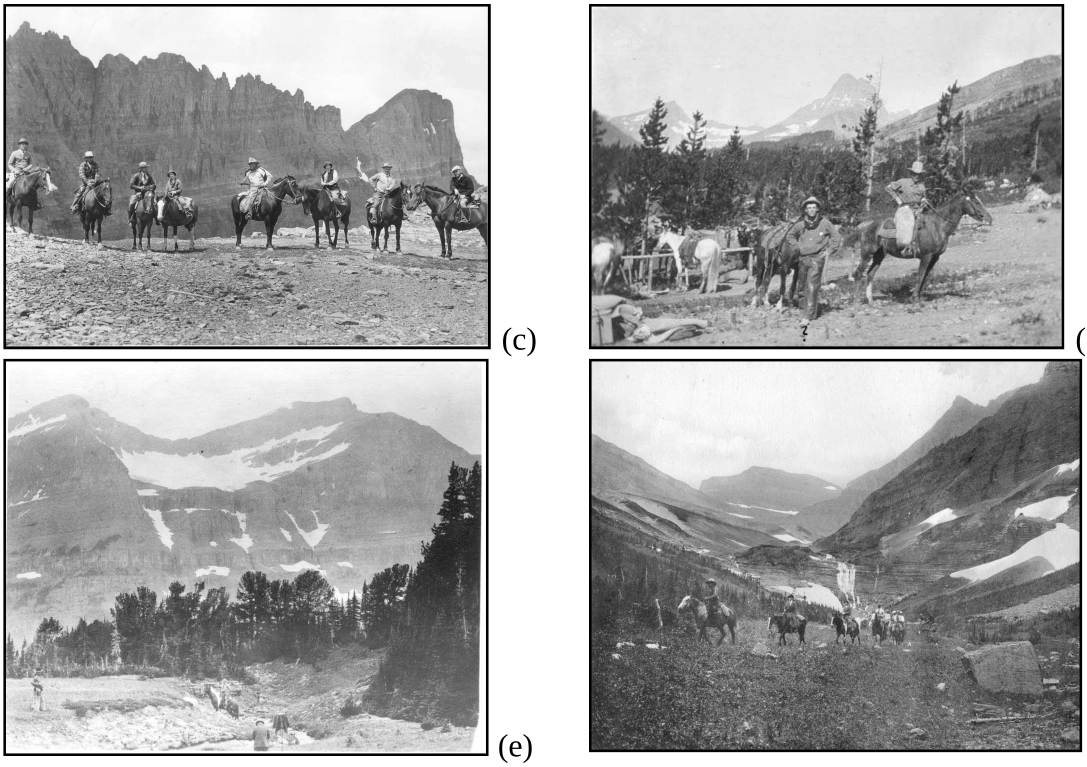


Fig. 3.3(a-f). Photographs of the early twentieth century horse troupes in GNP (Courtesy of the GNP archives).



(c) (d) (e) (f)

Fig. 3.3 (a-f).(Courtesy of the GNP). Continued

The total number of visitors to GNP is approximately 1.5 to 2.2 million people per year (Shaw 2001). High elevation plant communities can tolerate a threshold of impact via human and domestic animals without substantial alteration of plant communities (Olson-Rutz et al. 1996). Sustained damaged to meadow communities would be dependent on the duration and frequency of these impacts. Because the season for tourism is short, impacts sustained in the wilderness are not as damaging. The GNP trails do not open until the early summer when late season snows have melted and their conditions have been assessed for maintenance issues due to rockslides or rock falls as well as avalanches. Also, trail closures may occur periodically after trails open due to increased bear activity or fire outbreaks.

3.6 Preston Park Meadows –General Description

Preston Park (48°42'30" latitude, 113°37'30" longitude) is located in the east-central portion of GNP on the eastern side of the Continental Divide in the Lewis Range, just under Siyeh Pass (Fig. 3.4-Fig. 3.6). Preston Park is removed from the Continental Divide in both proximity and elevation. Preston Park meadows and ribbon forests are situated along an elevation gradient. The aspect of these meadows is predominantly south by southwest, but two meadows are west facing (Table 3.2). The slope of these meadows varies intra-meadow and inter-meadow (Table 3.2).

Table 3.2. The aspect and slope of the meadows in this study. The slope and aspect were calculated based on USGS 10m contours for the Logan Pass Quadrangle.

Meadow No.	Aspect	Slope degrees
1	Southwest	8 – 17
2	West	8 – 25
3	South x Southwest	0 - 8
4	Southwest x West	17-50
5	South x Southwest	8 - 33
6	Southwest x West	33 - 50
7	West	50 - 58
8	South x Southwest	8 - 50
9	South x Southwest	25 - 41

The pattern of the meadows and ribbon forest are dissimilar. Meadows have a rounded to elliptical pattern, and ribbon forest pattern is lateral and may have unusual, irregular bends due to topographic and geomorphic controls. Meadows range in elevation from 1,783 to 2,145 m. There are approximately nine subalpine meadows of interest along the Piegan Pass Trail ranging in size from 0.03 hectares to 3.23 hectares.

Ribbon forests are located just north of these meadows. Forests alternate with open meadows containing scattered conifers. These features are bisected by an incised stream.

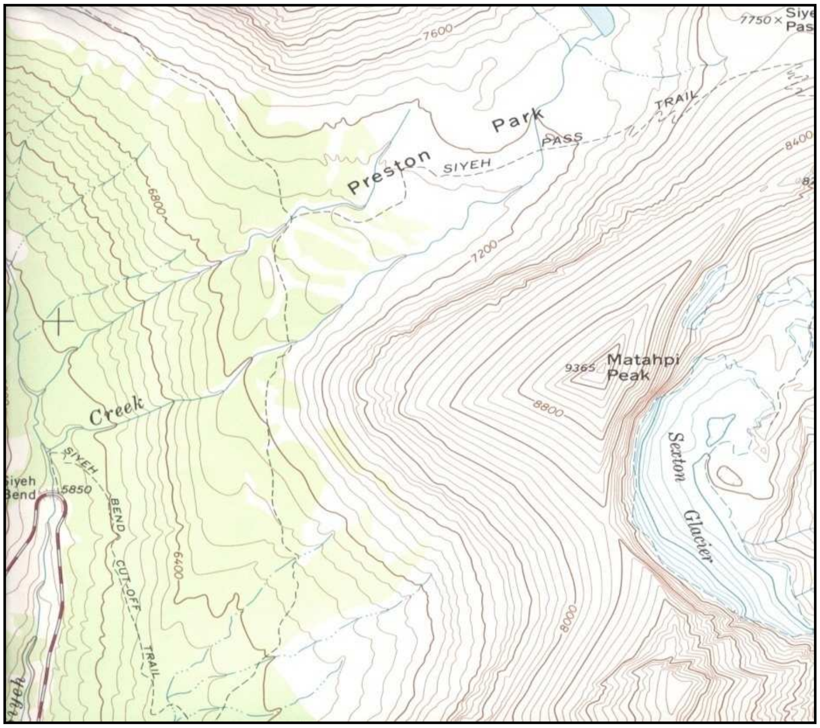


Fig. 3.4. USGS topo quad showing a subset of the Logan Pass, Montana quadrangle. Preston Park is situated near the Siyeh Pass Trail. Contour interval is 80 feet.

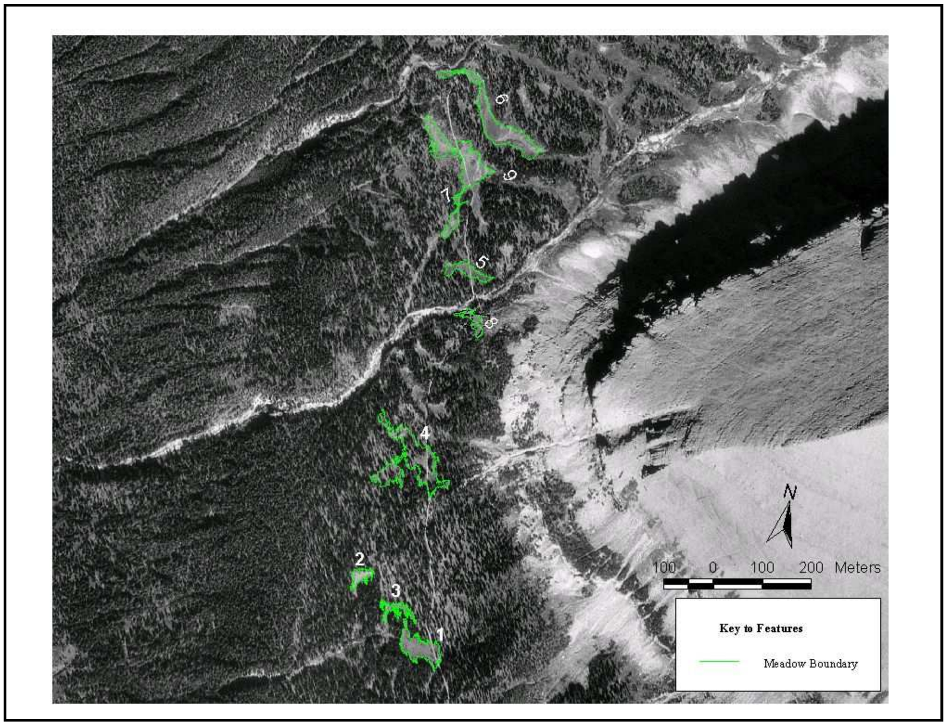


Fig. 3.5. Location of the nine sampled meadows along the elevation gradient, Preston Park, GNP, Montana.

Fig. 3.6. Location of Preston Park within the boundary of GNP.

The topography in Preston Park is complex and there is small-scale spatial variability in both soil types and in the soil moisture field (Fig. 3.7). Pleistocene glaciations traveled from a cirque flowing southwest. This glacial movement was across strata dipping 10 degrees in the same direction (Butler et al. 2003a, Whipple 1992). Butler et al. (2003a) found the coincidence of flow direction and dip created deeply plucked roche moutonee. Ribbon forests follow the base of these features with significant alteration by snowmelt and stream channels that incise across the floor of the park.

Tectonic uplift in this area exposes granite, argillite and other varieties of bedrock that become broken up due to weathering processes, such as frost heave. The weathering action leaves slopes of rock waste. Old rockslides on these slopes are found in and around meadows at mid-to-lower elevation in Preston Park. Rockslides cause talus to wash downslope and remaining rock is deposited near meadow boundaries. Parent material for these boundaries are Pleistocene/Quartenary till deposited as ground moraine (Vogler 1998). As these features become vegetated and stabilized, they have formed a higher “rim” around the meadow increasing the likelihood for snow catchments in meadow interiors. These higher ridges are stony with an average soil depth of 11cm when measured with probes. Soils have developed specific

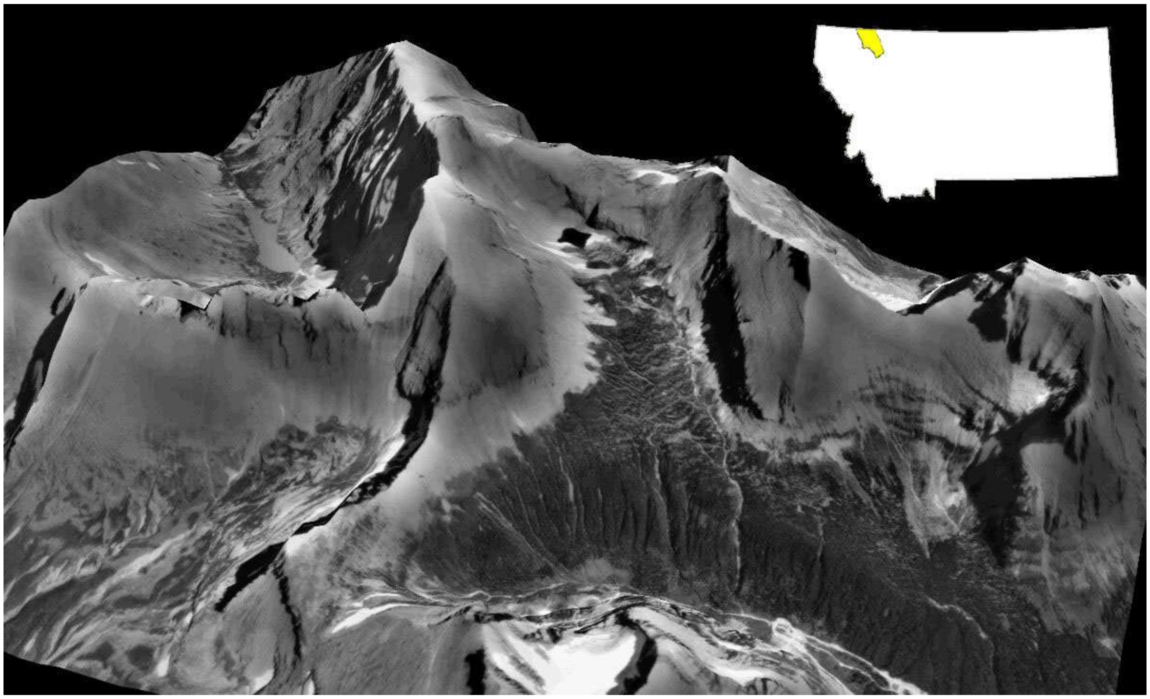


Fig. 3.7. A Digital Elevation Model (DEM) of Preston Park, GNP, Montana (courtesy of Dr. Stephen Walsh).

trends in this location. Hilltops are more coarse, stony and well-drained. Hillsides are more developed with loamy soils and are retain soil moisture. Butler et al. (2003b) found vegetation patterns at Preston Park site were associated with the interaction between glacial scouring and plucking and stratigraphy of this location. Fossilized stromatolites are found on the trailhead to Preston Park, evidence to the uplifting of a seabed.

Vegetation communities in Preston Park are populated with diverse, herbaceous species found here in large quantities once the trail passes the closed fir woodlands and forest, found on steeper hillsides, and breaks into the open meadows, glades, and ribbon forests. Dominant meadow herbaceous species include: *Aquilegia. flavescens*, *Anemone* *multifida*, *Erythonium. grandiflorum*, *Heracleum lanatum,* and both *Castilleja minata* (Scarlett paintbrush) and *Castilleja occidentalis* (Western Yellow paintbrush) (Kershaw et. al. 1998). These are moisture loving herbs.

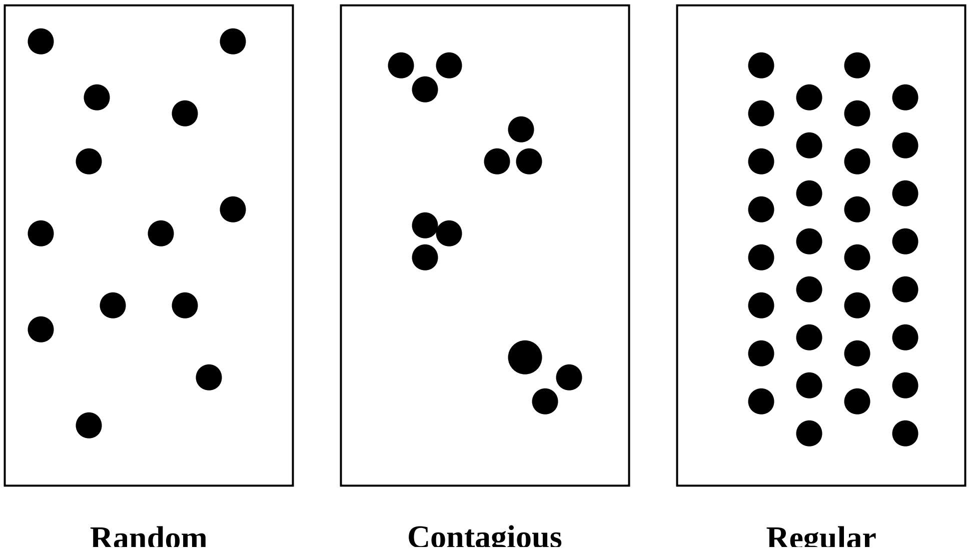
Based on current field observations Preston Park's meadows are heavily covered with *A. lasiocarpa* seedlings. Conifer species are an excellent invader in the subalpine ecotone. Seral tree species identified in the subalpine forests of Preston Park, Glacier National Park include the following: *Abies lasiocarpa* (subalpine fir), *Picea engelmannii* (Engelmann spruce), *Larix occidentalis* (Western larch), *Pinus contorta* (lodgepole pine) and *Pinus albicaulis* (whitebark pine). These species are located in subalpine zones at an elevation of 1,829 meters to 2,134 meters (Shaw and On 1979). *Pinus albicaulis* is a good colonizer for this cold and snowy location. These species are frost hardy and are well acclimated to the climate in the subalpine zone.

4. METHODS

Methods applied in this study were designed to describe the age, distribution, density and tree invasion pattern into subalpine meadows and to understand the association of this pattern with climate change. The plotless sampling strategy for tree density estimation is designed for simple application, to reduce costs, and to reduce time and labor in the field and is an efficient approach when collecting samples (Cottam 1947, Engeman et al. 1994).

The scale of the strategy was designed for the sampling of a single basin to target the meadows on an elevation gradient of the subalpine zone. Because of seasonal constraints, such as heavy snowfall in the high mountain environment, the timing of sampling was limited from early summer to fall when the Going to the Sun Road was open to the public. Data collection took place from summer 2001 to the summer 2003.

Spatial characterization of plant population size, plant density and spatial pattern requires a random sampling strategy to produce a non-biased estimate of the plant population. Methods such as the Nearest Neighbor are adequate to measure both the density and the dispersion pattern of a population from random. Dispersion patterns can be described as follows: contagious, random, and regular patterns (Fig. 4.1). A departure from a random pattern may show the effects of forces of climate, topography or disturbance on plant spatial pattern (Turner and Gardner 1990). A contagious pattern, or contagious dispersion, shows the variance is larger than the mean, and the population may be considered overly dispersed or clumped together (Turner and Gardner 1990).



Random

Contagious

Regular

Fig. 4.1. Spatial distribution types.

I employed several sampling strategies to describe plant patterns and the environmental and resource patterns associated with them. First, a general climate analysis was used to model temperature and precipitation trends. Second, both a Nearest-Neighbor technique and a belt transect technique were used to sample conifer invasion patterns in meadows. Third, dendrochronology techniques provided the date of establishment that can be analyzed in conjunction with the climate data. To determine the role climate serves in initiating conifer invasions into subalpine meadows, emphasis was placed on local trends in temperature and precipitation over the past century. Moreover, raw data were parsed into seasonal trends and examined in relation to the occurrence of conifer invasions.

4.1 General Climate Analysis

Climate data analysis was applied in this study to determine if increases in tree establishment are associated with climate change. Comparisons of conifer establishment dates to the climate trends of the corresponding periods were used to evaluate the role of regional climate patterns of conifer invasions into the subalpine meadows. Evaluation of climate trends may also indicate a relationship between climate and conifer invasion.

Historic climate data from neighboring climate stations of the Preston Park area were used to construct a historical climate model. Daily data were downloaded from the National Climate Data Center (NCDC 2006). Daily temperature, precipitation and snow depth data were available for the following Montana stations: Babb, East Glacier, Kalispell, Many Glacier, and St. Mary (Table 4.1) (Fig. 3.1). Daily temperature, precipitation and snow depth data were available for Lethbridge, Canada, and were downloaded from the Adjusted Historical Canadian Climate Data (AHCCD) website (AHHCD 2008) (Table 4.1).

Table 4.1. Stations examined for climate data analysis.

Station ID	Station Name	City	State	Start Date	End Date	Latitude	Longitude
240392	Babb 6 NE	Babb	MT	7/01/1948	2/28/2001	48.56	-113.22
244558	Kalispell Glacier Pk Int'l Ar	Kallispell	MT	1/01/1899	7/31/2002	48.18	-114.16
247292	St Mary	St Mary	MT	5/01/1981	9/30/2002	48.44	-113.26
244563	Kalispell	Kallispell	MT	1/01/1948	12/31/1952	48.12	-114.19
246615	Polebridge	Polebridge	MT	7/01/1948	7/31/2000	48.46	-114.17
245361	Many Glacier	Many Glacier	MT	8/09/1967	10/31/1980	48.48	-113.39
3033880	Lethbridge	Lethbridge	CA	6/01/1886	Present	49.37	-112.48

Data retrieved included: maximum mean temperature, mean temperature, mean minimum temperature, total precipitation, Pacific Decadal Oscillation (PDO) and snow depth. The daily data were aggregated into monthly values (Table 4.2). NOAA standard units were converted into metric units. Babb climate stations is the closest to the study site on the East side of the park, it was the control used for comparison for Preston Park ecological data. The Babb station has the highest elevation of the surrounding stations, 1,377 m, and is situated on the east side of the Continental Divide. Babb's distance is approximately 23.6 kilometers from Preston Park.

Table 4.2. Seasonal partition used to segregate seasonal data.

Season	**Months**
Winter	December, January, February
Spring	March, April, May
Summer	June, July, August
Fall	September, October, November

Long term trends in the climate data were shown by graphing the data over time. Graphs of plotted data were smoothed based on 2, 5 and 10-year averages. These data were used to show visual climate trends and were plotted with tree establishment trends. The 5-year average of climate was chosen based on the resolution of the available tree establishment data.

Seasonal means were calculated and used to identify climatic conditions associated with establishment pulses. The data were compared against establishment pulse using the overall climate data in order to show establishment pulse-climate correlation and the effects of general climate on establishment pulse.

4.2 Regression Analysis

Because Lethbridge is the closest station to Babb on the east side of the divide and has the longest data record (data available from 1886), it was chosen for data to model Babb data back in time. A simple linear regression was performed between the Babb station, the dependent variable, and the Lethbridge station, the independent variable to measure the strength of their linear relationship. The resulting regression coefficient and the constant were used to extend the observational record back in time for Babb matched to the length of surrounding station’s records into the 1880s. The predicted data in addition to the actual climate data for Babb were used to evaluate the role of local climate patterns of conifer invasions into the subalpine meadows. Dates from the model used were from 1882 to 1942.

4.3 Climate Data

The data used to model the predicted temperatures for Preston Park were based on data from the Babb and Lethbridge climate stations. The Babb dataset was chosen as the primary station because of its proximity to Preston Park, but the dataset is limited in time, 1944 to present. Babb climate station has the highest elevation of both stations, 1,377 m and is situated on the east side of the Continental Divide. Babb has the coolest temperatures, most likely due to its higher elevation. Lethbridge is situated on the east side of the Continental Divide and is located approximately 120 km distance northeast from Babb. Lethbridge climate station has an elevation of 929 m. Lethbridge has the longest data set, beginning in 1886 to present but it does have periods of missing data from the early 1900s and the 1920s (Fig. 4.2).

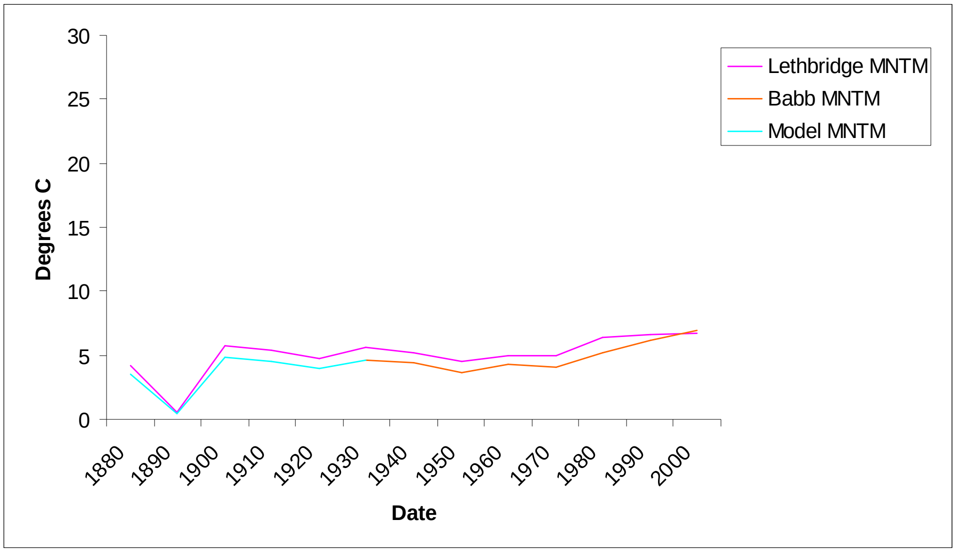


Fig. 4.2. Mean temperature for all the climate stations charted with the predicted model.

Temperatures at climate stations in the vicinity of GNP are highly correlated (Table 4.3). Linear regressions used to predict temperature for Babb based on Lethbridge are all highly significant and have very high R^2 values (Table). Lethbridge had a greater effect in the models for mean temperature and mean minimum temperature and was used for modeling Babb data (Table 4.4).

Table 4.3. Regression statistics listed for the climate stations based on mean monthly average temperature, mean monthly minimum temperature, mean monthly maximum temperature. Lethbridge is the independent variable, and the Babb model is the dependent variable.

Model Summary	**Adjusted R Square**	**Std. Error of the Estimate**	**B**	**F-stat**	**P**
Babb Model (MNMT)	0.947	1.98915		5721.52	< 0.001
Lethbridge (MNTM)			0.743		
Babb Model (MMNT)	0.976	1.162		14012.3	< 0.001
Lethbridge (MMNT)			0.867		
Babb Model (MMXT)	0.951	2.29649		6636.87	< 0.001
Lethbridge (MMXT)			0.366		

Table 4.4. List of regression coefficients and constants used to construct predicted data for Babb for maximum mean temperature, mean temperature and minimum mean temperature.

Climate variable	**Regression coefficient**	**Constant**
MMXT	0.874	1.269
MNTM	0.84	-0.012
MMNT	0.819	-1.855

In contrast to the temperature data, the relationship between the climate stations for total precipitation (TPCP) is weak. Although a significant regression model can be fitted to the data, its predictive power is very low (Table 4.5). Therefore, I will not use this model to explain the possible effects of climate on subalpine conifer establishment. I will use the raw data for Babb collected by both the local climate station and the National Weather Service (NWS) observation. These observations have been corrected for error by the NCDC and extend back in time to 1907. For precipitation the periods of 1882 to 1906 will be missing from the correlation and regression analyses.

Table 4.5. Regression statistics listed for the climate stations based on total precipitation (TPCP).

Model Summary	Adjusted R Square	Std. Error of the Estimate	β	Fstat	P
Babb Model (TPCP)	0.251	1.88008		154.83	<0.001
Lethbridge (TPCP)			0.383		

4.4 Mapping of Transects and Meadow Boundaries

4.4.1 Delineation of Meadow Boundaries

To assess spatial patterns of system structure it is necessary to examine a suite of spatially distributed data at a variety of spatial scales (Kennicutt and Wolff 1998). Meadow boundaries were delineated as the break from mature forest with an herbaceous and grass species dominant area. Analysis of meadow invasion pattern over space and time was examined using point data. Analysis of tree positions in meadows allows a better understanding of the processes driving these changes in pattern and of the environmental and resource variables that support them. Information of the invasion pulses can be mapped and may explain what role climate change has had in the past century on the meadows of today.

Data used are both vector and point based data. These data are useful for examining the following: spatial autocorrelation, frequencies along transects, proximity of individuals from meadow boundary, woody patch spatial trends, patch trends from meadow boundary, and spatial trends correlated to environmental data.

4.4.2 Tools Used to Map Meadow Boundaries

The standard field equipment used for the meadows were as follows: Trimble Geoexplorer GPS unit. Laboratory software used for displaying, creating and analyzing maps was ArcView 3.2 GIS. This software was used for mapping and analyzing point data, vector data and attribute tables. Walking the perimeter of the meadow/forest boundary, denoted by the height of the mature forest and the dominance of the herbaceous species, the GPS logged points constantly. These data were used to create a digital line map. One exception to these mapping procedures was the boundary of meadow 3, which was created using a USGS 1 m orthorectified image, an image in which terrain distortions have been removed, to digitize a digital line map of this meadow boundary.

4.4.3 Transect Delineation for the Nearest Neighbor Technique

Observed variation in the number of individuals presence and absence are often the result of tolerances of a species to environmental gradients (Gilbertson et al. 1985). Line and belt transects are best applied when zonation is pronounced, such as slopes, environmental gradients, soil moisture gradients, lithological gradients and impact gradients (ex. trampling), and it is especially useful across boundaries of vegetation types, such as transitions to forest to woodland to meadow (Gilbertson et al. 1985). Since the study area is zoned both by elevation and vegetation type, the systematic techniques of line and belt transects are ideally used for this study. Both types of transects were situated to capture maximum invasion pattern, and are generally associated across known environmental gradients.

Clearly defined transects are used to avoid overlap of samples measured and to reduce the likelihood of capturing the same sample twice. Transects were run from upper meadow/forest boundary to the lower meadow/forest boundary with the exception of meadow 7, which was situated in a drainage. Transect endpoints extended approximately 10 meters beyond the meadow margins. Transect lengths varied due to variations in meadow sizes. Transects were situated so as not to capture the same area twice. General topography and the situation of the Preston Park Trail caused some transects to deviate from a simple straight line, but these transects were delineated as straight as possible (Fig. 4.3).

Randomly generated sampling points permit the detection of spatial trends in each meadow, while adequately representing patterns of establishment. Once a transect was positioned, a random number generator (RNG) was used to define sampling points along the entire length of the transect at 1 to 9m intervals (Fig. 4.3). The position of trees near these sampling points was recorded with a GPS.

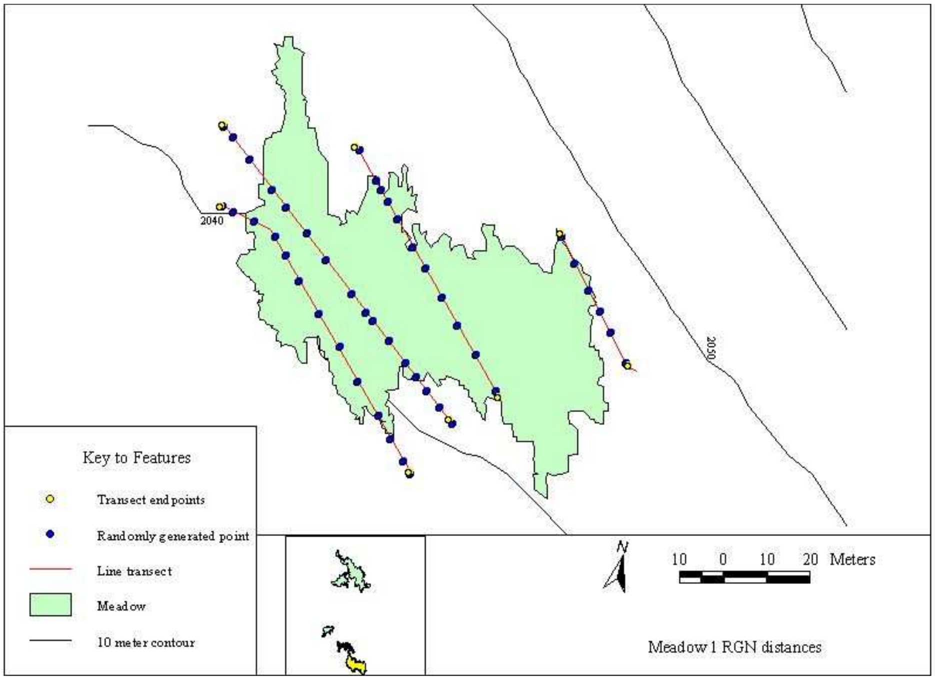


Fig. 4.3. Meadow 1 transect layout and random generated point locations.

4.5 Belt Transects

For lower elevation meadows a 10 m wide belt transect was delineated across the meadow/forest boundary and it was positioned to capture the greatest amount of seedling establishment. A large forest fire broke out in the adjacent basin while sampling, so it was necessary to speed the timing of data collection. Because meadow invasion was so dense at the higher elevations, a 5 m wide belt transect was deemed sufficient to capture density and pattern while allowing a shorter period of time to collect data for these meadows. The 5 m belt was delineated across the meadow/forest boundary and it was also positioned to capture the greatest amount of seedling establishment. The position of the belt was recorded with the GPS. Hand-drawn maps of the belt transects were used to determine the location of each individual with greater precision than a GPS which may log different trees at the same point. Therefore, the coordinates of each tree were excluded in the belt sampling, but the tree position was hand-drawn and noted relative to its neighbors. The belt transect data contains more sampling points, and was used to validate the sparser data of the nearest neighbor transects to ensure data accuracy.

4.5.1 Transect Delineation for the Belts

Each belt transect was positioned to capture the greatest amount of invasion in each meadow. Based on visual estimation of obvious pattern, a measuring tape was used to demarcate 10 m swath of the greatest meadow invasion from forest boundary-through the meadow- to opposing forest boundary. The transect boundary was flagged and recorded via a GPS at 2m intervals along the belt. A sketch of each 2X10 section of the belt was drawn in the field, and the location of each individual tree was plotted by hand (Fig. 4.4 and Fig. 4.5). A forest fire was adjacent to the sampling basin during the sampling period of the last three meadows. To insure these meadow data were collected before being burned, the belt transect was adjusted to a smaller 5 m swath to insure all remaining proposed meadows were sampled. Though smaller in size, the 5 m will still offer comparative data for spatial analysis.

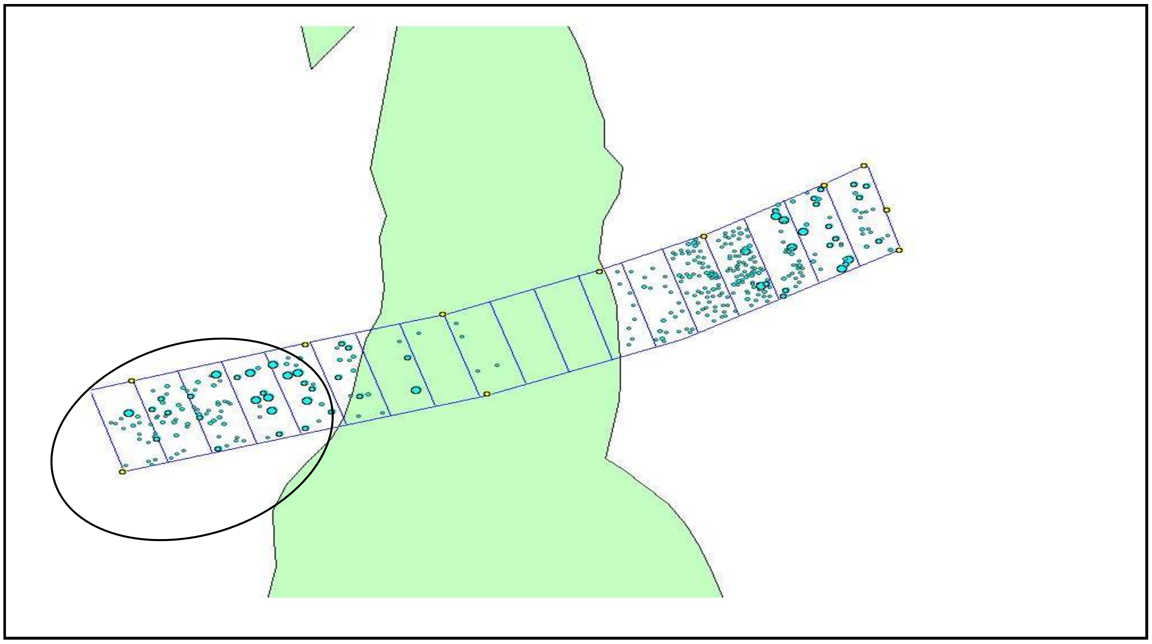


Fig. 4.4. Computer-drawn belt showing Meadow 5 belt transect sampling. The symbols represent individual trees. The green space is the meadow. The circled area represents the area enlarged in Fig. 4.5.

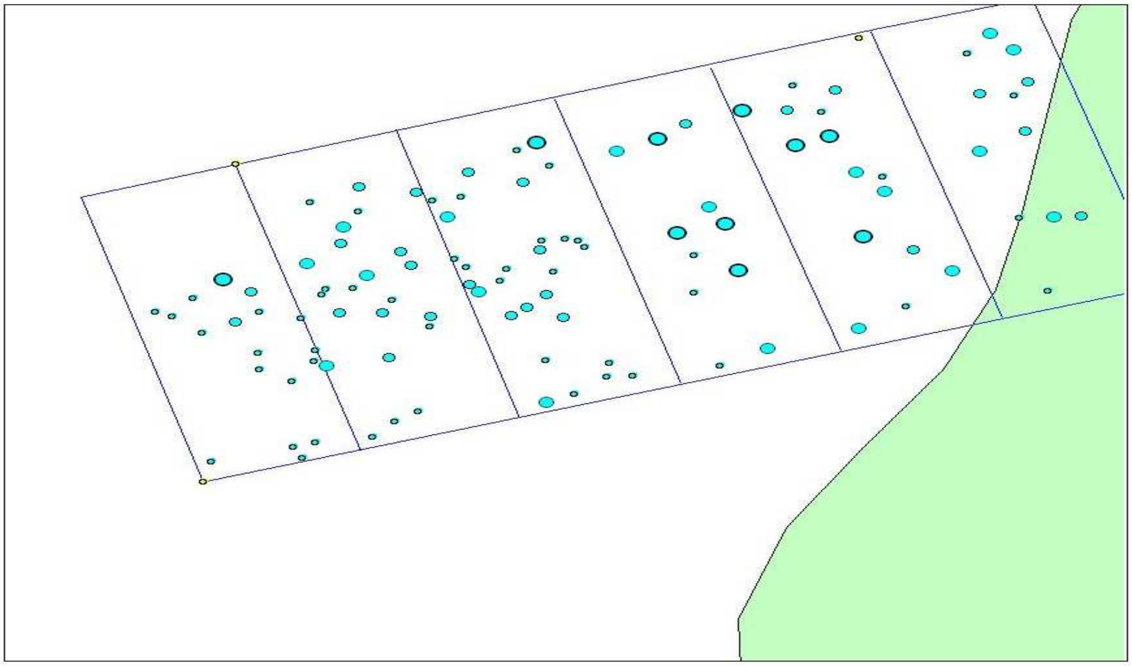


Fig. 4.5. Portion of hand-drawn belt showing a 10m by 2m swaths in Meadow 5. The symbols represent individual trees. Trees are graded by size with larger symbols being larger trees and smaller symbols being smaller trees respectively.

Each tree was sampled for data excluding the acquisition of the small diameter trees for dendrochronological analysis as because they could not be cut down for cross sections per the request of the National Park Service (NPS). The belt transects were then digitized using a Geographic Information System (GIS) (Fig. 4.6). Categorical maps based on compositional thematic data, such as tree size classes, tree age classes, and tree invasion patterns over time were evaluated for spatial configurations against system properties which exhibit preferred directional orientations, such as elevation patterns (Gustafson 1998). Attributes recorded for each tree were soil depth, diameter, and height (Fig. 4.7).

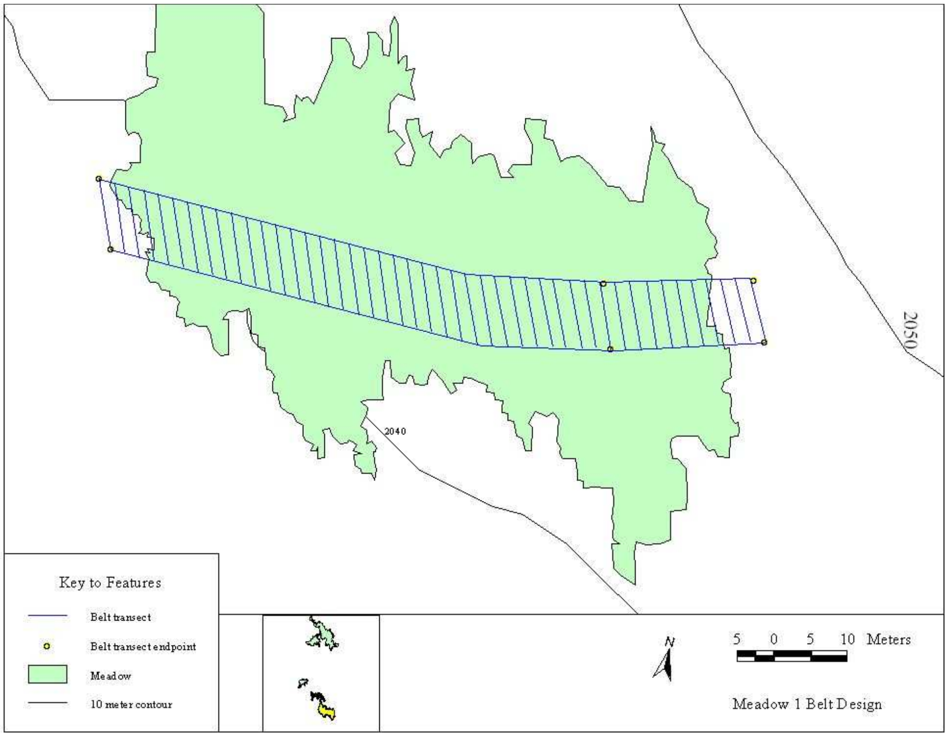


Fig. 4.6. Belt transect layouts within meadow 1.

Fig. 4.7. An example of a belt transect layout used in Meadow 9.

4.5.2 Nearest Neighbor Technique

The high densities of trees and saplings in the sample area restricted the use of typical plot methods, such as quadrats, so a plotless sampling methodology was implemented utilizing the Nearest-neighbor technique. The Nearest-neighbor technique examines “non-randomness” in vegetation with weak patterns not attributed to causal environmental factors as well as strong patterns caused by environmental factors (Kershaw and Looney 1966). Samples are taken at randomly generated points, and the distance from the nearest individual of a tree species to its neighbor are measured to determine tree density for a species (Gilbertson et al. 1985).

The nearest neighbor technique allows data collected to be analyzed for a departure of the spatial distribution of objects from random (Cottom and Curtis 1956, Southwood and Henderson 2000). The closest individual technique of the nearest neighbor method was employed for this study. A randomly generated point (P) on the transect was chosen, and the distance between this point and the nearest neighbor (N1) was measured. Then the distance between N1 and the second nearest neighbor (N2) was measured. All distances were measured by hand to ensure precision for the nearest neighbor points (Southwood and Henderson 2000). The closest-individual technique measures tree density and tree pattern for each meadow as it takes into account the additional sample spatially, and this information can be used to correct for bias due to object's non-random spatial distribution (Engelman et al. 1994, p.1770) (Fig. 4.8).

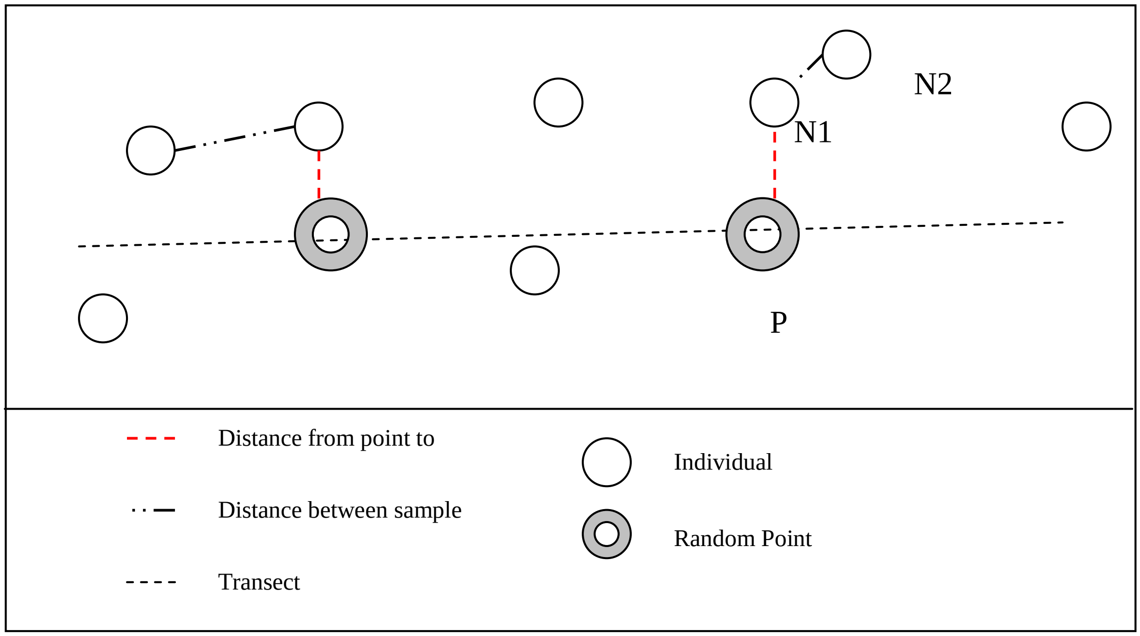


Fig. 4.8. The Nearest Neighbor method for plotless sampling describing how measurements were taken. A point is placed at random and the distances to the nearest individuals are measured.

4.5.3 Data Collected Using the Nearest Neighbor Technique

When a tree and its nearest neighbor were selected, the species of each was recorded. Its location in the meadow was noted based on the following: upper forest (UF), upper meadow (UM), mid-meadow (MM), lower meadow (LM), and lower forest (LF) (Table 4.6). If a meadow was situated in a drainage, then the classification was based on its proximity to the highest and lowest contour. If the individual was a seedling or a small tree, then the basal diameter was recorded. If the individual was mature and above 3.5 m tall, the dbh was taken. The height of the small trees was recorded. A core from the tree was extracted for dendochronological analysis. If a tree was situated on a rise (R), Depression (D), or flat surface (F), then this was noted (Table 4.6). A soil probe was used to record soil depth for both the tree and its nearest neighbor (Table 4.6).

Table 4.6. Field data to be collected for the Nearest Neighbor Transects.

1.0 Ecological	2.0 Resource	3.0 Mapping
Species	Soil depth	Seedling/tree positions (GPS)
Diameter from base for seedling, diameter at breast height (dbh) for mature individuals	Topographic Situation: R, D, F [a]	Transect endpoint locations (GPS)
Small increment diameter core from the base for the seedling, dbh for mature individual		Meadow boundary (GPS)
Distance to randomly generated point, distance to nearest neighbor,		Location within meadow: UF, UM, MM, LM, LF [b]
Height		

a=R (Rise), D (Depression) and F (Flat)

b= UF (upper forest), UM (upper meadow), MM (mid-meadow), LM (lower meadow), and LF (lower forest)

4.6 Data Collected Using the Belt Technique

Table 4.7 lists the data were collected for the belt transect, including the tree species, and its location in the meadow was noted based on the following: UF, UM, MM, LM, and LF. If the individual was a seedling, then the basal diameter was recorded. If the individual were mature and above 3.5 m tall, the dbh was taken. The height of the trees was recorded. If a tree was situated on the following: R, D, or F, then it was noted. A soil probe was used to record soil depth for both the tree and its nearest neighbor.

Table 4.7. Field data to be collected for the belt transect.

1.0 Ecological	2.0 Resource	3.0 Mapping
Species	Soil depth	Seedling/tree positions (fine scale mapping by hand)
Diameter from base for seedling, diameter at breast height (dbh) for mature individuals	Topographic Situation: R,D,F[a]	Transect endpoint locations (GPS)
Height		Meadow boundary (GPS)
		Location within meadow: UF, UM, MM, LM, LF[b]

a=R (Rise), D (Depression) and F (Flat)
b= UF (upper forest), UM (upper meadow), MM (mid-meadow), LM (lower meadow), and LF (lower forest)

This method determines the spatial distribution and pattern, which allows the density of trees can be estimated. The information gathered from this technique was mapped and used for statistical analyses on invasion pulse: size class distributions, age class distributions, density-distributions, abundance, the relationships of distributions to measured environmental variables, and the changes in patterns and relationships with elevation.

4.7 Dendrochronology Techniques

Dendrochronology determines tree age to analyze the spatial and temporal changes of conifer invasions. These spatial and temporal changes in tree pattern are associated with physical processes, such as the climate and other environmental conditions. Dendrochronology provides establishment chronologies and is used to correlate conifer invasion with climate changes. Specifically, comparison of tree establishment chronologies to climate was used to correlate trends and to determine tree invasion history (periods of invasion), track meadow pulses, and compare the invasion pulses of meadows with elevation. Using a small diameter increment bore made this technique less destructive or invasive, and it considerably reduced the possible adverse impacts of the study on the meadows.

4.8 Dendrochronolgical Data Collected

Increment cores were collected from small trees between one to three meters tall using a small diameter increment borer. Only one core was taken per tree, and these cores were located facing away from park trails. Cores were removed in areas where rings will not be convoluted: below branches and opposite sides of the trunk exposed to steep terrain. For seedlings and saplings the cores were taken to the pith and as near to the base as possible. For mature trees the cores were taken at breast height. Cored trees were plugged with adhesive polymer to deter bacteria that could initiate rot as per GNPS request.

Following standard dendrochronological procedures, the cores were air-dried and mounted into a slotted mount. Mounting of conifer species required the orientation of the core to be similar to its orientation in the tree; and it is necessary to align the core with a vertical arrangement of the cells visible at the end of the core (Stokes and Smiley 1968, Grissno –Mayer 1996). Once mounted, the cores were sanded with a belt sander to achieve a fine surface on the core and to make the cells distinct and visible.

Using a boom-arm stereozoom microscope, tree rings were counted at least three times. Ring widths were measured twice to perform skeleton plot analysis for cross-dating procedures to ensure periods are not missing and to assign a true year of tree ring formation (Sheppard 2002). Age data were added to data tables for analysis (Fig. 4.9).

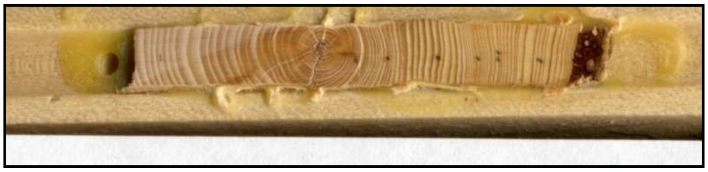


Fig. 4.9. Image of a prepared core that has been dated. Each symbol on the core marks ten years of tree ring growth. The doubled mark represents 50 year segments.

Skeleton plotting is the characterization of “non-average” tree ring growth showing years in which certain rings stand out and are recorded on a graph. Skeleton plotting is somewhat subjective and requires experience and consistent practice. Average ring widths are unmarked with narrow rings being noted with a vertical mark

(Fig. 4.10). The more narrow the ring then the taller the mark. Rings that are considered very wide or rings that may be absent or false are also noted. These marks create a pattern that can be compared from tree to tree (Sheppard 2006) .

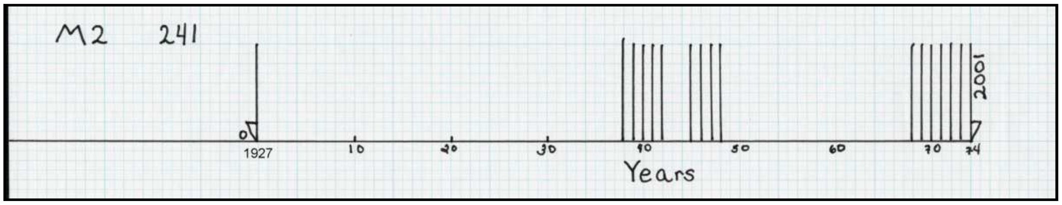


Fig. 4.10. Image of skeleton plot for the tree core shown above (Fig. 4.9).

4.9 Data Analysis

4.9.1 Analysis of Establishment Data

The methods listed above yield residual climate, modeled climate data subtracted from the mean data, and age data analyzed for temporal and spatial patterns in establishment for forest and meadows over an elevation gradient. The residuals of the establishment data were correlated with the residuals for climate using Pearson’s bivariate correlation. Pearson’s bivariate correlation produced correlation coefficients used to determine linear associations. The establishment data were grouped in the following categories: Total (meadow + forest), forest and meadow. These forest and meadow categories were subdivided further to explore trends due to elevation: lower forest, lower meadow, upper forest and upper meadow. Climate categories were mean maximum temperature (MXMT), mean temperature (MNTM), mean minimum temperature (MMNT), total precipitation (TPCP), and Pacific Decadal Oscillation (PDO). Finally, all categories were analyzed for trends at both the decade and pentad levels. Once significant relationships were found, a stepwise multi-regression analysis was used to determine the strength or influence the independent variables in climate have on the dependent variable of establishment.

The methods listed above also yield age class and size class distributions based on information gathered from the conifers in the meadows. When mapped, age and size class distributions yield spatial and temporal patterns of tree establishment. These patterns are analyzed against climate in order to determine establishment trends in association with climate. Variability in age class may reflect interannual establishment, mortality, or recruitment to sapling or tree size classes (Johnson et al. 1990, Veblen and Daniels 2004).

4.10 Analysis of Spatial Pattern of Establishment

The measurement of point pattern combined with establishment dates gathered from the age class data and climate allow the determination of long term conifer invasion trends. Point pattern analyses that measures clustering were used to compare meadows to determine if there is an overall spatial pattern, such as clumped, random or regular patterns of establishment.

4.11 Density Mapping

The second-order neighborhood spatial analysis on Ripley’s K function is a useful method to analyze non-regular patterns of recruitment of woody species in harsh physical environments. A circle of radius *t* is placed around each sample point, which in this study represents a tree, and the number of neighboring trees within the circle is counted. Points positioned close to the boundary of the sampling plot require a weighted edge correction (Haase 1995, Haase et al. 1996):

$$K(t) = \sqrt{[K(t)/\pi]} - t$$

“If the distribution of the points is Poisson random, the expected value of the cumulative function K(t) equals πt^2, i.e. the area of a circle of radius t, which gives a linear plot of $\sqrt{K(t)}$ versus t. It has become common practice to plot the derived sample statistic $\sqrt{[K(t)/\pi]} - t$ because this expression has zero expectation for any value of t when the pattern is Poisson random (Skarpe 1991).” (Haase et al. 1996).

For statistical significance, the lowest and highest values of the spatial statistic using 99 randomizations to define the lower and upper boundaries of the 95% confidence interval were used. If the sample statistic deviates outside the confidence interval, then there is a departure from random pattern. If the departure from the sample statistic is positive, then a clustered distribution is suggested. If the departure from the sample statistic is below the confidence interval, then a regular or uniform pattern is suggested. If the sample statistic remains within the boundary of the confidence interval, then a random pattern is suggested (Haase et al. 1996).

Morans I tests for clustering at more global scales, but the Anselin Local Morans I (ALMI) is more useful in this study because it tests for clusters at local scales (Anselin et al. 2004). The ALMI is a local statistic for spatial autocorrelation that depicts spatial clusters of trees of similar diameters (positive z scores) and spatial outliers of trees with different sized diameters (negative z scores). The ALMI is calculated for each tree based on distance for point locations, and it is useful for identifying neighboring tree structure (Anselin et al. 2004). For example, a spatial distribution of significant spatial outliers may indicate tree islands (a significant pattern of large and small trees).

The Anselin Local Moran's I statistic

$$1)\qquad I_i = \frac{\chi_i - \overline{X}}{S_i^2} \sum_{j=1, j\neq i}^{n} w_{i,j}(\chi_i - \overline{X})$$

where χ_i is a feature *i* attribute, $\overline{X}$ is the corresponding attribute mean, $w_{i,j}$ is the weight between features *i* and *j*.

$$2)\qquad S_i^2 = \frac{\sum_{j=1, j\neq i}^{n} w_{i,j}}{n-1} - \overline{X}^2$$

where *n* is equal to the total number of features.

$$3)\qquad ZI_i = \frac{I_i - E[I_i]}{\sqrt{V[I_i]}}$$

where:

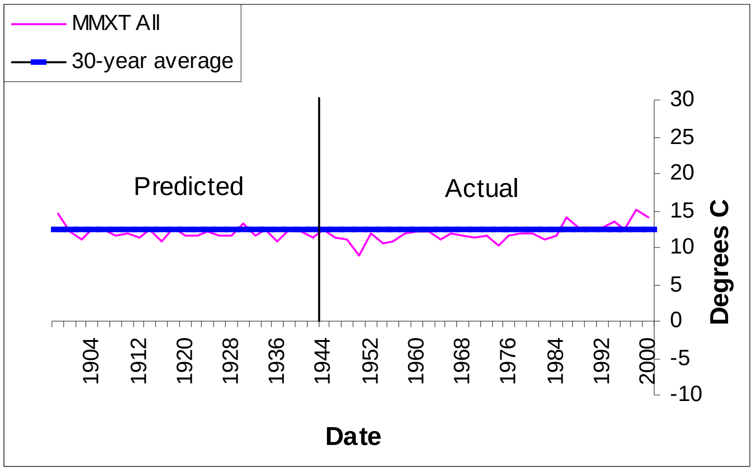
$$4)\qquad E[I_i] = -\frac{\sum_{j=, j\neq 1}^{n}}{n-1}$$

5) $V[I_i] = E[I_i^2] - E[I_i]^2$

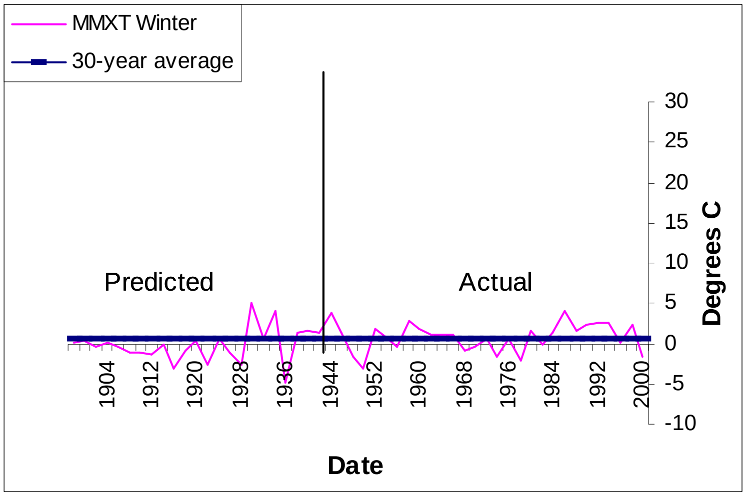
5. RESULTS

5.1 Climate Data

Results of the combined predicted and actual climate data show the following trends. Temperatures in the 1950s and the 1980s were higher than average and these temperatures have remained elevated through 2000. Cooler than average periods occurred in both the 1940s and 1970s (Fig. 5.1). Winter mean maximum temperature shows peaks in the late 1920s, early 1930s, 1940s and the 1980s through 2000 (Fig. 5.1). Spring mean maximum temperature shows the early 1900s and 1920s are warmer than the rest of the overall plotted data, but peaks are shown in the 1940s, 1960s, and 1990s (Fig. 5.1). Summer mean maximum temperature shows peaks in the 1960s and 1970s as well as an increased warming trend towards 2000 (Fig. 5.1). Fall mean maximum temperature shows peaks in the 1930s through the 1950s as well as the 1960s. Notable cooler than average periods occurred in the 1980s (Fig. 5.1). Similar annual and seasonal trends in temperatures were found in both the mean temperature and mean minimum temperature as compared to mean maximum temperature. Similar trends in annual and seasonal temperatures were found for both the 5-year and 10-year moving averages.

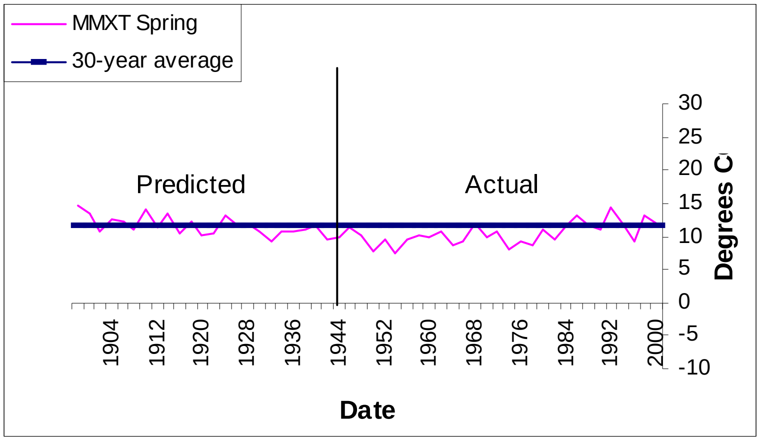


a) All Seasons

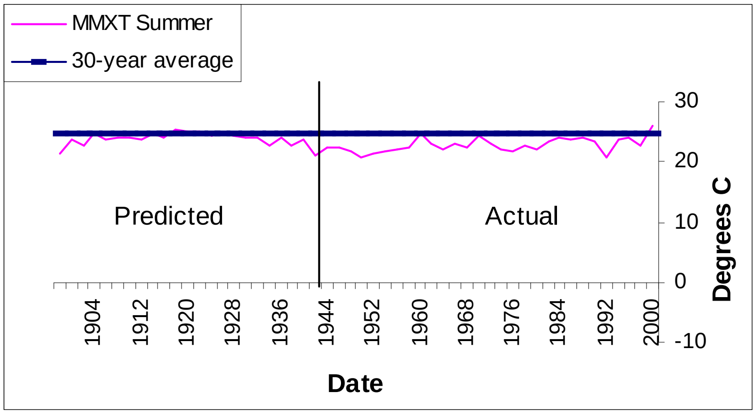


b) Winter

Fig. 5.1(a-e). Mean maximum temperature shown in both annual and seasonal graphs. The 2-year moving average of actual and predicted temperatures is shown.

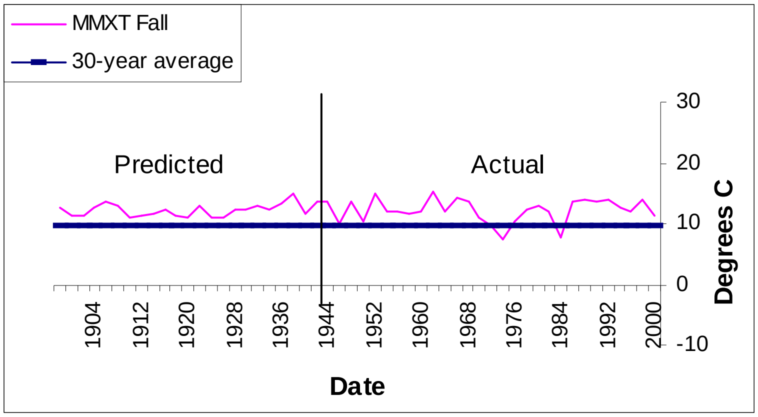


c) Spring



d) Summer

Fig. 5.1 (a-e) Continued



e) Fall

Fig. 5.1 (a-e) Continued

5.2 Establishment Data

The reverse J curve below is useful to study dynamics of populations. Counts above the curve show greater than predicted growth. Counts below the curve show less than expected growth. This curve is a representation of what we expect for forest age structure, with young trees that are actively regenerating a site. When all samples are pooled the age structure indicates periods of lower than expected establishment in decades: 1782, 1792, 1802, 1822, 1862, and 1872 (Fig. 5.2). Greater than expected establishment is shown for years 1882 to 1952.

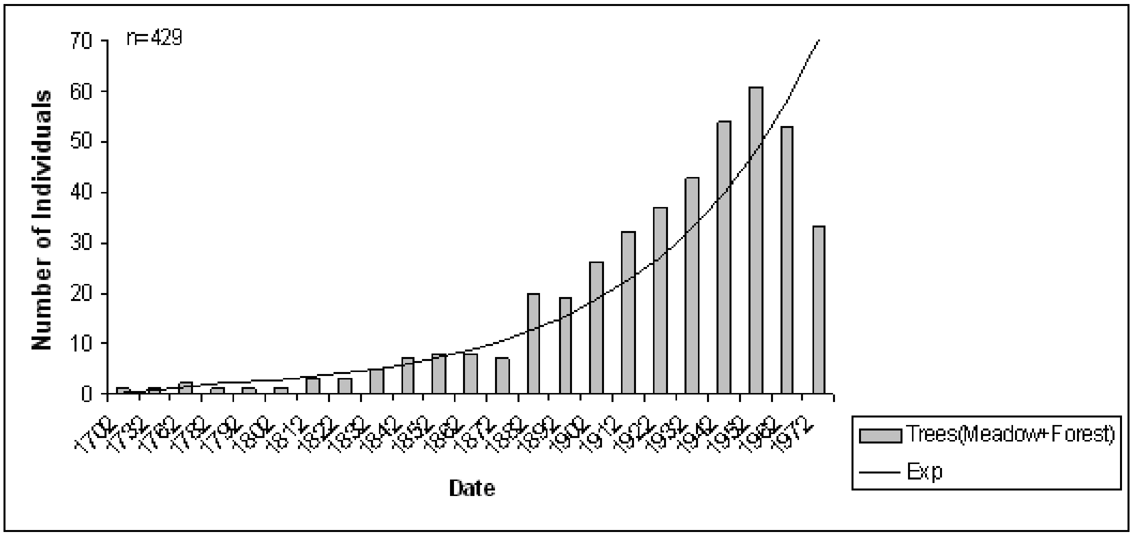


Fig. 5.2. Exponential curve of age data for both meadows and forests in Preston Park.

A similar analysis, but for forest sites only, indicates lower than expected establishment in the decades 1782 through 1862 (Fig. 5.3). Greater than expected establishment is shown for years 1872 to 1952. There is a decline in establishment after the late 1940s. The forests respond to climate a decade earlier than the total data combined.

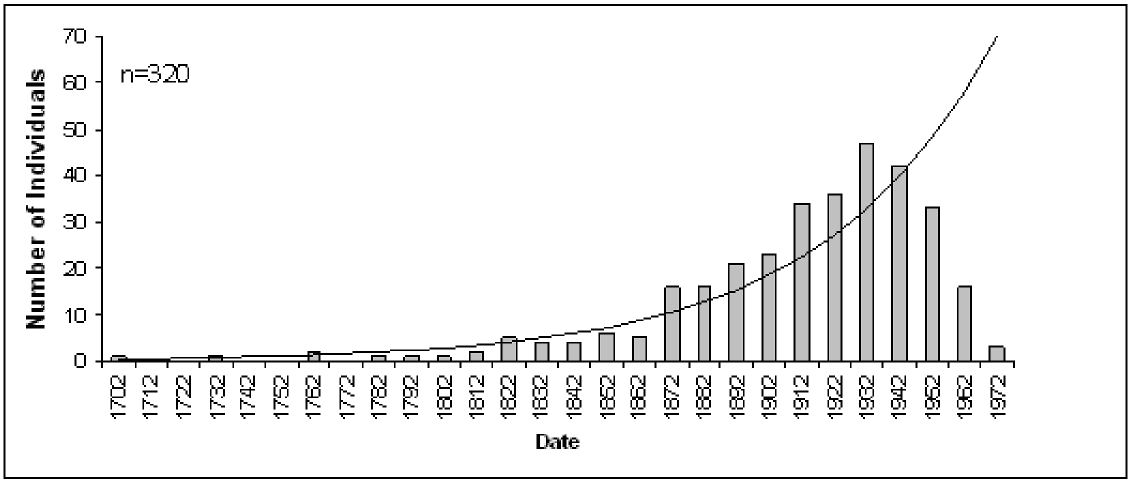


Fig. 5.3. Exponential curve of age data for forests in Preston Park.

For the meadow areas, there is less than expected establishment for the following decades: 1862, 1872 1892, 1922, 1932, and 1942 (Fig. 5.4). Greater than expected establishment occurs in 1862, 1912, 1952, 1962, and 1972. The meadows show a peak in establishment much later than forests with greater than expected establishment highest in 1912 and 1952.

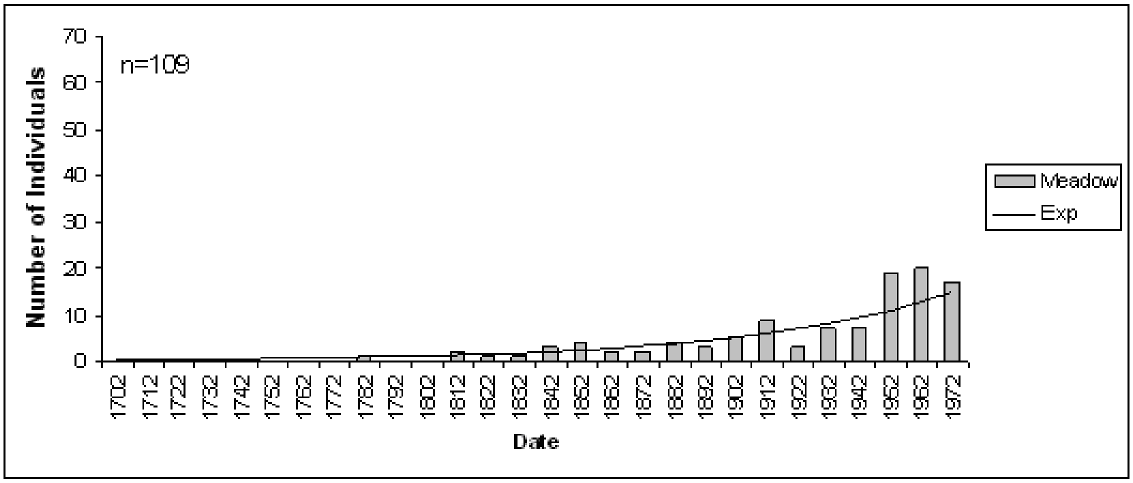


Fig. 5.4. Exponential curve of age data for meadows in Preston Park.

5.3 Site-Level Establishment Trends

Each meadow shows different trends in recruitment over time. Meadow 1 peaks for establishment start in 1926 with the highest peak in 1940. Peaks for Meadow 1 flatten by 1972 (Fig. 5.5). Meadow 2 peaks for establishment start in 1911 with the highest peaks in 1928, 1935 and 1942. Peaks for Meadow 2 become flat in 1970 (Fig. 5.5). Meadow 3, due to its smaller size, did not have enough data to calculate the exponential curve for residuals. Meadow 4 shows establishment in the early 1800s circa 1826 with peaks present in 1862, 1880, 1885, 1891. The highest peak is in 1912, but decreases over time with smaller peaks in 1919, 1925, and 1937 (Fig. 5.5). Meadow 5 shows higher than expected establishment in 1837 with peaks in 1935, 1948, 1964, 1972, and 1979 with the largest peak in 1956 (Fig. 5.5). Meadow 6 shows higher than expected establishment present in 1911 with larger peaks in 1946, 1957, 1960, 1963 and 1966 with the largest peak in 1960 (Fig. 5.5). Meadow 7 has greater than expected establishment starting in 1858 with small peaks in 1901, 1915, and 1962, but these peaks are less pronounced than peaks found in larger meadows at both high and low elevations (Fig. 5.5f). Meadow 8 has greater than expected establishment starting in 1858 with peaks in 1903, 1934, 1938, 1945, 1953, 1967 and 1974 with the largest peak in 1934 (Fig. 5.5). Meadow 9 has greater than expected establishment starting in 1826 with peaks in 1955, 1964, and 1971 (Fig. 5.5).

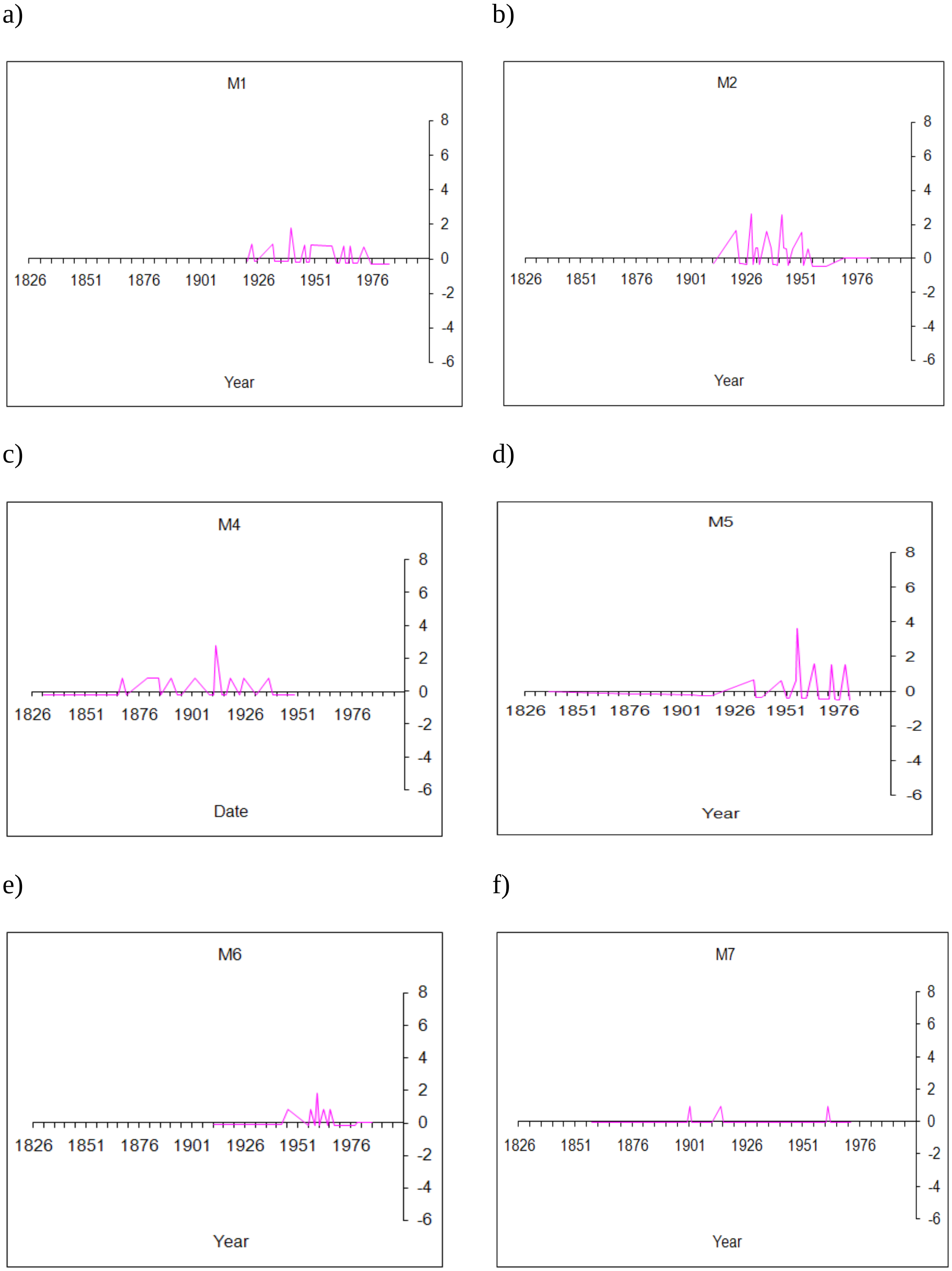


Fig. 5.5(a-h). Residuals for the exponential power curve for individuals in each meadow over time.

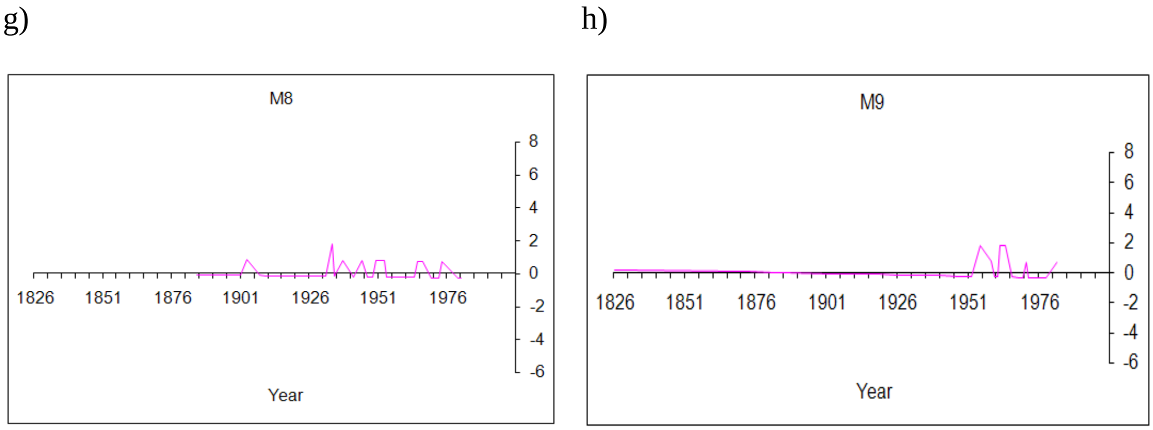


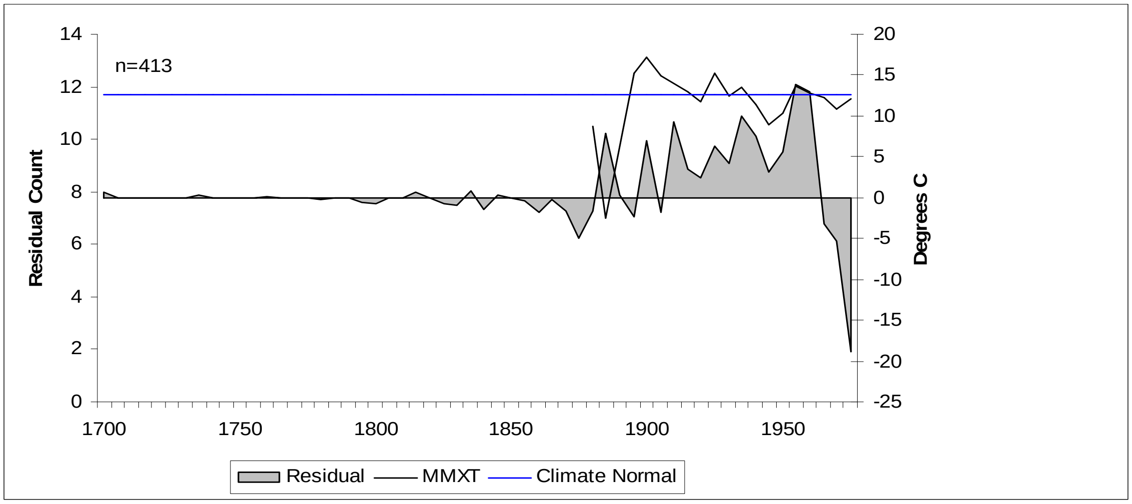
Fig. 5.5 (a-h). Continued

Establishment data for each meadow showed an increase in establishment over time. Depositional meadows and forests peaks in establishment occurred in the 1930s to the 1950s (Meadows 1, 2, 3, 4, and 8). Erosional meadows and forests peaks in the 1960s through the 1980s (Meadows 5, 6, 7, and 9). Meadow 7 is an exception with peaks in the 1920s and 1930s, then a decrease in establishment over time until the 1960s and 1970s when this meadow has a secondary peak (Fig. 5.5). Meadow 3 has limited data but shows an increase in individuals in the 1960s and 1970s.

5.4 Climate Residual Data

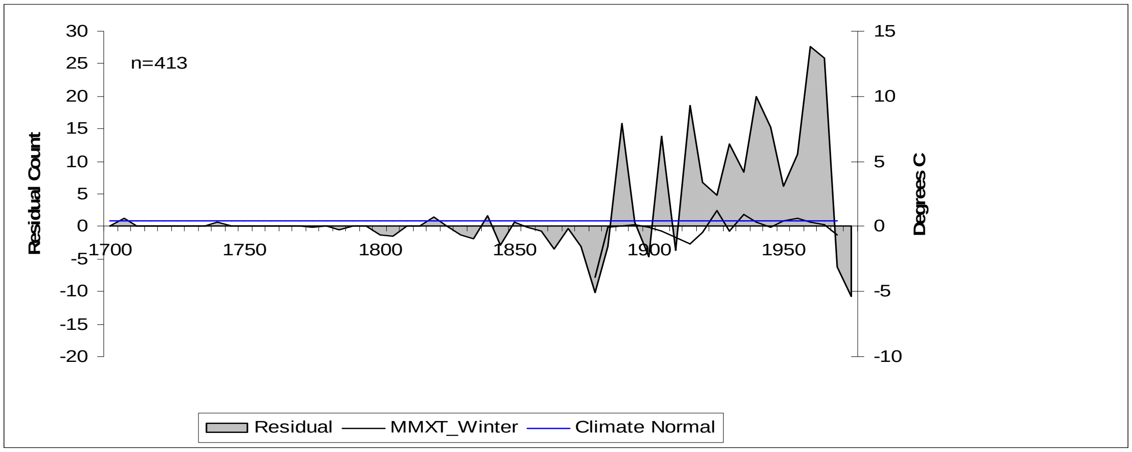
Using mean maximum temperature as an example, residuals of establishment shows below expected establishment for the periods from 1800 to 1875(Fig. 5.6). Around 1885 establishment increases over time with the exception of 1895 and 1905. Notable establishment peaks are: 1910, 1930, 1935, and all of the 1950s. The increase in establishment is consistent over time until 1960 when residuals become negative.

Notable negative peaks are 1960 and 1975. For all climate MMXT high peaks occur in 1920, 1925 and 1955 and low peaks occur in 1920, 1945, and 1975. Mean maximum temperature in winter show low peaks in 1885 and 1920 with high peaks in 1930, 1940, and 1960 (Fig. 5.6). Mean maximum temperature in spring shows temperatures below climate normals with low peaks in 1935, 1950 and 1960s (Fig. 5.6). Mean maximum temperature shows temperature below climate normals wFig. 5.6). Mean maximum temperature for fall was above climate normals in 1900, 1915, and 1935 (Fig. 5.6).

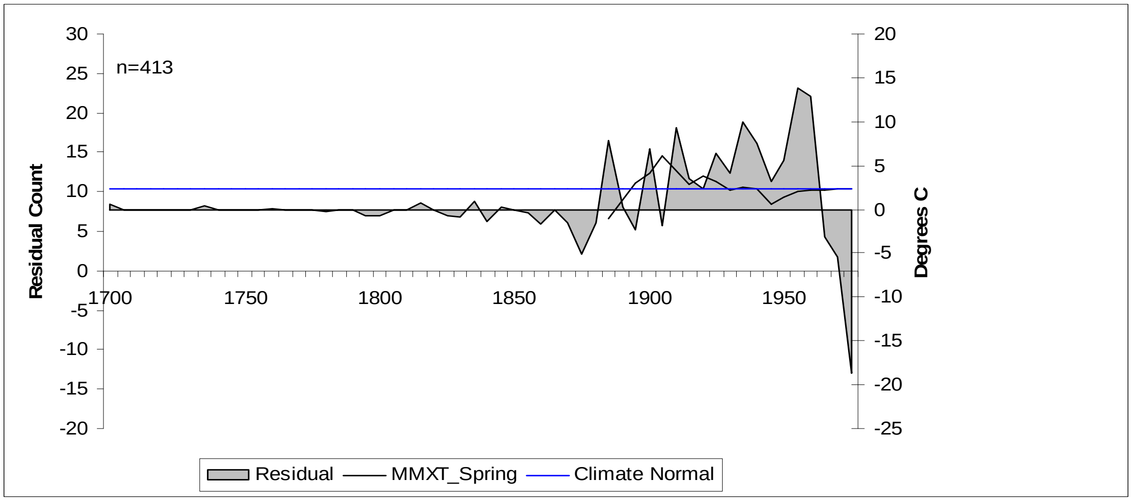


a) Annual

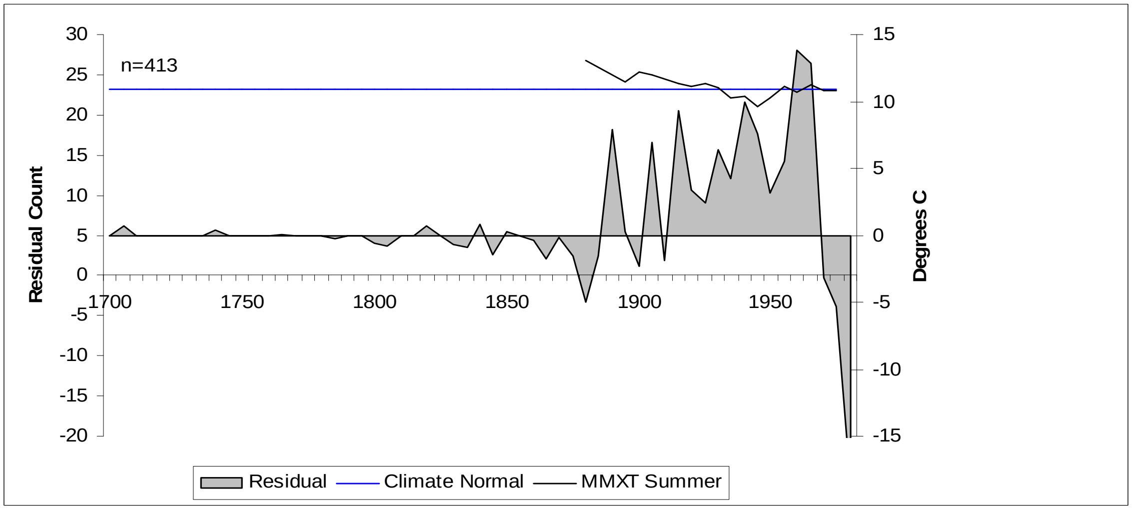
Fig. 5.6 (a-e). Pentad residuals of establishment plotted with mean maximum temperature (MMXT).



b) Winter

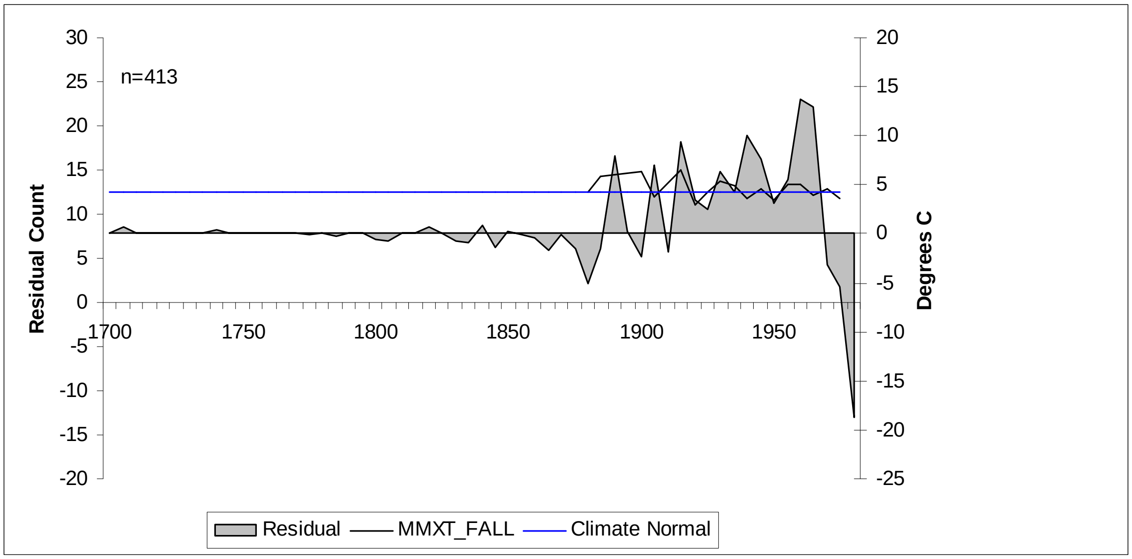


c) Spring



d) Summer

Fig. 5.6 (a-e). Continued



e) Fall

Fig. 5.6 (a-e). Continued

Because a pith estimator was used to calculate missing rings on many cores, the tree ring resolution was not accurate to within a year. The annual data were not used in the analysis, but pentad data were used. Due to limitations placed on sampling procedure via National Park Service restrictions, contemporary establishment was not adequately captured within the last 28 years. To determine the latest date of which establishment is adequately represented in my data I calculated the standard deviation of the residuals of the reverse j curve for all establishment data. Any year within a standard deviation below the predetermined threshold value of -1.87 showed outliers and was considered a year of insufficient data. These years were removed to maintain the rigor of the analysis (Fig. 5.7) (Table 5.1).

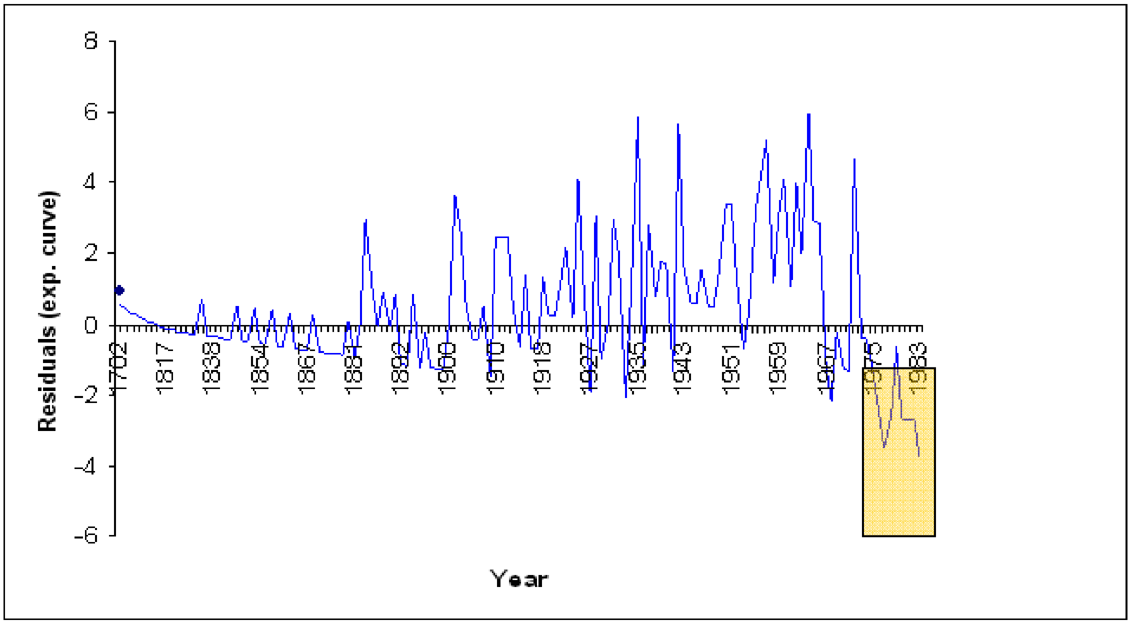


Fig. 5.7. Shaded area shows outliers of years due to sampling inadequacy.

Table 5.1. List of dates with standard deviations beyond tolerance threshold of -1.87.

Year	Number of Individuals	Residual
1976	2	-2.49
1977	1	-3.53
1978	2	-2.57
1980	2	-2.65
1981	2	-2.69
1982	2	-2.73
1983	1	-3.77

5.5 Correlation of Climate Data with Residual Data

The decadal data showed no significant trends in the Pearson’s bivariate correlation at the $p \leq .05$ level of significance. There is no discernable linear relationship between establishment and climate for the categories: total, meadow, and forest, lower forest, lower meadow, upper forest, and upper meadow. These data are not sufficient to explore the relationship between climate and establishment at the decadal time scale.

For pentads, however, significant correlations exist. Forest data showed a positive correlation to fall mean maximum temperatures ($p \leq 0.05$). Forest data showed highly significant relationship to total precipitation and winter precipitation ($p \leq 0.01$). Finally, forest data show a positive significant relationship to Pacific Decadal Oscillation (PDO) ($p \leq 0.05$). Meadow data showed negative correlations to winter, spring and summer PDO ($p \leq 0.05$). Total data shows a significant, positive trend with total and winter precipitation ($p \leq 0.05$) (Fig. 5.8).

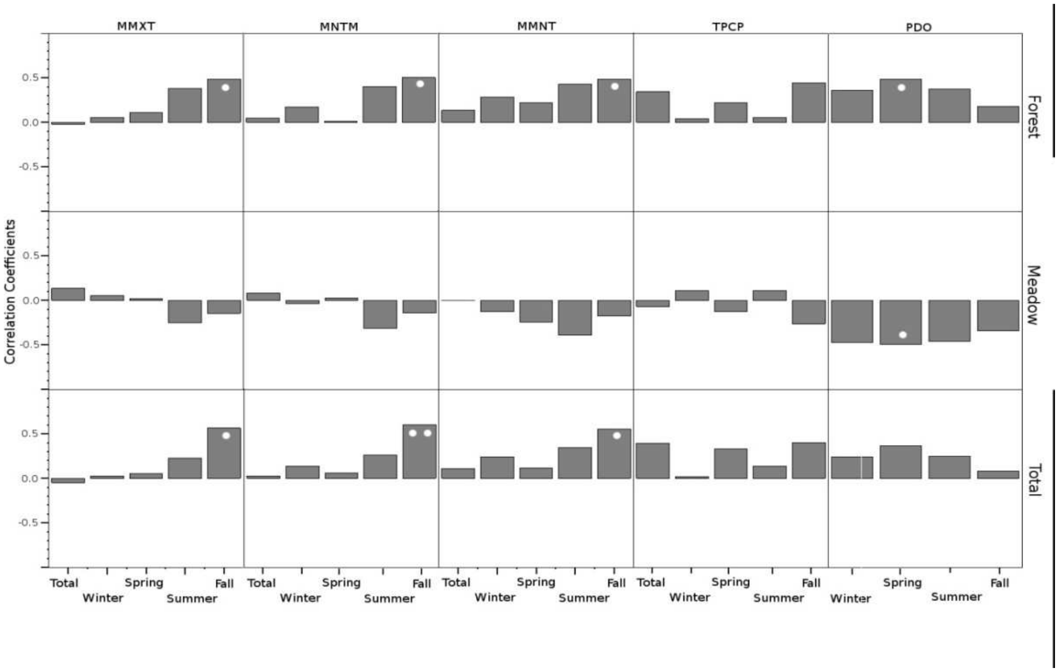


Fig. 5.8. Correlation coefficients of residual establishment data for forest, meadow and total (forest + meadow) categories plotted against climate data (mean maximum temperature, mean temperature, mean minimum temperature, total precipitation and Pacific Decadal Oscillation) for pentad. * is significant to $p < 0.05$ level, ** is significant to the $P < 0.01$ level.

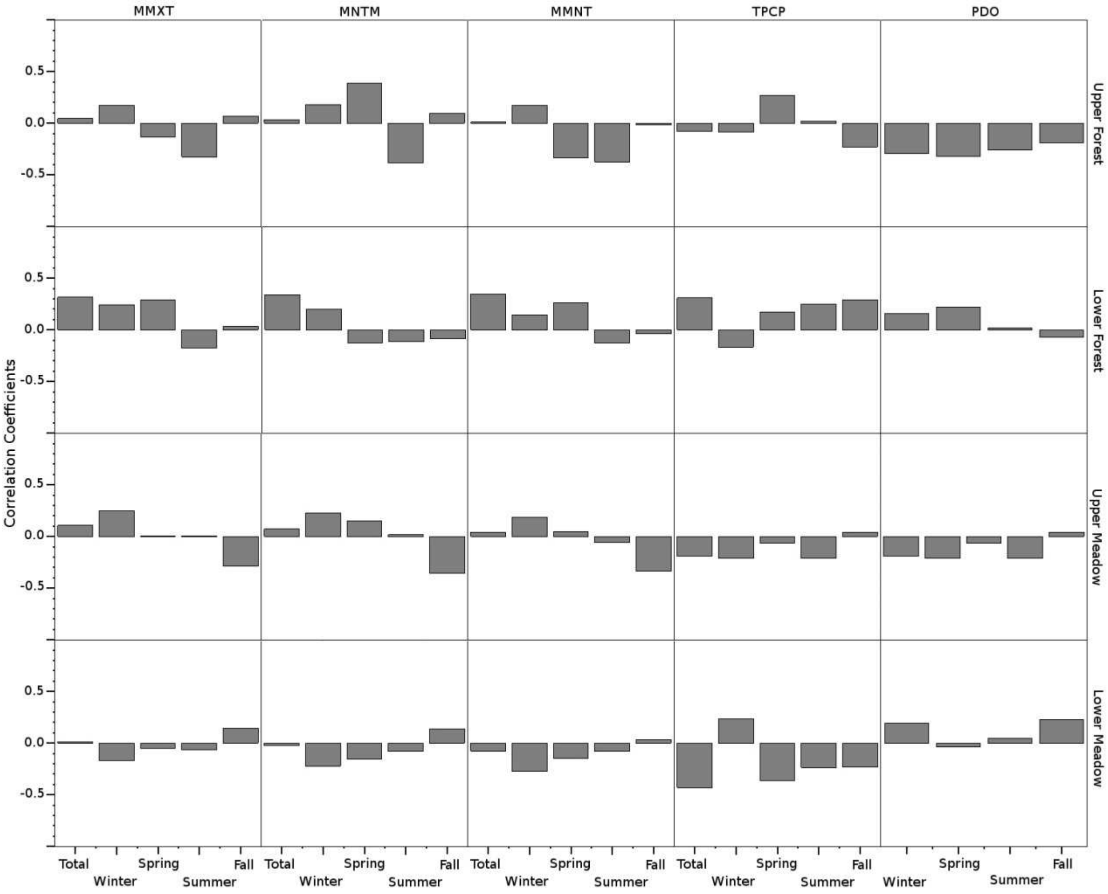


Fig. 5.9. Correlation coefficients of residual establishment data for high elevation forest, low elevation forest, high elevation meadow and low elevation meadow categories plotted against climate data (mean maximum temperature, mean temperature, mean minimum temperature, total precipitation and Pacific Decadal Oscillation) for pentad. * is significant to p < 0.05 level, ** is significant to the P < 0.01 level.

When the data are considered by their position (UF, UM, MM, LM, LF), there are significant relationships for only the lower elevation forests and lower elevation meadows (Fig. 5.9). Lower elevation forests had a significant, positive correlation with total precipitation only ($p \leq 0.05$). Lower elevation meadows had a significant negative correlation with total precipitation only ($p \leq 0.05$).

5.6 Stepwise Regression Analysis of Climate and Establishment

Stepwise regression analysis of establishment and climate data show significant R^2 values for two categories: total and meadows. For both meadows and forests combined, fall mean temperature showed the strongest relationship in predicting establishment ($r^2 = 0.35$), (Table 5.2). For meadows mean temperature in the spring showed a similar trend in predicting establishment for the forest category ($r^2 = 0.27$) (Table 5.3).

Table 5.2. Regression statistics of the total category establishment data against climate variables (annual and seasonal).

Category		Adj. R^2	Std. EE	β	F-stat	P	t	P
Total	MNTM(Fall)	0.35	13.95	0.63	7.95	0.015	2.81	0.015

Table 5.3. Regression statistics of the meadow category establishment data against climate variables (annual and seasonal).

Category		Adj. R^2	Std. EE	β	F-stat	P	t	P
Meadow	MNTM(Sp)	0.27	3.37	-.57	5.72	.03	-2.39	.03

5.7 Age Class

5.7.1 Age Class – Total, Forest, and Meadow Populations

Age classes for all meadows from the years 1702 to 1983 show the greatest number of individuals in the 26 to 50 year age class (n=132, mean age 39), but there are a large number of individuals for the 51 to 75 year age class (n= 119, mean age 62). The least number of individuals were found in the 151 to 200 year age class (n=18, mean age

167), 201 to 250 age class (n=5, mean age 219), and the > 251 age class (n=2, mean age 283). The 0 to 25 age class may be under represented due to sampling inadequacy (n=13, mean age 22) (Table 5.4).

Table 5.4. Summary statistics for the total age class.

Age Class	Min	Max	Mean	SD
< 25	20	25	22	1
26 – 50	26	50	39	6
51 – 75	51	75	62	7
76 - 100	76	100	86	6
101 - 150	101	150	119	14
151 - 200	152	187	167	10
201 - 250	201	241	219	15
> 251	266	301	283	17

Age classes for forests from the years 1702 to 1983 show the greatest number of individuals in the 51 to 75 year age class (n=103, mean age 62), but there are a large number of individuals for the 26 to 50 year age class (n= 82, mean age 40). The least number of individuals were found in the 151 to 200 year age class (n=12, mean age 166), 201 to 250 age class (n=4, mean age 219), and the > 251 age class (n=2, mean age 283). The 0 to 25 age class may be smaller due to sampling inadequacy but this age class would not survive well under a closed canopy, old growth forest dominated by larger individuals (n=13, mean age 22) (Table 5.5).

Table 5.5. Summary statistics for the forest age class.

Age Class	Min	Max	Mean	STD
0 – 25	20	25	22	1
26 – 50	27	49	40	6
51 – 75	51	75	62	7
76 - 100	76	100	86	7
101 - 150	101	150	118	13
151 - 200	152	187	166	9
201- 250	201	241	219	17
≥ 251	266	301	283	17

Age classes for meadows from the years 1702 to 1983 show the greatest number of individuals in the 26 to 50 year age class (n=50, mean age 23). There are older tree classes in the meadows with the age class 101 to 150 years having the second largest number of individuals (n=18, mean age 121) and the 51 to 75 age class (n=16, mean age 60) and the 76 to 100 year age class (n= 13, mean age 76) representing the remainder meadow population. The least number of individuals were found in the 201 to 250 year age class (n=1, mean age 220). Samples from small diameter individuals were difficult to obtain, thus the 0 to 25 age class may be under represented due to sampling inadequacy (n=5, mean age 23) (Table 5.6).

Table 5.6. Summary statistics for the meadow age class.

Age Class	Min	Max	Mean	SD
<= 25	22	24	23	0
26 – 50	26	50	38	6
51 – 75	51	75	60	6
76 - 100	78	93	86	4
101 - 150	101	150	121	17
151 - 200	155	186	168	13
201 - 250	220	220	220	0
>=251	0	0	0	0

The greatest percentage of individuals were found in the 26 to 50 year age class in meadows (relative frequency = 45.87). The 51 to 75 age class in forests had the second greatest percentage of individuals (relative frequency = 32.19) followed by the 26 to 50 age class for total individuals (relative frequency = 30.77). The least percentage of individuals is found in two age classes the 201 to 250 age class (total relative frequency = 1.17, forest relative frequency = 1.25, meadow relative frequency = 0.92), and the ≥ 251 (total relative frequency = 0.47, forest relative frequency = 0.63, and meadow relative frequency = 0) (Table 5.7).

Table 5.7. Relative frequency calculations for total individuals, forest and meadow categories.

Age Class	Total	Forest	Meadow
0 – 25	3.03	2.5	4.59
26 – 50	30.77	25.62	45.87
51 – 75	27.74	32.19	14.68
76 - 100	17.02	18.75	11.93
101 - 150	15.62	15.31	16.51
151 - 200	4.20	3.75	5.50
201- 250	1.17	1.25	0.92
≥ 251	0.47	0.63	0

5.7.2 Higher and Lower Elevation Age Class – Total Population

Age classes for the high elevation – total population from the years 1702 to 1983 show the greatest number of individuals in the 26 to 50 year age class (n=76, mean age 39). Three of the older age class categories have similar trends: 51 to 75 year age class (n=33, mean age 61), 76- 100 years (n=26, mean age 88) and 101 to 150 years (n=29, mean age 117). The least number of individuals were found in the ≤ 251 year age class (n=2, mean age 283) (Table 5.8).

Table 5.8. Summary statistics for the high elevation age class – total population.

Age Class	Min	Max	Mean	SD
<= 25	21	25	23	1
26 – 50	26	48	39	6
51 – 75	51	75	61	7
76 - 100	76	100	88	6
101 – 150	101	147	117	12
151 – 200	152	177	164	8
201 – 250	201	241	219	17
>=251	266	301	283	17

Age classes for the low elevation – total population from the years 1702 to 1983 show the greatest number of individuals in the 51 to 75 year age class (n=86, mean age 62). The second greatest category of the older age class categories is 26 to 50 year age class (n=56, mean age 39), 76- 100 years (n=26, mean age 88) and 101 to 150 years (n=29, mean age 117). The least number of individuals were found in the 201 to 250 age class (n=1 , mean age 220). There were no representative individuals for the ≤ 251 year age class. (Table 5.9).

Table 5.9. Summary statistics for the low elevation age class – total population.

Age Class	Min	Max	Mean	SD
<= 25	20	24	22	1
26 - 50	27	50	39	6
51 - 75	51	75	62	6
76 - 100	77	100	85	6
101 - 150	101	150	120	16
151 - 200	155	187	168	11
201 - 250	220	220	220	0
>=251	0	0	0	0

The greatest percentage of total individuals were found in the 26 to 50 year age class in the higher elevation forest and meadows (relative frequency = 41.08). The 51 to 75 age class in lower forests and meadows had the second greatest percentage of individuals (relative frequency = 35.25) followed by the 26 to 50 age class for lower forests and meadows (relative frequency = 22.95). The least percentage of individuals is found in three age classes: the lower forest and meadow ≤ 25 year age class (relative frequency = 2.05), the 201 to 250 age class for both higher elevation forests and meadows (relative frequency 2.16) and lower elevation meadows and forest (relative frequency = 0.14), and ≥ 251 year age class higher elevation forests and meadows (relative frequency = 1.08), and lower elevation forests and meadows (relative frequency = 0) (Table 5.10).

Table 5.10. Relative frequency calculations for total individuals subdivided into higher and lower elevation categories.

Age Class	Higher	Lower
<= 25	4.32	2.05
26 - 50	41.08	22.95
51 - 75	17.84	35.25
76 - 100	14.05	19.26
101 - 150	15.68	15.57
151 - 200	3.78	4.51
201 - 250	2.16	0.41
>=251	1.08	0

5.7.3 Higher and Lower Elevation Age Class – Forest Population

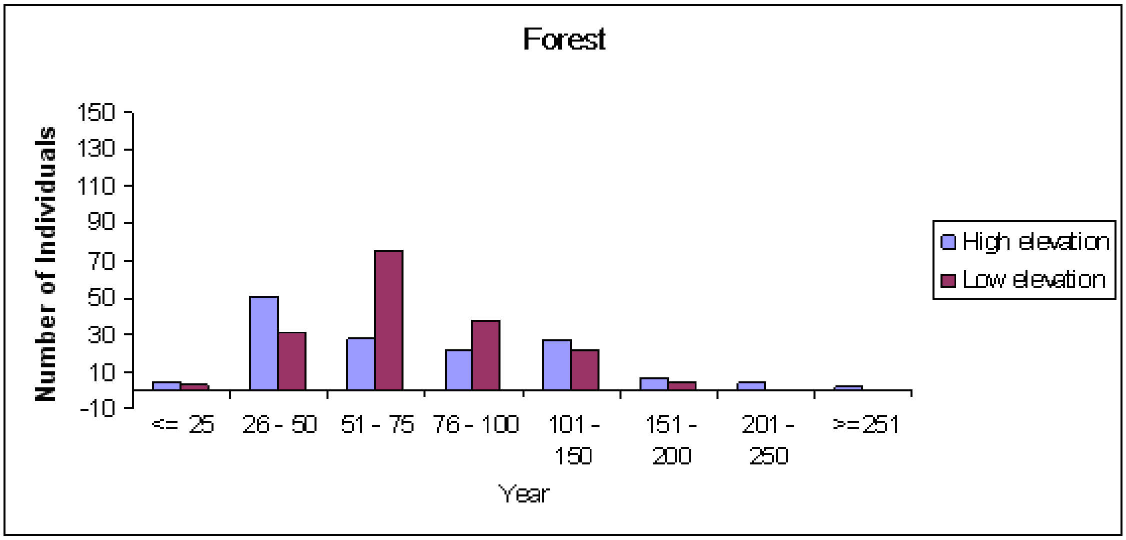


Fig. 5.10. Age classes for the high and low elevation forest category.

Age classes for the high elevation forest population from the years 1702 to 1983 show the greatest number of individuals in the 26 to 50 year age class (n=51). The numbers of individuals in the high elevation forest category decrease over time with the least number found in the ≥ 251 year (n=2). Age classes for the low elevation forest population shows the greatest number of individuals in the 51 to 75 year age class (n=75). No individuals from this category were found in the 201 to ≥ 250 year age classes (Fig. 5.10).

5.7.4 Higher and Lower Elevation Age Class –Meadow Population

Age classes for the high elevation meadow population from the years 1702 to 1983 show the greatest number of individuals in the 26 to 50 year age class for both high and low elevation (n=25, n=25 respectively). The second greatest increase in individuals is in the 101 to 150 year category in the low elevation forest category (n=16). The lower elevation meadow has the greatest number of individuals over time (Fig. 5.11).

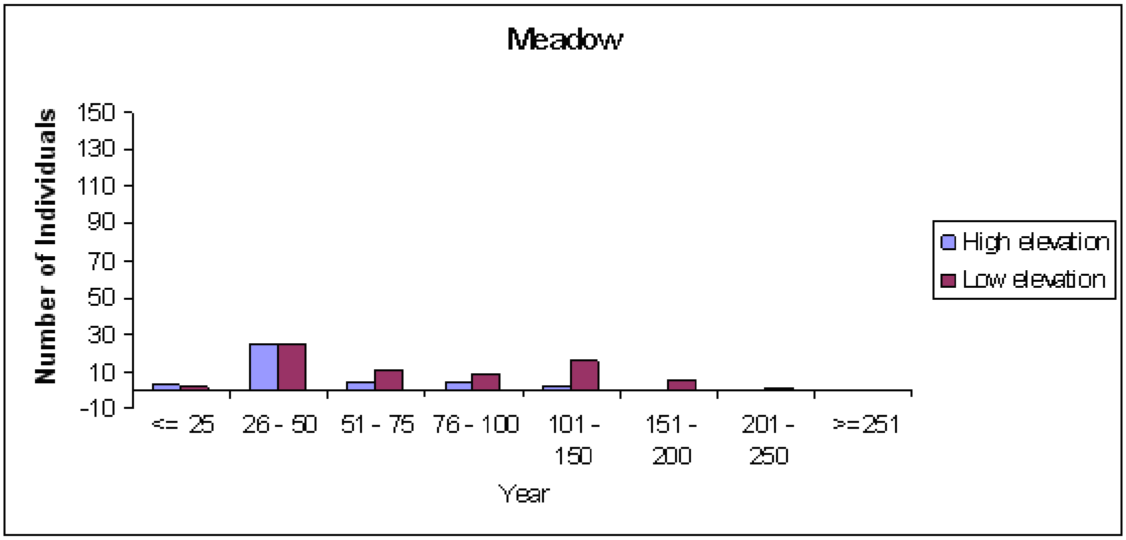


Fig. 5.11. Age classes for the high and low elevation meadow category.

5.8 Size Class

5.8.1 Total, Forest, and Meadow Populations

Size class categories for the total category show the greatest number of individuals in the ≤ 10 cm (total n=3276, forest n=2150, n=1126). The number of individuals decrease dramatically for the 11 to 20 cm (total n=244, forest n=156, n=88). Few individuals are found in ≥ 41 cm category for forest (n=10) (Fig. 5.12).

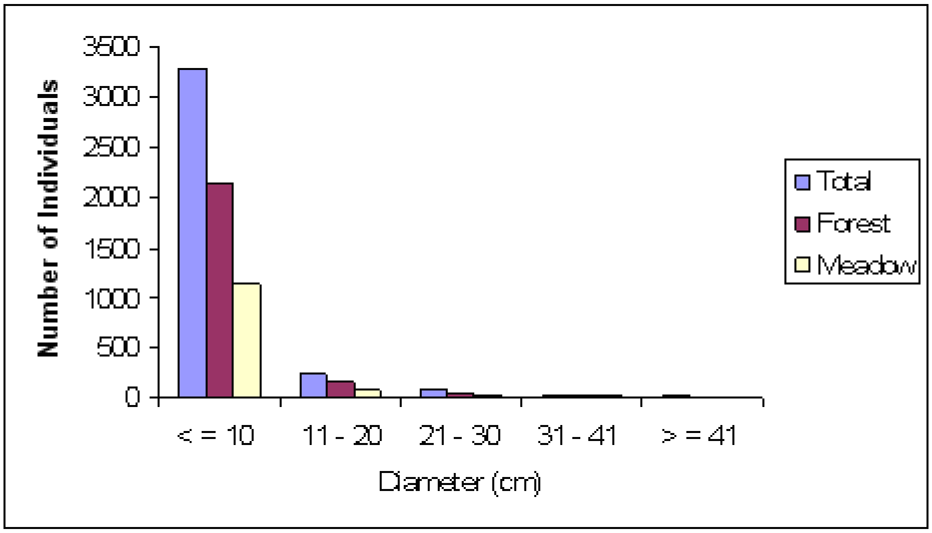


Fig. 5.12. Size classes for the total (forest+ meadow), forest and meadow categories.

5.8.2 Higher and Lower Elevation Size Class – Total Population

Size class categories for all higher and lower elevation categories show similar trends with the greatest number of individuals in the ≤ 10 cm (higher elevation n=1839, lower elevation n=2150). The number of individuals decrease dramatically for the 11 to 20 cm (higher elevation n=75, lower elevation n=169). No individuals are found in ≥ 41 cm category (n=10) (Fig. 5.13).

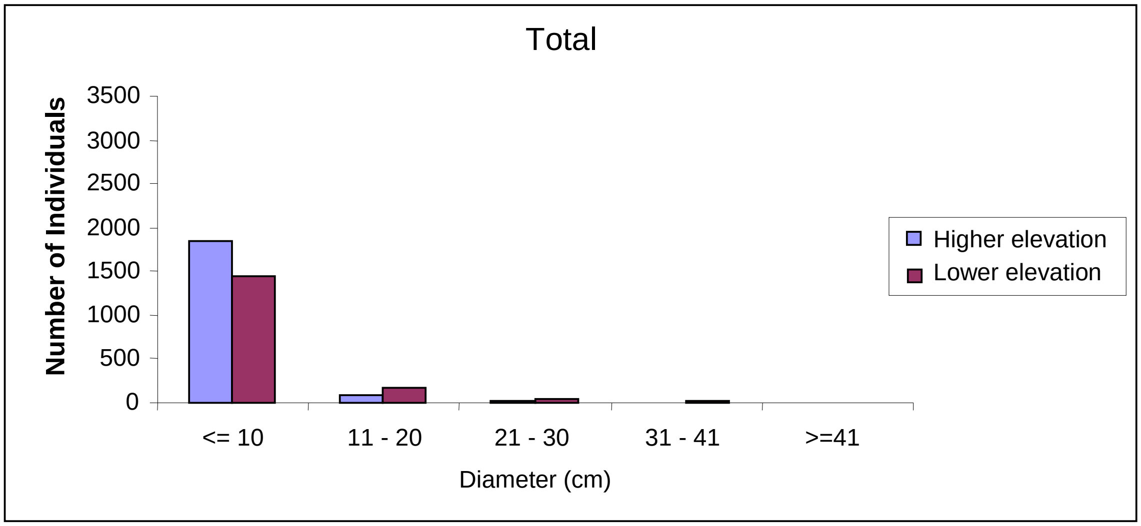


Fig. 5.13. Size classes for the total categories split into high elevation and low elevation.

5.8.3 Higher and Lower Elevation Size Class – Forest and Meadow Populations

Size class categories for all higher and lower elevation categories show similar trends with the greatest number of individuals in the ≤ 10 cm (lower elevation forest n=897, higher elevation forest n=1253, lower elevation meadow n=540, higher elevation meadow n=586). The number of individuals decrease for the 11 to 20 cm (lower elevation forest n=94, higher elevation forest n=62, lower elevation meadow n=75, higher elevation meadow n=13). One category has individuals in the ≥ 41 cm category (upper forest n=4) (Fig. 5.14).

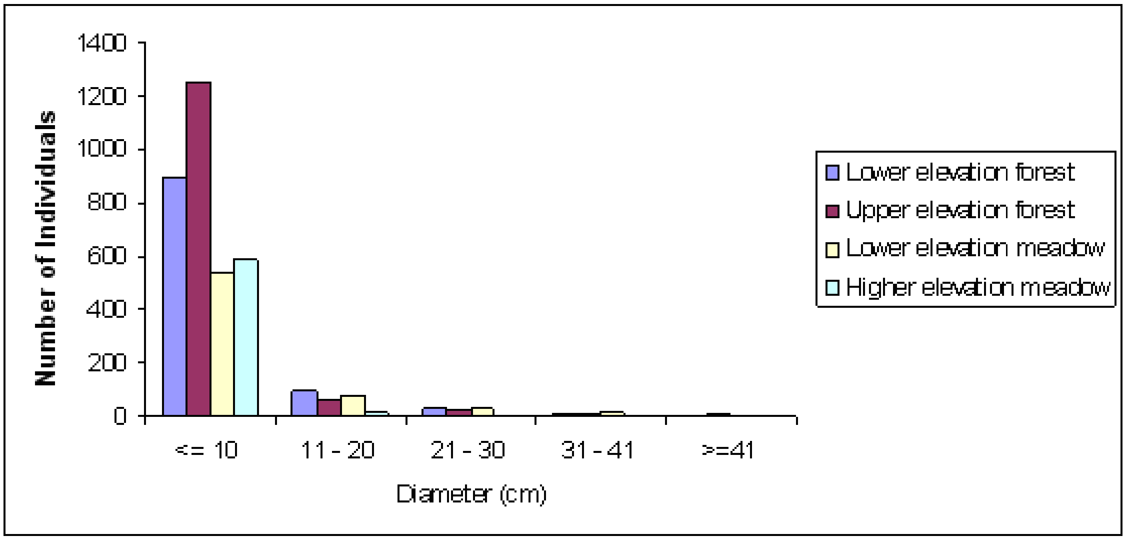


Fig. 5.14. Size classes for the forest and meadow categories split into high elevation and low elevation.

5.9 Mapping Establishment

The goal of the mapping portion of this section is to determine where *Abies lasiocarpa* seedling abundance is positioned in the meadows as well as characterize the age and size of both seedlings and larger individuals. The age and size structure of seedlings and their spatial distribution along the elevational gradient provides a comparison of ecological factors and tree population dynamics influencing establishment patterns (Wallenius et al., 2002). Tree succession is distributed from forest boundaries via dispersal and towards meadow centers. The greatest amount of establishment is found along forested boundaries and is sequestered near larger individuals, which may protect smaller seedlings from adverse site conditions during establishment. There was not a significant, strong relationship found between tree size and tree age.

5.9.1 Size Class Maps

Understanding the spatial tree size structure of tree establishment in meadows and ribbon forests is important as current patterns further influence recruitment patterns and the ecological and successional processes in these habitats (Wallenius et al., 2002). The *Abies* dominated forests of the lower elevation meadows overall show an overall pattern of size classes 31-40 cm, 41-80 cm located in forest margins as is expected for forest structure. Surrounding these larger diameter trees are a smaller number of individuals in the 21-30 cm size class. There are a large number of individuals in the 0-10 cm size class that are dispersed throughout forest margins and meadow interiors (Fig. 5.15-Fig. A.4). There are two exceptions to these patterns. Meadow 4 has a more irregular shape and has larger sized individuals from the 21-30 cm and the 31-40 cm size classes located well within meadow interiors. Individuals from the 0-10 cm size classes seemed both clustered heavily around the larger individuals and dispersed more randomly throughout the meadow (Fig. A**.1**). Meadow 8 showed clustered establishment of both larger diameter and smaller diameter individuals at the higher elevation forested boundary. This meadow lacked the largest diameter individuals at the higher elevation forested margin, but had a clustered number of individuals in the 11-20 cm, 21-30 cm, and 31-40 cm size classes (Fig. A.3). These larger individuals were found in approximately 20 m into meadows, and 0-10 cm size class individuals were clustered around larger individuals. The smallest size classes were located in more open areas of the meadow with all age classes becoming sparser at the lower elevation forest boundary (Fig. A.3).

The higher elevation meadows reflect a similar distribution of size classes with the 31-40cm and the 41-80 cm size classes individuals found at forest margins (Fig. A.2-Fig. A.4). The 0-10 cm and the 11-20 cm diameter trees and seedlings are clustered around larger individuals. With the exception of meadow 6, all higher elevation meadows had the 0-10 cm diameter seedlings infiltrating the meadow interiors. Meadow 6 was located close to meadow 8 and it shows a similar pattern of clustered individuals in the 11-20 cm, 21-30 cm, and the 31-40 cm size classes as well as one individual in the 41-80 cm size class found at the lower elevation forested boundary. The 11-20 cm, 21-30 cm, and the 31-40 cm size classes were found in both lower and upper sections of meadows and forests, and smaller individuals were clustered around larger individuals and were more prevalent in the upper elevation eastern direction of the meadow. The smallest size classes were located in more open areas of the meadow with all age classes becoming sparser at the lower elevation forest boundary (Fig. A.2). The highest elevation ribbon forests of 5 and 9 and meadow 7 show the largest amount of recruitment for the 0-10 cm size class with much of the recruitment located in the upper and lower meadows and diminishing towards mid-meadow locations (Fig. A.2, Fig. A.3, and Fig. A.4). The number of trees measured reflects this pattern with the greatest number of samples collected in Ribbon forests 5, 9 and meadows 7 and 8 (Table 5.17).

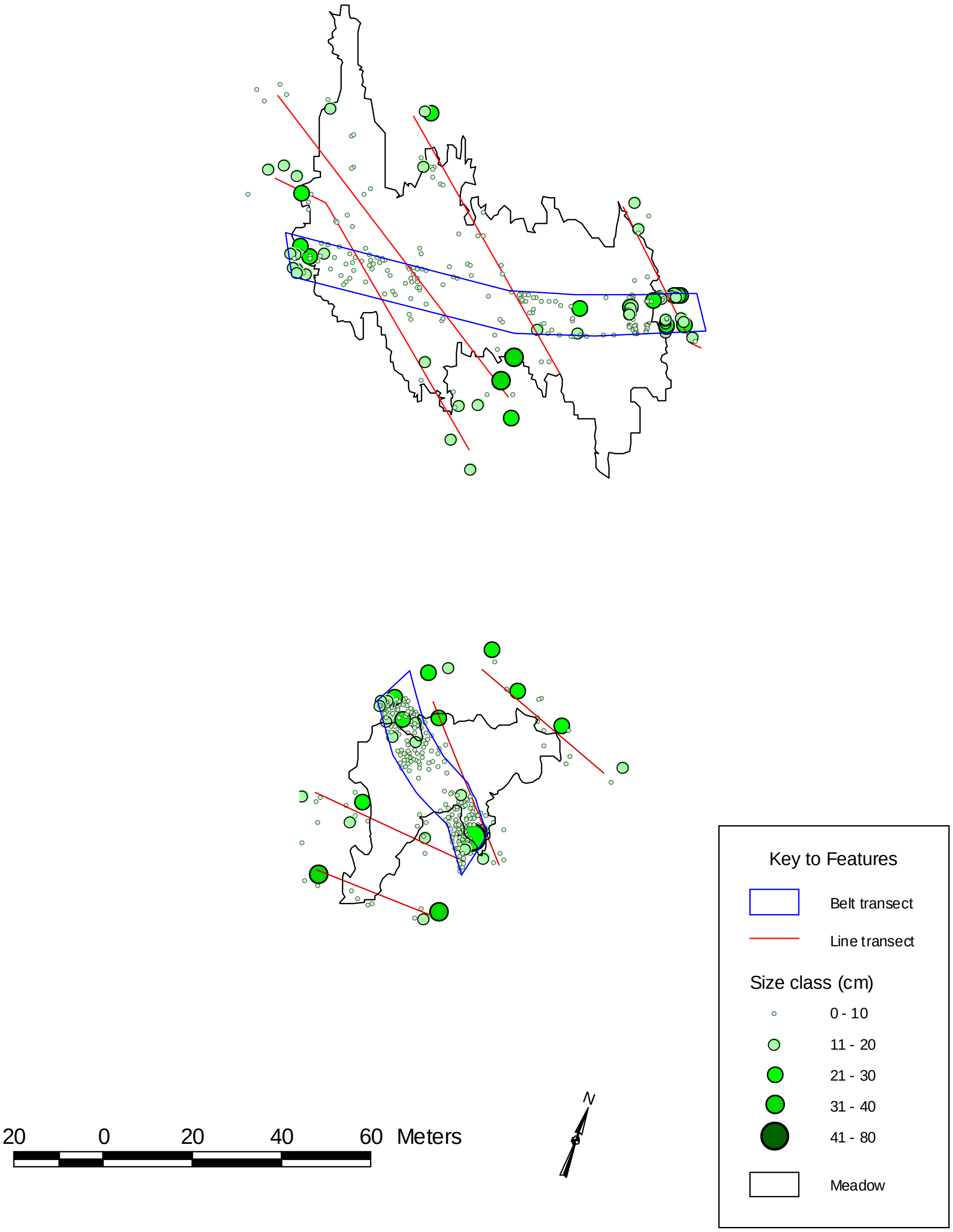


Fig. 5.15. Size class maps of seedling and tree diameters (cm) in meadow/forest boundaries of meadows 1 and 2 in Preston Park.

5.9.2 Age Class Maps

Spatial tree age structure of tree establishment in meadows and ribbon forests is important to understand current aged forest patterns and how they further influence recruitment patterns and the ecological and successional processes in these habitats (Wallenius et al. 2002). A caveat of this study was the difficulty in obtaining the samples of small trees 2 cm diameter or less. These maps reflect the tree and seedling invasion for collected samples of diameters 2 cm in diameter or greater. Thus there are fewer samples represented for the 0-26 year age class.

Lower elevation meadows show few individuals in the 201-250 and 251-400 age classes (Fig. A.4-Fig. A.7). Meadows 1, 3, and 6 have the few representative individuals for the 201-250 year and the 251-400 year age class with meadow 6 having the most individuals (n=6). Meadow 6 had older age classes most present in the lower elevation forest boundary (Fig. A.6). Lower elevation meadows had older individuals in the 101-150 and the 151-200 year age classes surrounding meadows in the forest margins. The exceptions to this pattern are meadow 4 and meadow 6 which show the 101-150 and the 151-200 year age classes are present throughout the whole meadow: lower forest, lower meadow, mid-meadow, upper meadow and upper forest (Fig. A.6-Fig. A.7). These age classes were dense in the upper and lower meadows and become sparse toward meadow center. Meadow 4 had 51-75 year and the 76-100 year age classes grouped around the larger trees, which indicates tree islands in meadow interiors. All lower elevation meadows had a greater number of individuals in the 51-75 year age class and a few individuals in the 26 – 50 year age class grouped around the older classes. Meadow 1 is the only meadow with recruitment of these age classes found consistently across the meadow spatially with presence in the following categories: lower forest, lower meadow, mid-meadow, upper meadow and upper forest. The remaining lower elevation meadows were missing the 26 – 50 year and the 51-76 year age class in meadow interiors.

Higher elevation meadows had older individuals in the 101-150, 151-200, 201-250, 251-400 year age classes in the forest margins surrounding meadows (Fig. A.7-Fig. A.9). The exception to this pattern is Meadow 7, this meadow is more narrow with had a sharp drainage bisecting the length of the meadow. The higher elevation part of the meadow had two individuals in the older age classes located in the meadow center (Fig. A.8). All higher elevation meadows had recruitment in the 26-50 and the 51-75 year age classes. The pattern of these individuals showed recruitment along forest margins and upper and lower meadow boundaries. Meadow central interiors were sparse of recruitment.

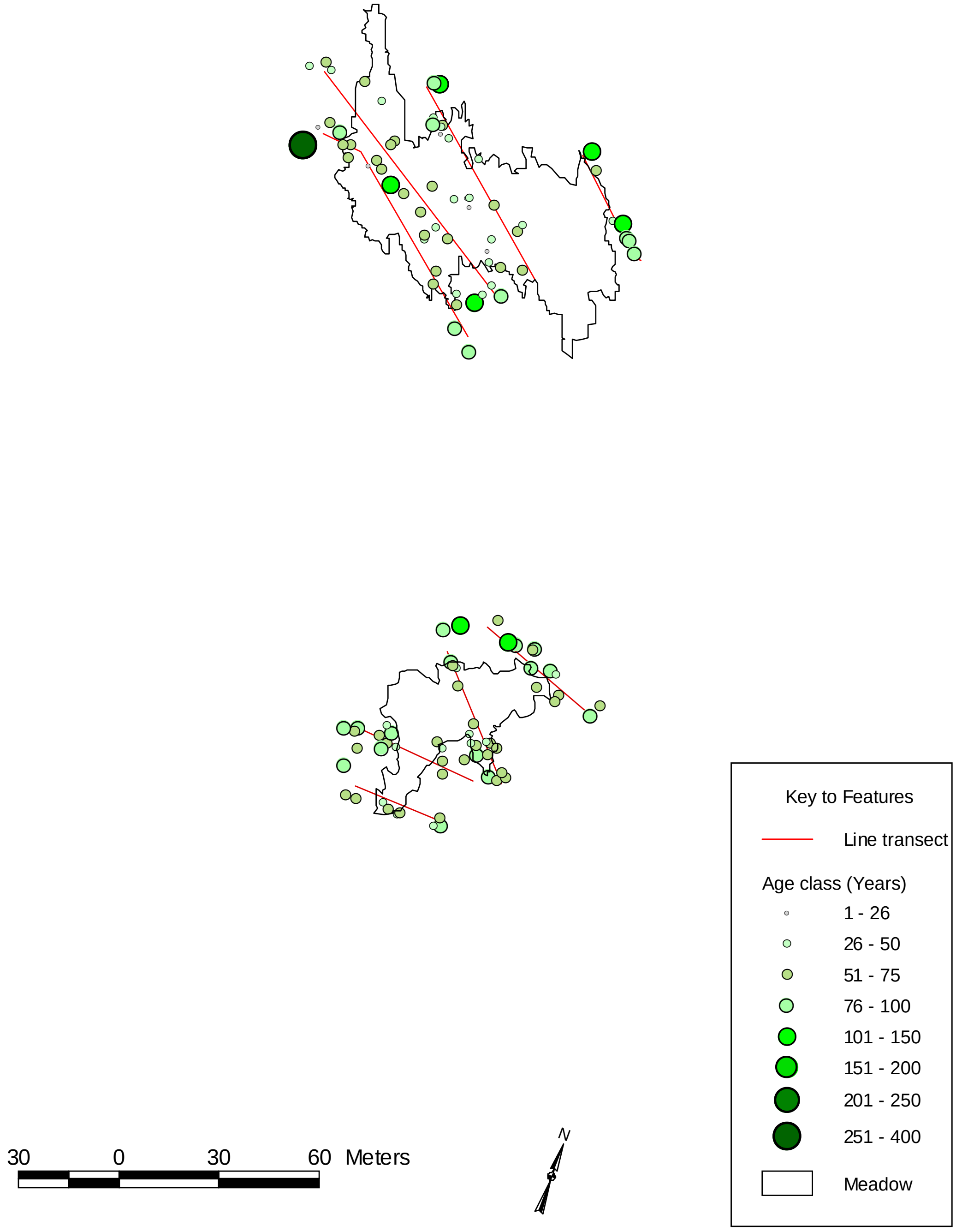


Fig. 5.16. Age class maps of seedling and tree diameters (cm) in meadow/forest boundaries of meadows 1 and 2 in Preston Park.

5.10 Location of Establishment in Meadows

Tree and seedling recruitment in meadows and ribbon forests show a pronounced number of trees located in the upper forest (n=1,653, 44.9% of the total population) followed by mid-meadow (n=1,122, 30.5% of the total population) and lower forest (n=759, 20.6% of the total population). The least number of trees were located in lower meadows (n=78, 2.1% of the total population) and upper meadows (n=70, 1.9% of the total population) (Fig. 5.17 and Fig. 5.18).

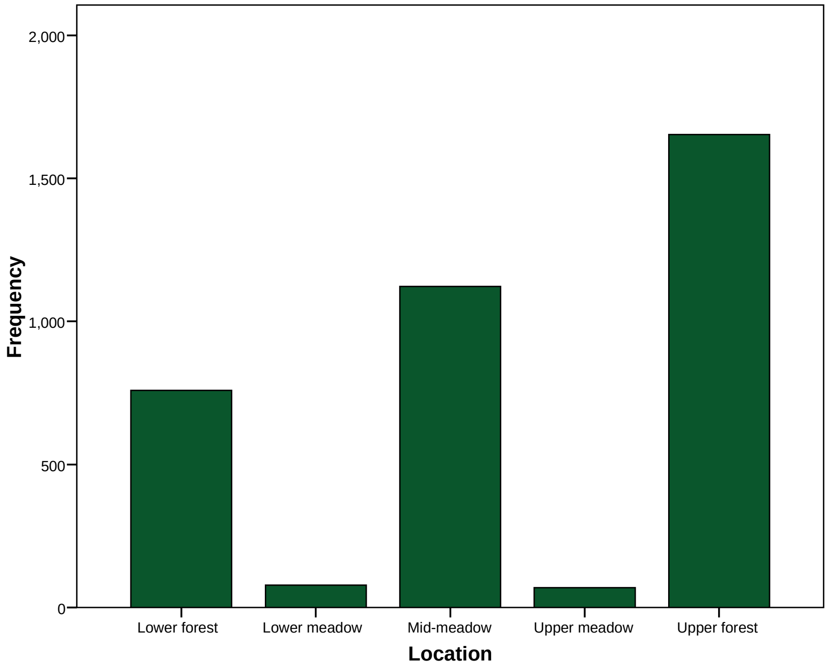


Fig. 5.17. Frequency of trees and seedlings for meadows and ribbon forests parsed in the five location categories: lower forest, lower meadow, mid-meadow, upper forest, and upper meadow.

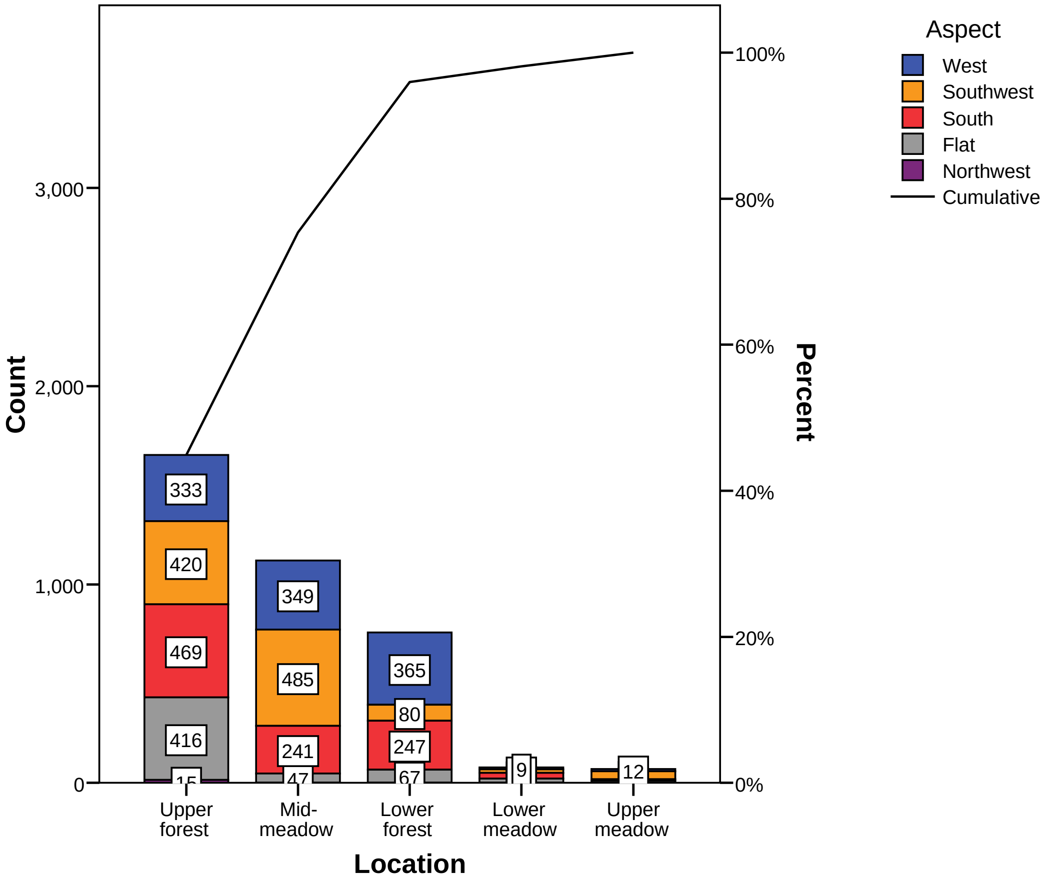


Fig. 5.18. Pareto analysis of both location in meadow and aspect in meadows and ribbon forests of Preston Park. Pareto charts are used to show categories of one variable summarized within categories of another variable. The line represents the cumulative percentage.

The majority of tree and seedling is found on three aspects: west (n=1,068, 29% of total population), southwest (n=1,044, 28.3% of total population), and south (n=993, 27% of total population). A large number of trees were found in the flat category (n=562, 15.3% of the total population). Few individuals were found in the northwest aspect (n=15, 0.4% of the population (Fig. 5.18 and Fig. 5.19).

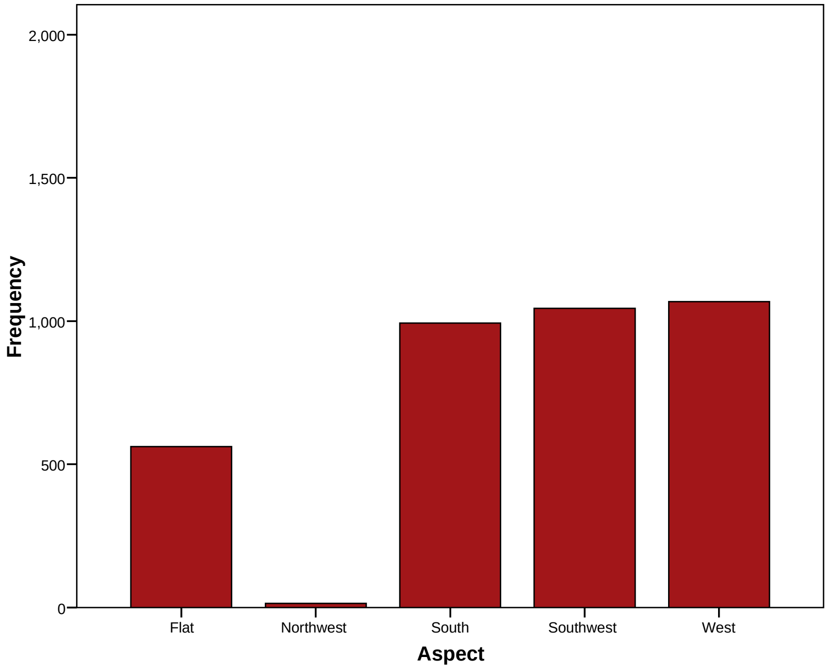


Fig. 5.19. Frequency of trees and seedlings for meadows and ribbon forests parsed by aspect: flat, northwest, south, southwest, and west.

Location of individuals in each meadow shows distinct similarities and dissimilarities. Meadow 1 has the greatest number of individuals in lower forest and mid-meadow locations (Fig. 5.20). Few individuals are found in the lower meadow and upper meadow locations. Meadow 2 has the greatest number of individuals in the lower forest and upper forest locations. Meadow 2 has no individuals in the lower meadow location (Fig. 5.20). Meadow 3 has fewer individuals overall, and has the greatest number of individuals in the upper forest and lower forest locations (Fig. 5.20).

Meadow 4 has the greatest number of individuals in the mid-meadow location (Fig. 5.20). Meadow 5 was unusual in that it has no individuals in the lower meadow location. Meadow 5 has the greatest number of individuals in the upper forest location. Fewer individuals are found in the lower forest and mid-meadow locations (Fig. 5.20). Meadow 6 has the greatest number of individuals in the upper forest location. It has few individuals in the upper meadow and lower meadow location (Fig. 5.20). Meadow 7 has no individuals in either the lower or upper meadow. It has the greatest number of individuals in the lower forest location, and has a great number of individuals in the mid-meadow and upper forest locations as well (Fig. 5.20). Meadow 8 has the greatest number of individuals, both in situ and for all meadows, in the upper forest location. Meadow 8 also has a great number of individuals in the mid-meadow location (Fig. 5.20). Meadow 9 has the greatest number of individuals in the mid-meadow location, and it has a great number of individuals in the upper forest boundary. Few individuals are found in the upper meadow or lower meadow locations (Fig. 5.20).

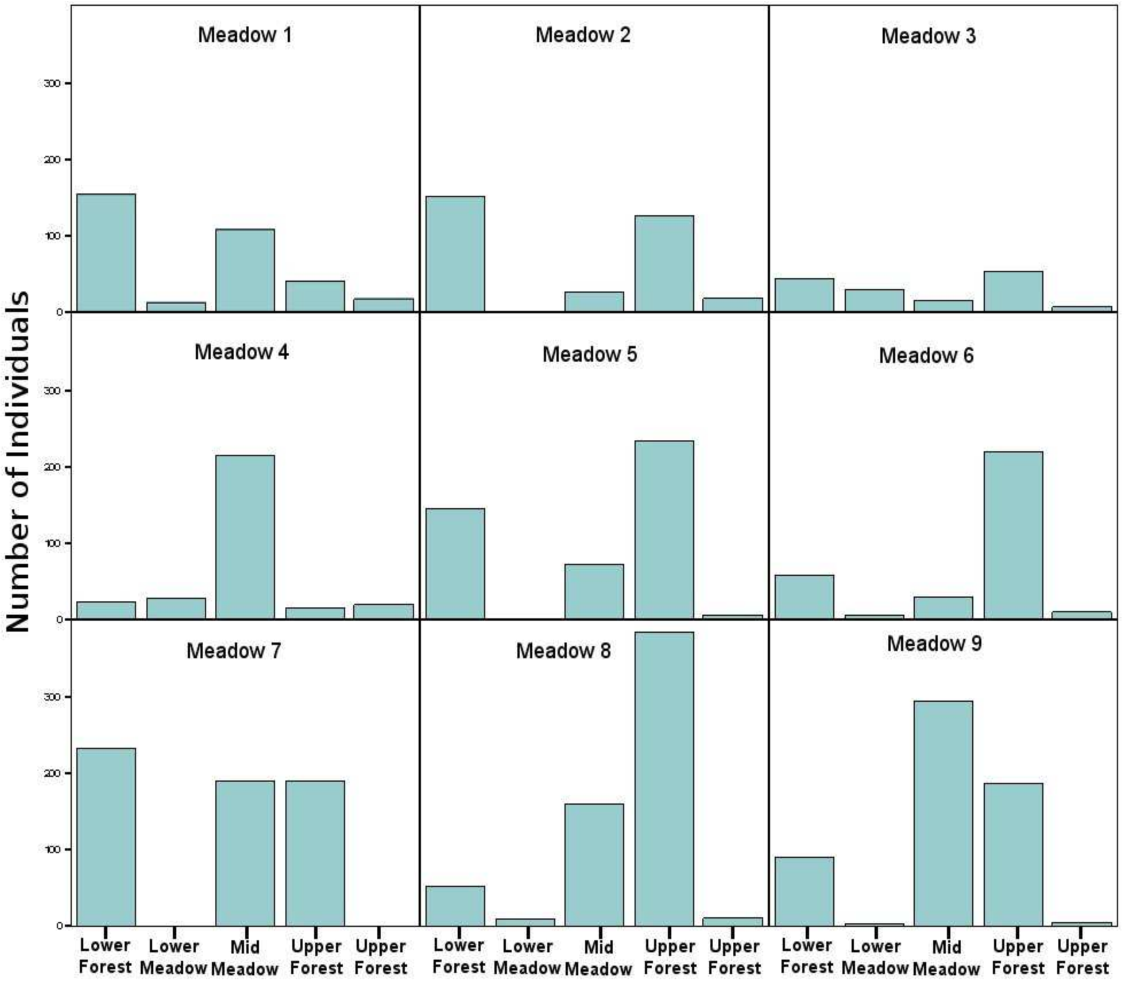


Fig. 5.20. Location of individuals (trees and seedlings combined) in Preston Park meadows and ribbon forests**.**

5.11 Soil Depth Classes by Location

Establishment of trees and seedlings occur in the 10 – 20 cm depth class and the 20 – 30 cm depth class. Partitioning the soil depth category by location of trees and seedlings in meadows and forests, lower elevation recruitment is occurring in greater numbers in the 0-10 cm, 10 – 20 cm, and 20 – 30 cm depth classes. Recruitment of trees and seedlings in the lower forests and lower meadow locations are greatest in the 10 – 20

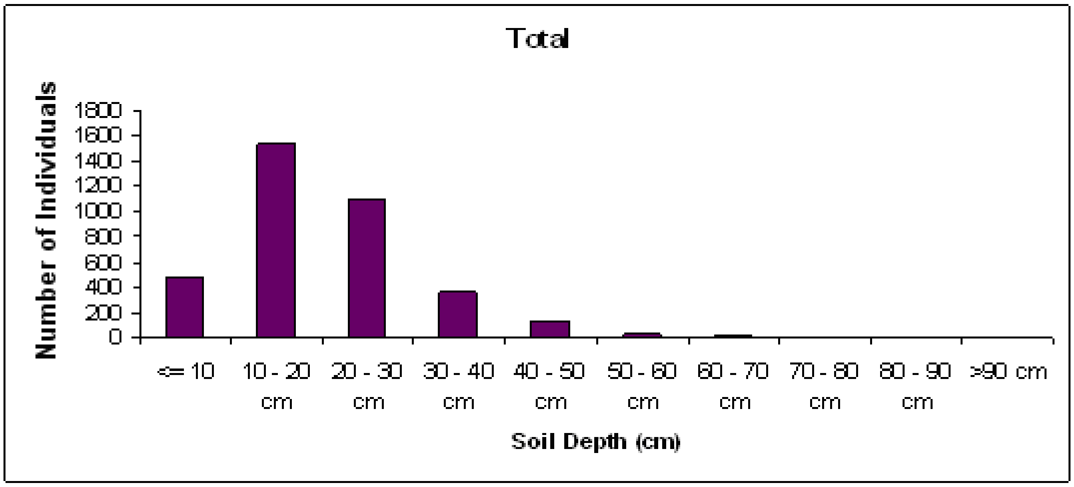


Fig. 5.21. Number of individuals in the soil depth classes in Preston Park meadows.

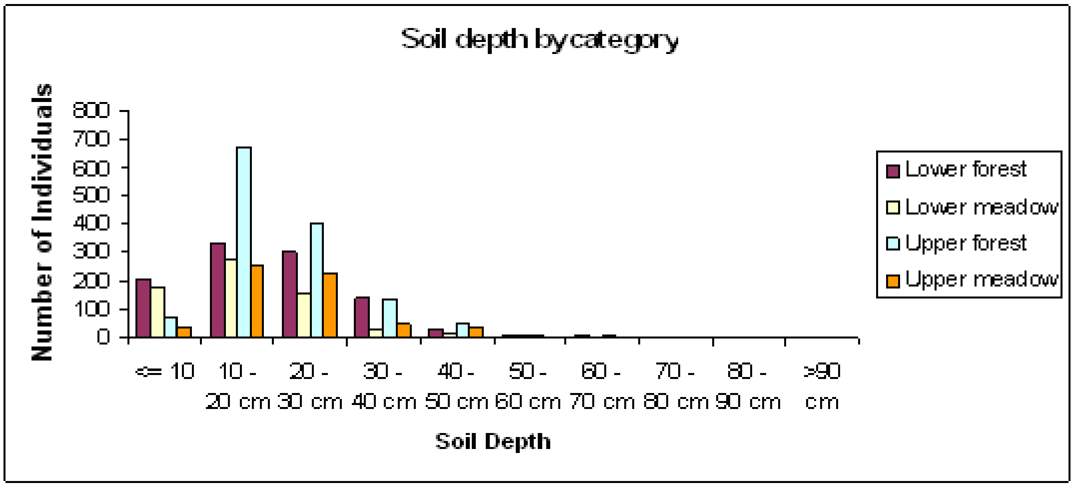


Fig. 5.22. Number of individuals in the soil depth classes in Preston Park meadows parsed by location in meadow.

and the 20 -30 cm depth classes. The greatest number of individuals in these depth categories was found in the upper forest boundary. Notable trends were the 50 – 60 cm and the 60 – 70 cm depth classes. All individuals in this class were found in meadow 1, the wet meadow (Fig. 5.21 and Fig. 5.22).

The tree and seedling density seems to align with deeper soil resources and topography. Meadows 1, 2, 3, 5, 6, 7 and 9 show deeper soils within forest boundaries with soils becoming more shallow towards meadow interiors (Fig. 5.23-Fig. A.10, Fig. A.12-Fig. A.14, and Fig. A.16). Meadows 4 and 8 do not show deeper soils in forest boundaries where population density is low (Fig. A.11 and Fig. A.15). Meadows 4 and 8 have changes in topography in these locations with a steep change in slope (Fig. A.11 and Fig. A.15). The most dense patches, or tree islands, located in the meadow boundary are found in more deep soil patches for meadows 1, 2, 3, 4, 6, 8, and 9 (Fig. 5.23-Fig. A.11, Fig. A.15, and Fig. A.16). Tree islands in all meadows are located in areas with deeper soil.

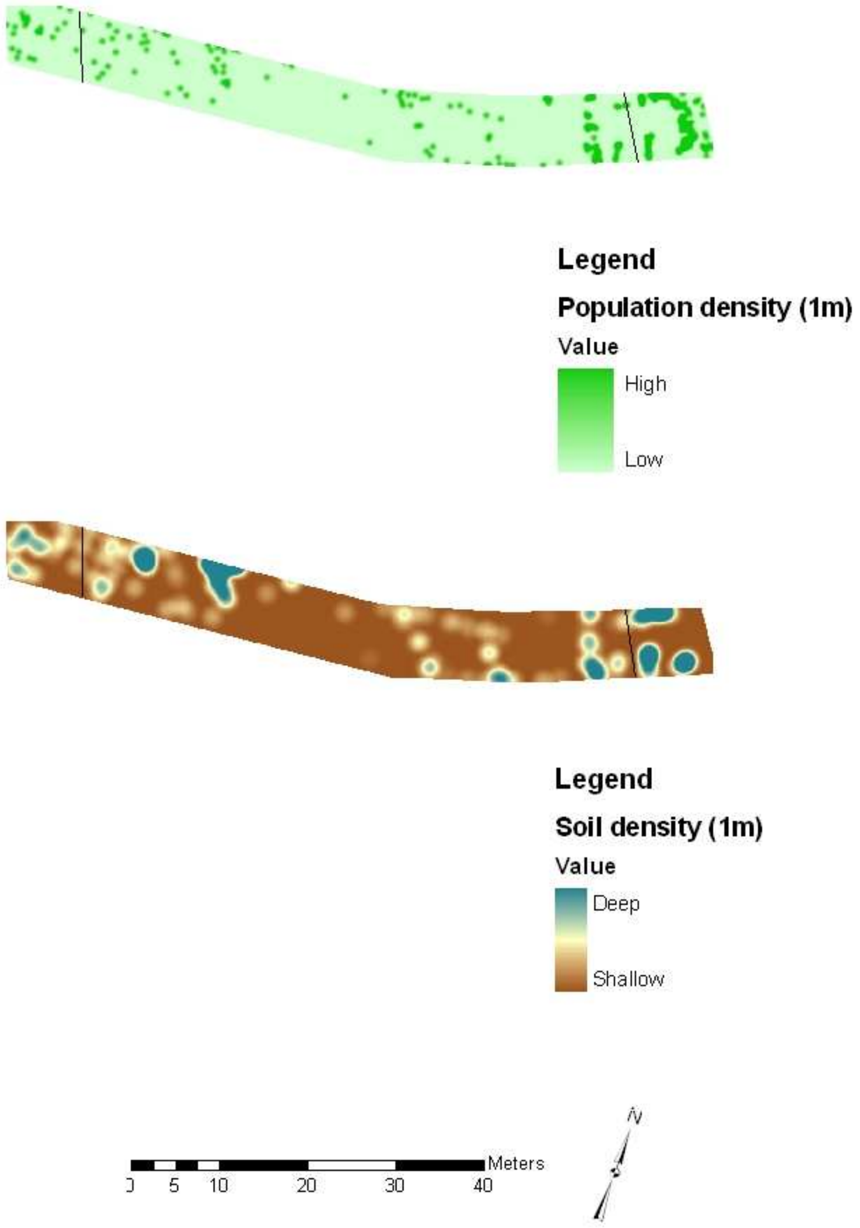


Fig. 5.23. Tree and soil density maps in the meadow 1 belt transect in Preston Park. The back line indicate the meadow-forest boundary.

5.12 Analysis of Spatial Pattern

This section describes the spatial pattern of invasion into meadows. By determining if the spatial pattern is categorized as random, regular or clumped, then it may be possible to infer mechanisms driving the spatial pattern of *Abies lasiocarpa* invasion. For example, if the spatial pattern of *A. lasiocarpa* distribution is regular or dispersed, then an argument may be made that plant to plant competition is thinning the numbers of the population. Two key questions addressed by this research are 1) Is there facilitation or competition between large trees and seedlings? And 2) How does pattern change with elevation?

5.12.1 Scale Dependent Pattern of Tree Invasion

The second order spatial analysis revealed significantly clumped distributions consistently over scales for meadows 1, 4, 6,7, 8, and ribbon forest 9 (Fig. 5.24). Meadow 2, a dry meadow, showed a clumped pattern over 2m, random pattern from 3 to 4 m, and regular pattern from 4m and greater (Fig. 5.24). Meadow 5 exhibits clustering spatial associations until 8.5 m distance, then a random pattern of spatial associations is present(Fig. 5.24). Meadow 3, a small meadow, shows a random pattern over the 0 to 2m range of distance and 5 to 6 m range of distance (Fig. 5.24).

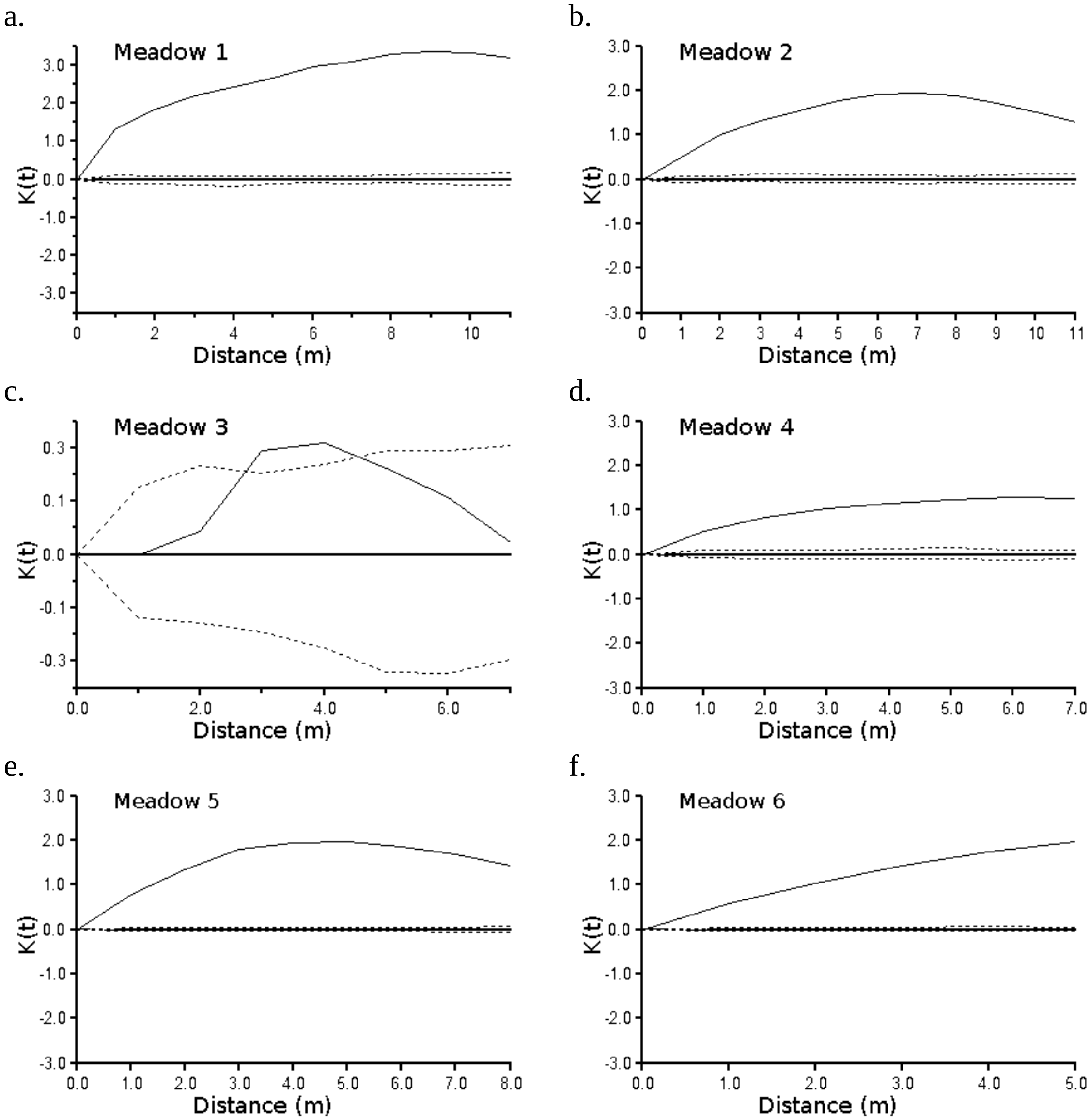


Fig. 5.24 (a-i). Second-order neighborhood analysis results for *Abies lasiocarpa* in each meadow-forest boundary. Positive K(t) values indicates clustering while negative K(t) values indicate regular dispersion. Dashed line indicates the 95% confidence interval for departure of randomness constructed using Monte Carlo simulations. The x-axis denotes the distance (m) for the radius of the neighborhood for a given L(d) value.

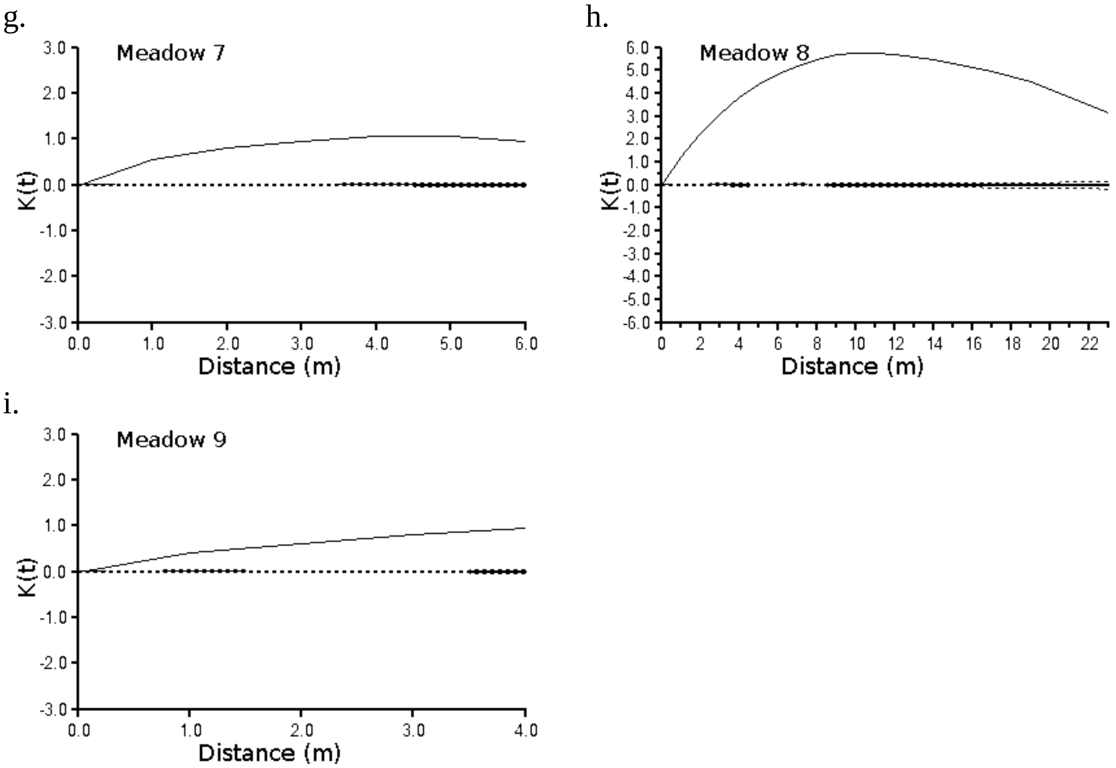


Fig 5.24(a-i). Continued.

The second order spatial analysis revealed significant trends in spatial patterns for large (> 5 cm diameter) versus small trees (≤ 5 cm diameter). Meadow 1 show a strong spatial associations for large and small trees across the entire range of the neighborhood (Fig. 5.25). Meadow 2 small trees show a strong spatial associations for large and small trees across the entire range of the neighborhood (Fig. 5.25). Meadow 3 shows a random pattern of trees across the neighborhood with the exception of 3 to 4.5 m where strong spatial associations are shown (Fig. 5.25). The small and large trees show a greater extent of clumping over the 3 to 4.5 m distances (Fig. 5.25). Meadow 4 large trees show a lesser extent of clumping over 6 m distance and random pattern over greater distances (Fig. 5.25). Meadows 5, 6, and 7 show clumped spatial associations for small seedlings and larger trees the entire range of the neighborhood (Fig. 5.25). Meadow 7 shows a random pattern for both small and large trees over total distances (Fig. 5.25). Meadow 8 shows one of the strongest spatial associations as compared to all the meadows across the entire range of the neighborhood (Fig. 5.25). Meadow 9 shows a weak, positive spatial associations between seedlings and larger trees across the extent of the neighborhood (Fig. 5.25).

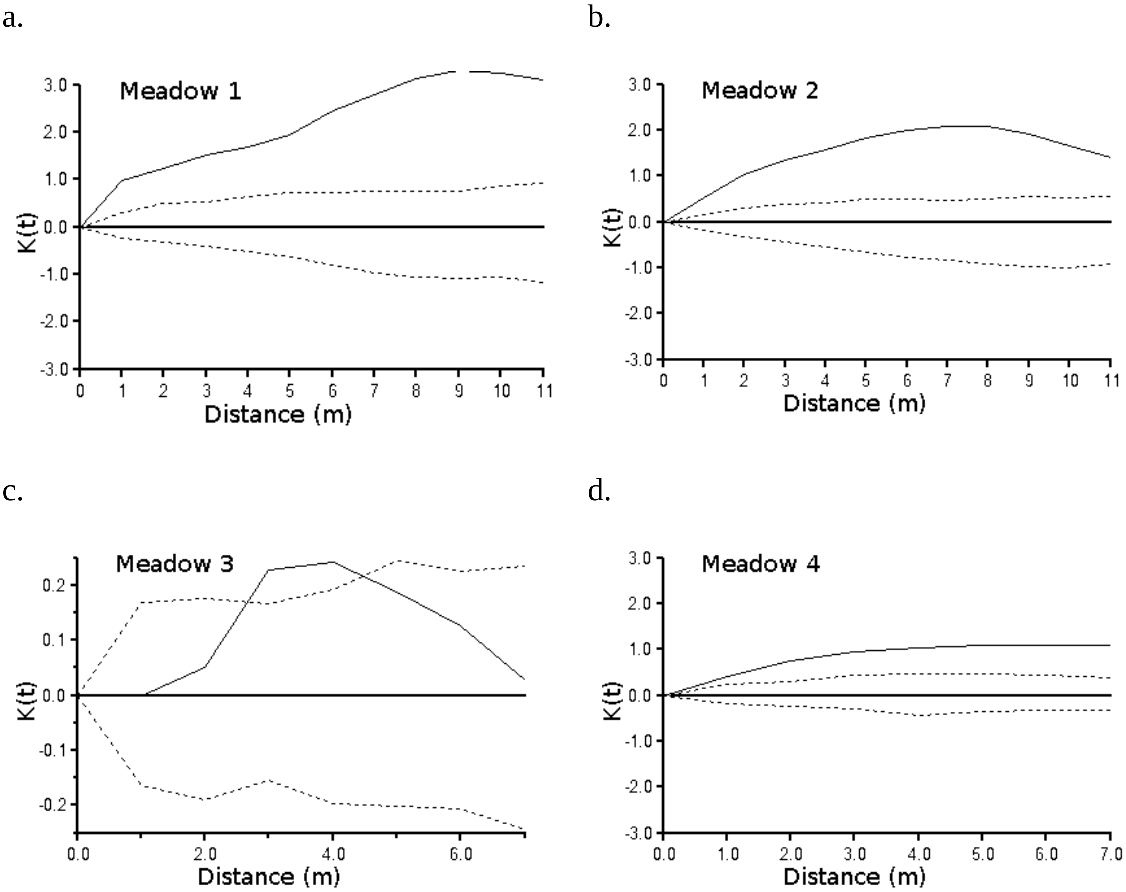
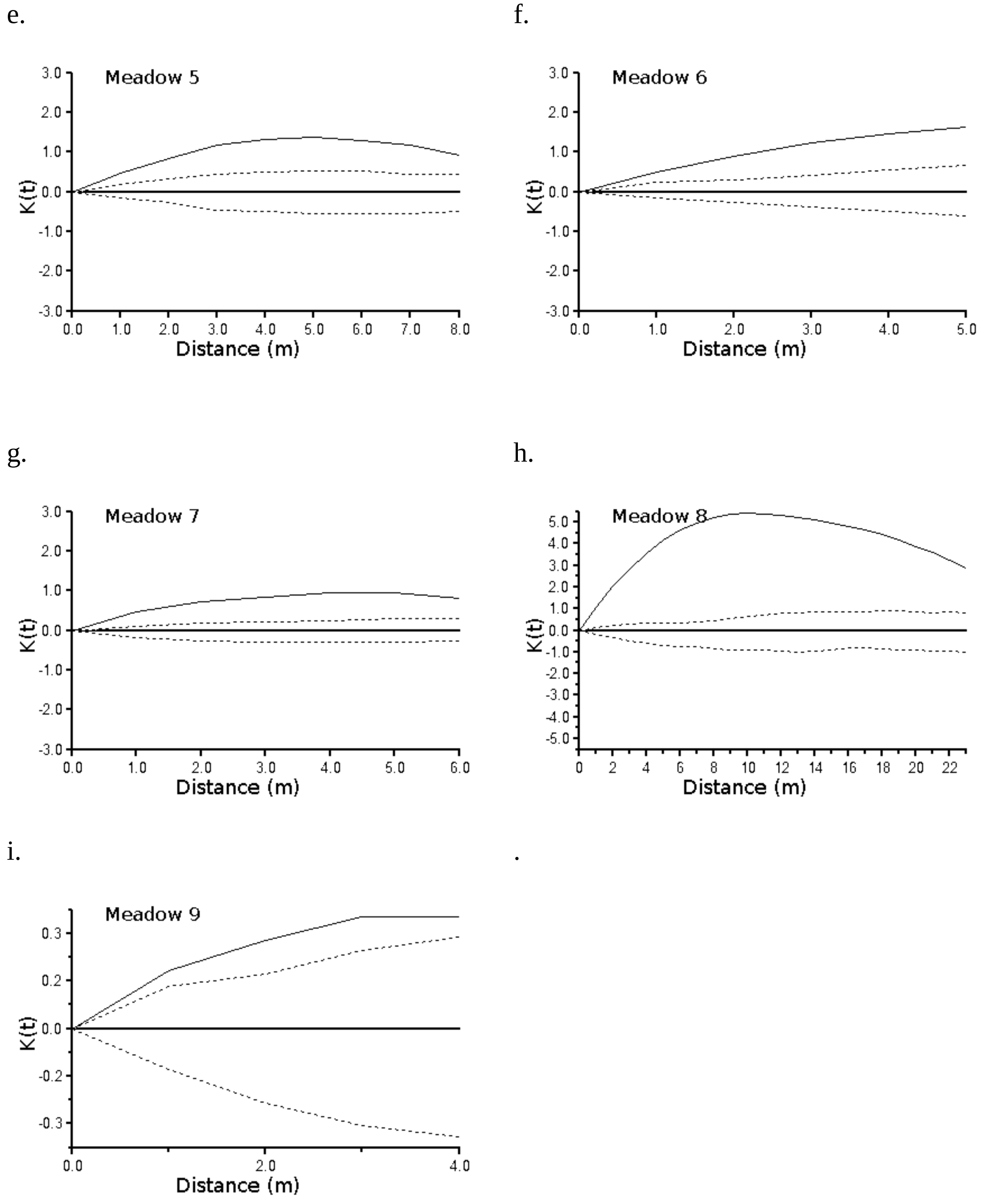


Fig. 5.25(a-i). Bivariate second-order neighborhood analysis results for *Abies lasiocarpa* in each meadow-forest boundary subdivided by <5cm diameter class or > 5 cm diameter class. Positive K(t) values indicates clustering while negative L(d) values indicate regular dispersion. Dashed line indicates the 95% confidence interval for departure of randomness constructed using Monte Carlo simulations. The x-axis denotes the distance (m) for the radius of the neighborhood for a given K(t) value.



e.

f.

g.

h.

i.

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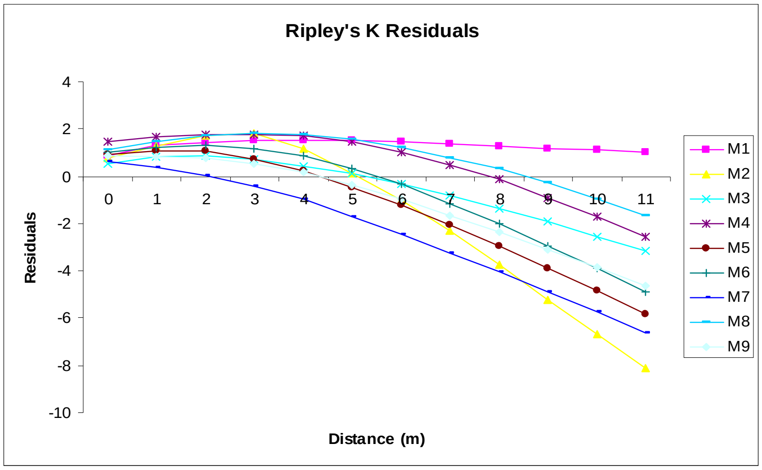
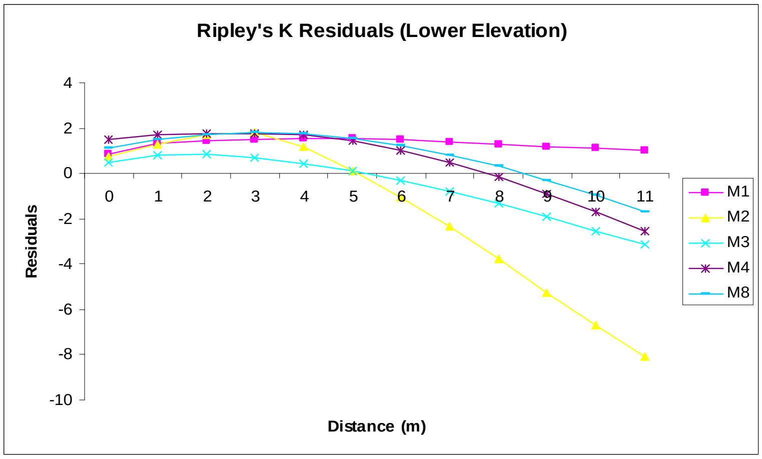
Fig. 5.25 (a-i). Continued.

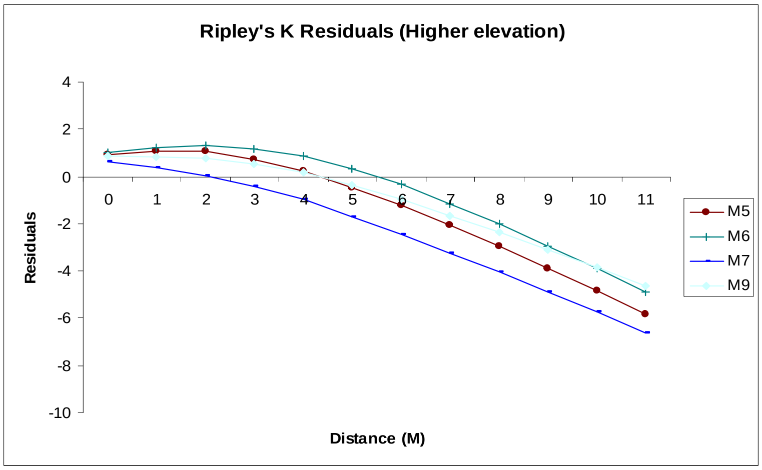
The multi distance spatial cluster analysis function yields both observed and expected values. Residuals of the Ripley's K function were calculated by subtracting the actual values from the predicted values to show departure from random patterns over distance, and these patterns show trends in each meadow and along the elevation gradient. Meadow 1, a wet meadow, is the only meadow that shows consistent clumping patterns across all distances. The remaining meadows all show clumping up to 2 to 8m in distance with greater distances having regular patterns. Meadow 7 has the greatest extent of a regular pattern (Fig. 5.26 (a-c). Grouping the residual data by lower elevation, depositional meadows and higher elevation, erosional meadows show there is a strong visual trend with lower elevation meadows having greater clumping over longer distances than higher elevation meadows which have a more pronounced regular pattern (Fig. 5.26 (a-c)). The lower elevation Meadow 2, a dry meadow, shows similar distribution patterns to the higher elevation meadows (Fig. 5.26 (a-c)).



a.



b.



c.

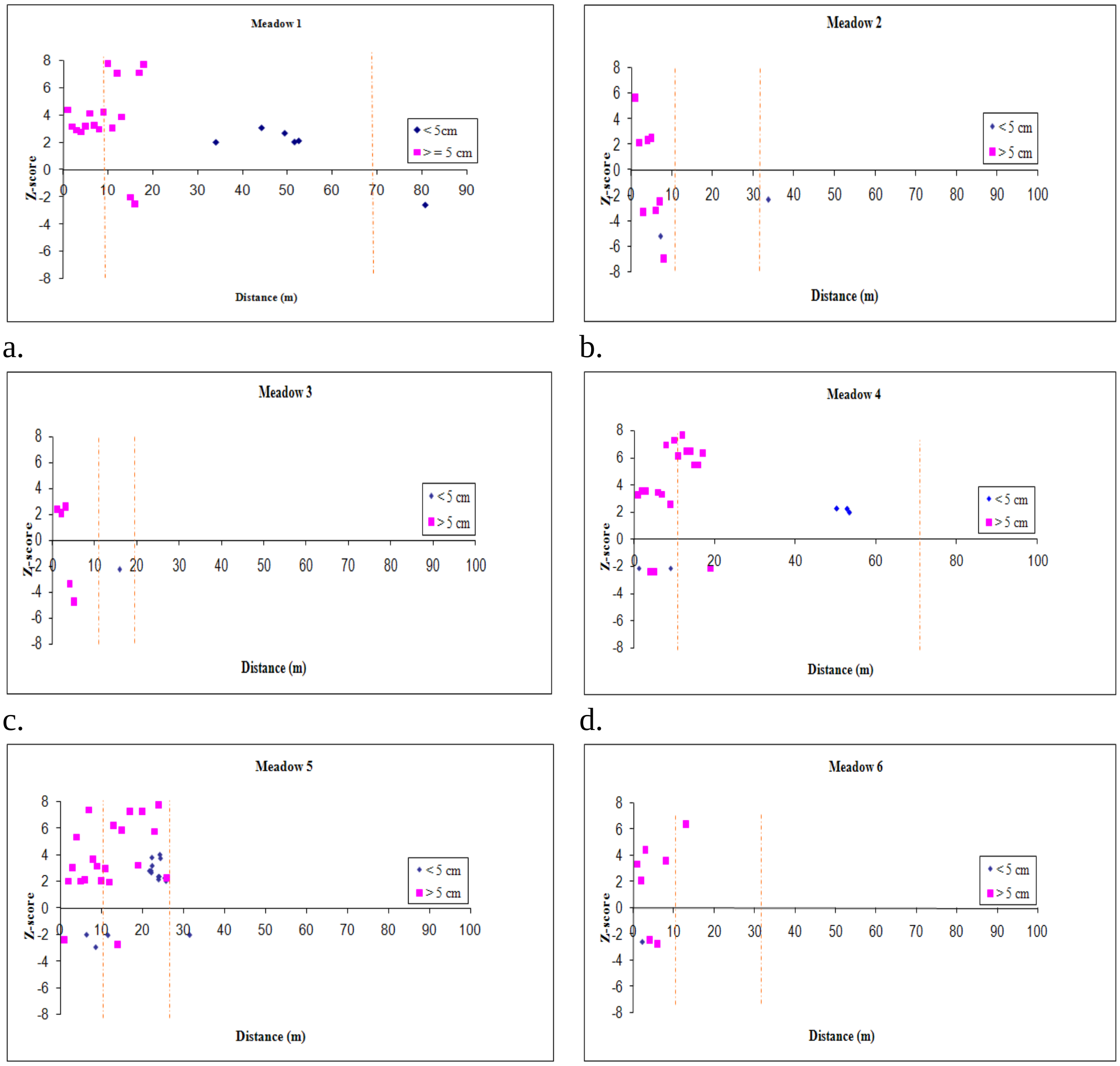
Fig. 5.26 (a-c). Ripley's K residual grouped a) all meadows, b) lower elevation meadows, c) higher elevation meadows.

5.13 Spatial Autocorrelation of Tree Size

Spatial autocorrelation analysis of tree sizes was used to examine possible size structure in the forest and tree islands. Spatially distributed variables, such as age and size, show spatial dependence at some scale (Wallenius et al. 2002). The Anselin Local Moran's I (ALMI) test was utilized to detect spatial autocorrelation in tree size, and visualize significance and cluster maps (Anselin et al. 2004). The ALMI statistic identifies clusters in local patterns or spatial outliers (Fig. 5.27).

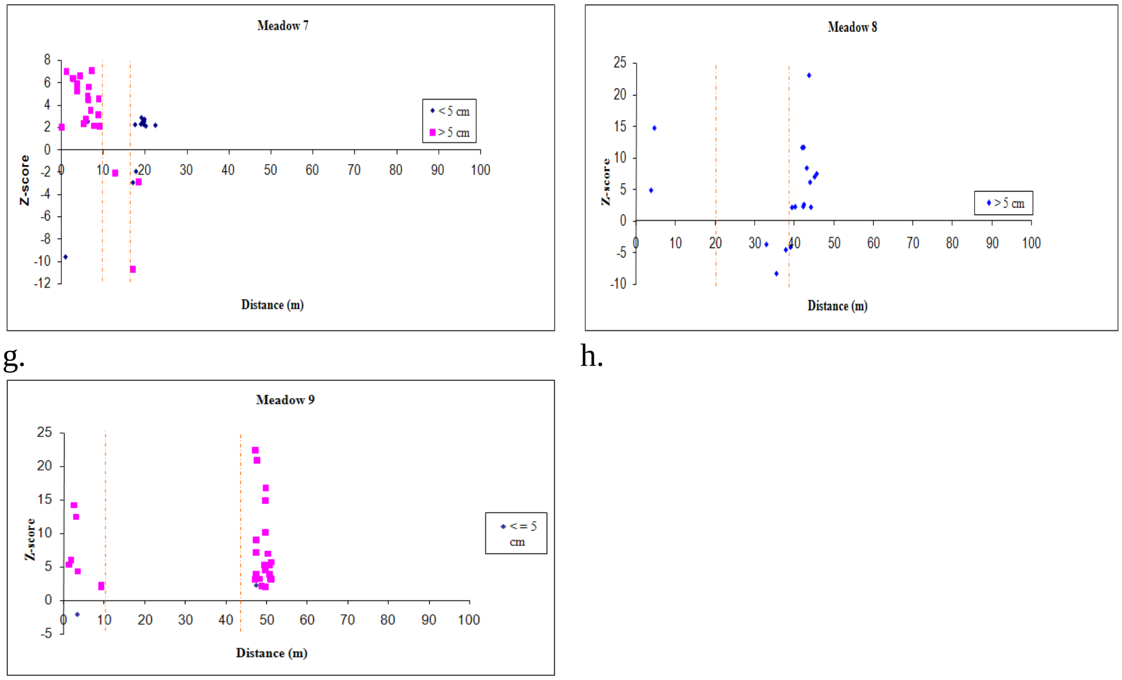
A high, positive z score for the point, in this instance the variable is diameter (cm), indicates surrounding features have a similar value. A low, negative z score for the point indicates surrounding points have a dissimilar value. The z scores do not reflect the actual diameters of trees, and only reflect if their neighbors are similar or dissimilar in diameter (cm). Size class maps were paired with the ALMI statistic to visually compare diameters of trees to the degree of similarity or dissimilarity of features.

In meadow 1, the higher elevation forest boundary, which starts at point 0, has more similar-sized individuals in the 11-20cm size-class (Fig. 5.28). Dissimilarity in diameter increases from forest boundary into meadows as the size of individuals decreases, and these values remain constant with increasing similarity across the meadow until 80m distance. Z-scores become more mixed in similarity/dissimilarity denoting a layering of size classes for the remaining 15m of the belt. This pattern captures the pattern of tree islands and the presence of smaller individuals in the lower forest boundary.



a. b. c. d. e. f.

Fig. 5.27 (a-i). Scatterplot of the z-scores that fall outside of the 1.97 and -1.97 tolerance limit across belt transect distances. The dotted line represents the forest-meadow boundary.



g.

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Fig 5.27 (a-i). Continued

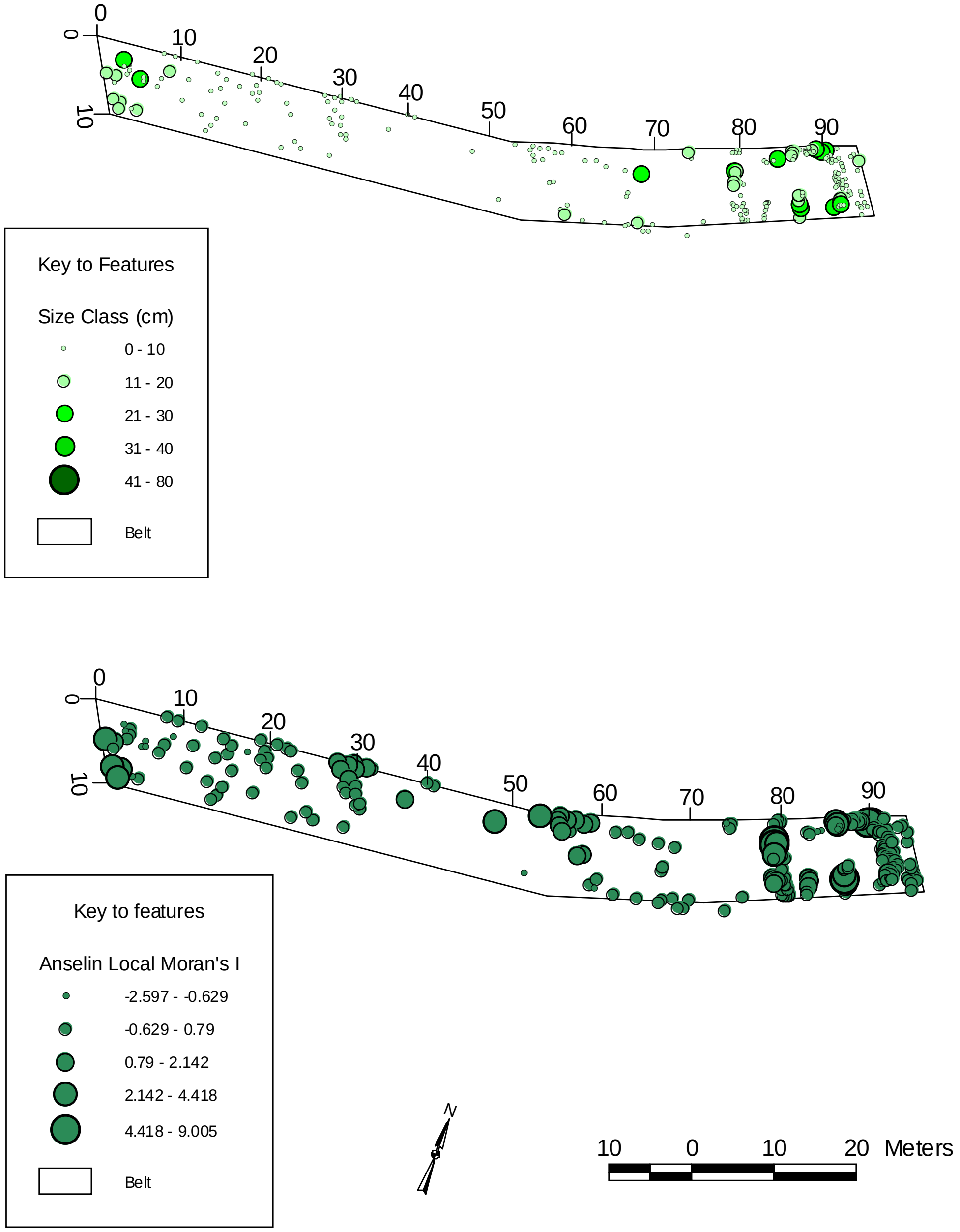

Fig. 5.28. Meadow 1 size class (upper) and Anselin Local Moran's analysis of clusters (lower).

Meadow 2’s lower elevation boundary, starting at 0m, shows both high and low spatial autocorrelation of tree size (Fig. A.17). The size class map of the meadow 2 belt reveals some heterogeneity in individuals sizes with a mix of a few 31 to 40 cm individuals surrounded by a greater number of 0 to 10 cm size class. Z-scores show increasing dissimilarity across the lower and mid-meadow. The higher elevation meadow-forest boundary shows greater dissimilarity in diameter.

Meadow 3’s z-scores reveal strong spatial similarity in tree size across the belt (Fig. A.18). A few instances of great dissimilarity occur in the lower meadow and forest boundary and the upper meadow and forest boundary. These distances are 2m, 10m, and 20 m with 20 m denoting lower elevation meadow-forest boundary. There are fewer larger individuals in the 11 to 20cm and the 21 to 30 cm diameter size-classes dispersed at these distances surrounded by the 0-10 cm size classes contributing to the pattern of dissimilarity.

Meadow 4 has a more complex pattern. There is less similarity throughout the entire belt (Fig. A.19). The AMLI statistic shows more heterogeneous pattern of size class structure with clumping of dissimilar values at 5m, 55m, and 60m. The size class distribution map reveals a mixture of individuals with a greater number of 0-10cm diameter individuals surrounding 21 to 30 cm and 31 to 40 cm size classes in these locations. The 65 m to 75 m of the belt shows similarity in its pattern of size structure.

The AMLI statistic for meadow 5 does not have strong, negative z-score (Fig. A 20). There are areas along the belt that show more variability in size class structure at 3 to 5 m, 15 to 20 m, and 25 to 30 m. The size class distribution maps show a few numbers of individuals in the 11 to 20 cm size class surrounded by a greater number of individuals in the 0-10 cm size class, but the overall pattern of the meadow reveals no strong trends in similarity of size class structure.

The AMLI statistic for meadow 6 does reveal a strong negative z-score and strong positive z-score which indicate both great dissimilarity and similarity in size structure of meadow invasion respectively (Fig.A 20). The greatest variability of size class structure is found at the lower forest-meadow boundary, starting at 40m, but the forest regeneration is sparse compared to the higher elevation meadow-forest boundary. There is greater clustering at the higher elevation meadow-forest boundary, but the size structure is not as variable in its distribution.

Meadow 7 shows strong negative z-scores and shows variability in size structure throughout the forest-meadow boundary (Fig. 5.29). Meadow 7 has so many individuals along the boundary that it exhibits a regular spatial distribution pattern. Based on the size class distribution map, the variability present in the size structure for the meadows is concentrated in the 0 to 10 cm size class.

The AMLI z-scores for meadow 8 show both strong, negative and strong, positive z-scores (Fig. A.22). The size structure shows more variability at the lower elevation meadow-forest boundary, starting at 35m, but the forest structure is sparse. There is greater variability and clustering of the size structure at the higher elevation forest-meadow boundary from 0-15m. The lower elevation meadow has few individuals suggesting the forest regeneration pattern is occurring from the high to the low elevation gradient for this meadow.

The AMLI z-scores for ribbon forest 9 shows dissimilarity in higher elevation forest-meadow boundary, starting at 0 to 5m, with little variability in size structure found again until 45 to 55 m in distance at the lower elevation boundary (Fig. A.23). There is greater clustering of similar size structure at the lower elevation boundary.

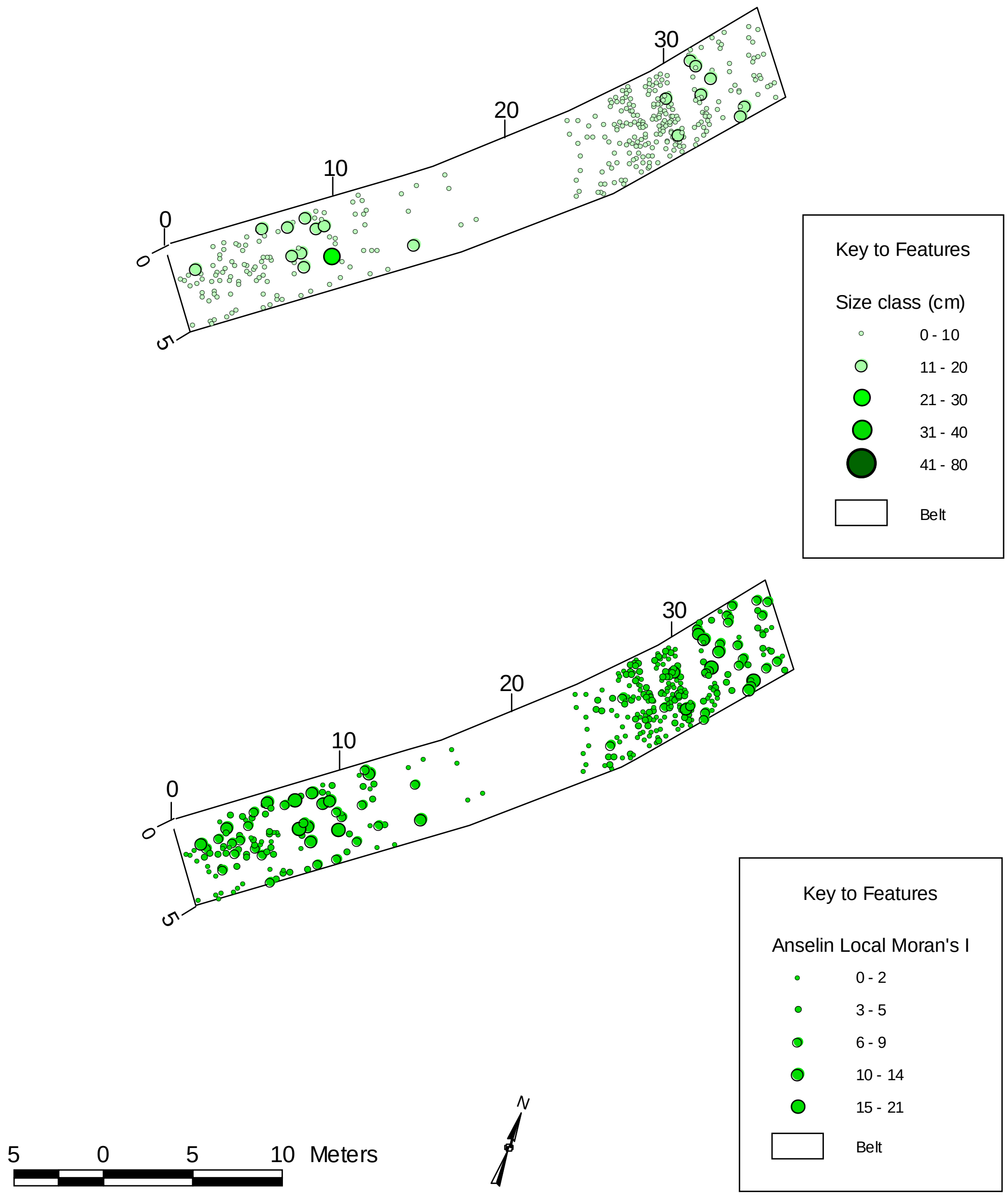

Fig. 5.29. Meadow 5 size class (upper) and Anselin Local Moran's I analysis of clusters (lower).

6. DISCUSSION, SUMMARY AND CONCLUSIONS

6.1 The Effects of Climate on *A. lasiocarpa* Establishment

The earliest establishment period for seedlings is in subalpine forests, which began after the 1850s. Recruitment in both the upper and lower forest boundaries follows directly after the end of the Little Ice Age as the climate became warmer (Bekker 2005, Hall and Fagre 2003). Data are lacking for determining establishment for forests after the 1950's, so it is difficult to discern if climate change is more or less favorable for regeneration. The main establishment period for subalpine meadows began in the early part of the 1900s showing a lag in both establishment relative to forests, which may suggest a stabilized forest under the climate regimes in the area. Meadows then show decreased establishment in the 1950's through the 1970's (Fig. 5.4). The study does not have adequate data to capture the invasion pattern after 1976, though un-sampled, small seedling pattern may reflect a changing climate that is favorable for contemporary establishment in subalpine meadows.

Changes in climate may be related to forest establishment in Preston Park, Glacier National Park. The positive correlation between establishment and fall mean maximum temperature, fall mean minimum temperature, and fall mean temperature supports the hypothesis that temperature influences *A. lasiocarpa* recruitment in subalpine forests and into subalpine meadows. Temperature increase extends growing season length for forests. Warmer, fall maximum mean temperatures at this site promotes warmer soils and lengthens the growing season. Warmer summer and fall temperatures may encourage faster leaf, shoot, and stem growth (Körner 1998). Warmer fall temperatures are associated with higher levels of solar radiation reducing photoinhibition after cold, evening temperatures (DeLucia and Smith 1987). Given the positive relationship with seedling recruitment and fall temperature categories, then seedling recruitment in subalpine forests is increased due to bountiful seed crops from previous years and a longer, critical snow-free period for propagules to germinate and become well established (Fig. 5.8).

There is no positive correlation between total precipitation and establishment, which does not support the hypothesis of precipitation influencing *A. lasiocarpa* recruitment into forests and meadows. For forests and meadows these data suggest that precipitation does not influence *A. lasiocarpa* establishment, and this relationship between establishment and total precipitation is similar in both higher and lower elevation forests of the subalpine zone in GNP (Fig. 5.8). Perhaps these areas experience an earlier snowmelt date and experience soil moisture stress earlier in the growing season (Fig. 5.8). However, there is a strong positive correlation between forest establishment and spring value of the Pacific Decadal Oscillation index, which indicates warmer, wetter conditions are positively influencing establishment (Fig. 5.8). The strong, negative correlation between meadow establishment and PDO in spring indicates cooler and drier conditions, and seems to indicate a decrease in snowpack depth, which in turn increases *A. lasiocarpa* establishment in meadows (Fig. 5.8). The relationship between negative PDO and establishment is most evident in meadows of the subalpine zone. Correlations of PDO and establishment for both forests and meadows do not show significant trends for upper and lower elevation.

The negative PDO and establishment relationship reflects the importance of snowpack characteristics on growing season by its presence on the landscape (Hansen-Bristow 1986, Peterson and Peterson 2001). Pederson et al. (2004) found PDO cycles can alter snowpack and snow water equivalent in GNP. Another research study located in eastern GNP found correlations of negative PDO cycles with establishment at treeline locations (Alftine et al. 2003). Overall, the PDO regional climate phenomenon seems to have significant influence on the establishment of subalpine forests and meadows.

Based on establishment dates and on the relationships between establishment and climate, the change in seasonal temperature and precipitation show a warmer, wetter climate favoring *A. lasiocarpa* establishment at the subalpine meadow-forest interface over a century-long period. Peak establishment in meadows occurs at a later and over a shorter period from the 1920s to 1960s (Fig. 5.5, Fig. 5.6). The climate-establishment relationship does show a spatial and temporal lag effect between forests and meadows, which is pronounced along the elevation gradient.

Climate is considered one of the important driving factors in structuring species patterns on the landscape, especially patterns of tree migration into the subalpine and alpine zones (Daniels and Veblen 2004, Innes 1991, Kupfer and Cairns 1996, Körner 1998, Stevens and Fox 1991). In recent papers discussing plant hierarchy theory, climate is considered a top-down control that organizes macroscale patterns of plant diversity, and influences environmental heterogeneity that in turn influences nonequilibrium processes at the mesoscales and microscales respectively (Whittaker 2001, Sarr et al. 2005). Temperature and precipitation, the latter factor influencing moisture availability, affect plant growth, maintenance and reproductive processes (Woodward 1987, Sarr et al. 2005). Temperature and precipitation are considered primary variables driving seedling establishment into subalpine meadows (Rochefort et al. 1994, Rochefort and Peterson 1996). In Preston Park, periods of extremely low temperatures and low moisture availability during the growing season do not support a high diversity of species; *A. lasiocarpa* is stress tolerant therefore it persists on the landscape. Under hotter, drier conditions of climate, it regenerates; therefore it dominates the landscape.

6.2 Temporal and Spatial Patterns of *A. lasiocarpa* Distribution

Basal diameter and age class maps show larger and older individuals of *A. lasiocarpa* are located in lower and upper forest boundaries on higher slopes across the elevation gradient for meadows 1 (Fig. 5.15-5.16), 2 (Fig. 5.16 and Fig. A.17), 5(Fig. 5.29 and Fig. A.2), 6 (Fig. A.6 and Fig. A.20), 8 (Fig A.7 and Fig. A.22), and 9 (Fig. A.7 and Fig. A.23). Meadows 1 and 4 (Fig. 5.28 and 5.16; and Fig. A.19 and Fig. A.5) do show larger and older individuals located in tree islands in the central meadows. Based on the bivariate second order neighborhood analysis all meadows, with the exception of meadow 3, show strong spatial associations between seedlings and trees across the entire range of neighborhood for the transect (Fig. 5.25). Based on the ALMI results and size class maps, there is higher spatial auto correlation of large trees in forest boundaries, but the spatial patterns of larger and smaller trees are mixed in the upper and lower slopes of the meadow-forest boundaries (Fig. 5.27, Fig. 5.28, and Fig. A.17-A.23). Central meadows show more spatial autocorrelation in seedlings with the exception of tree islands.

The patterns of establishment across the elevation gradient reflect larger, older trees recruiting seedlings in more immediate proximity to the large individual (Fig. 5.15, Fig. A.1-Fig. A.8, Fig. 5.25). Near forest edges individuals tend to occupy available spaces (Fig. 5.24). This recruitment is spreading into the slopes of the meadow boundaries and central meadow locations as tree islands (Fig. 5.27). At higher elevations and in ribbon forests, larger and smaller trees are more clustered together (Fig. 5.27). In all meadows seedlings recruit with greater density around these larger trees, but meadow 2 shows dispersion with greater distances from large individuals into more open sites (Fig. 5.27). The meadow 2 pattern of closely clumped small trees around larger individuals shows avoidance of less favorable sites. Seedling recruitment in close proximity to larger trees in meadows across the elevation gradient, points strongly to the effects of positive feedback with intraspecific interactions.

The above patterns indicate that tree establishment for all sites show an "in-filling" process. An "in-filling" pattern is a result of seedlings establishing in more open gaps around larger individuals or patches of trees (Liguna et al. 2008, Slatyer and Noble 1992). Larger trees establish on more favorable sites. Over time large individuals ameliorate site conditions creating sites conditions favorable to seedling establishment, or "in-growth" trees, i.e. "smaller diameter, shade tolerant species in high density clusters" (Smith et al. 2005). As climate favors reproduction for *A. lasiocarpa*, seeds of neighboring *A. lasiocarpa* individuals become deposited around larger trees on these favorable sites (Table 5.4 - Table 5.6). In meadow 4, the pattern of large and small individuals located across the meadow boundary suggests that the presence of larger trees throughout both forest and meadow boundaries recruit small individuals heavily in all meadow locations (Fig. A.19). The increased tree island expansion seems to be infilling meadows and closing forest canopy more rapidly. For example, meadow 3 is small in size, and shows a greater amount of “in-filling” with greater canopy closure showing a more random pattern (Fig. 5.26). Meadow 3 is small compared to the rest of the meadows in the study, so canopy closure is more likely. Meadow 3 had many large individuals in the meadow interior, which is a pattern reflecting the closure of a climax canopy.

6.3 The Role of the Regeneration Niche and Biotic Succession

The colonizer *A. lasiocarpa* has become a single canopy, self replacing species in Preston Park. Continued dominance is noted by the presence of seedling establishment into meadows (Watt 1947). The presence of a greater number of seedlings near larger trees shows the larger individuals increase seedling survival and increase seed deposits in the existing seed bank in close proximity (Maher and Germino 2006, Tranquillini, 1979). Propagules seemed to be recruited heavily from the surrounding forests and from individuals well established in meadow interiors. *Abies lasiocarpa* can reproduce and recruit seeds under more shaded canopies. Seedling response to neighboring plants is important in structuring forests in the regeneration niche (Maher and Germino 2006). Canopies can serve seedlings in many ways. Via contagious dispersion the snowpack melts earlier surrounding the larger individual, making surrounding sites open and available to seeds earlier in the growing season (Payette et al. 2001). Once established, seedlings are shade tolerant, performing quite well in heavily shaded openings of the forest or in the shadows of trees on the edge of open sites in central meadow locations.

6.4 Biotic Controls that Structure Subalpine Forests and Meadows

Intraspecific interactions and life history are important controls of *A. lasiocarpa* establishment patterns. Stress tolerance, facilitation and competition are mechanisms used by plants to survive in unproductive habitats (Grime 2001). In habitats where stress conditions prevail, seedling establishment advances under protective canopies of well established trees that reduce water and heat stress (Callaway and Walker 1997, Franco and Nobel 1989, Grime 2001).

Stress tolerance and facilitation are two mechanisms used by *A. lasiocarpa* in establishment of subalpine meadows. Adult populations of winter hardy species have a high frost tolerance and are acclimated to cold environments (Levitt 1972). Yet seedlings of this population are susceptible to injury or mortality due to the stressful environmental conditions during winter, as well as high light and temperature stress during the summer. The forest edge effect improves microsite and microclimate conditions and reduces limitations for *A. lasiocarpa* to establish (Liguna et al. 2008). Tree patches are known to ameliorate microsite conditions in the high mountain environments to facilitate invasion. For example, the presence of a larger neighbor may capture wind-blown snow, affecting snow thickness, which produces a “nurse” effect by both insulating and protecting young trees from extreme cold and dessication from winds (Callaway 1998). As the snow melts under the canopy, and it will melt more slowly because of the shade, the remaining snow becomes a source for soil moisture for a longer time period in the growing season. Also larger individuals buffer the effects of a high irradiance environment, which can both be deleterious to younger *A. lasiocarpa* seedlings. Solar radiation can also dry soils more rapidly early in the growing season creating drought stress for young seedlings with less established root systems.

The presence of dead and dying stands of *P. albicaulis* may show that this species had been influential in initiating *A. lasiocarpa* invasion on the landscape and facilitating *A. lasiocarpa* growth in these subalpine meadows, but it has been out competed in climate more favorable to *A. lasiocarpa* at the higher elevation (Callaway 1998, Maher and Germino 2006, Maher et al. 2005). In harsh environments with low resources, then the release of stress by a neighbor providing shelter from environmental stresses may be more important in maintaining seedling survival than the role of competition (Callaway 1998). At both the higher and lower elevation sites seedlings and saplings of *A. lasiocarpa* establish in close spatial proximity to large trees. The dense clusters for all meadows, with exception of meadow 3, show that at the seedling stage the facilitative effects of larger individuals are important for seedling survival.

Competition is thought to be important under conditions where resources limit productivity (Tilman 1982, Weins 1977). Tilman (1982) defined strong competitors as those individuals having the ability to tolerate extremely low resource levels. Such a definition focuses more on a mechanistic view of competition, but this view becomes more complex in light of plants modifying the environment to less favorable conditions making it unsuitable for the fitness of neighbors (Grime 2001).

Plant competition occurs in both below-ground and above-ground locations. Upon germination and establishment, seedlings require minimal space and resources, thus these individuals may occur more closely together in space without affecting each other. Competitive initiation may first occur in the soils via root interaction (Grime 2001). If soils and habitat are poor and do not promote productivity, then plant canopies will remain underdeveloped with competition more confined to below-ground environments. If soils promote higher productivity, then competitive canopy interactions will occur. Canopies encroaching on neighbors affect the quality of light and thus plant responses to this competition may alter canopy composition (Ballare et al. 1987, Novoplansky et al. 1990). Extensive shading from dense canopies also has the caveat of extensive root systems, and this may also indicate a scarcity of water and nutrient depletion of resources (Grubb 1994). Regardless of below ground scarcity of resources, an extensive canopy is a competitive advantage for capturing both space and light resources.

Such scarcity of resources due to consumption by plants amplifies the competitive effect when considering intra-specific competition. Environmental conditions may reduce the competitive ability of smaller individuals within the same species. Though *A. lasiocarpa* is a hardy and long lived competitor, smaller individuals do not have the ability to competitively exclude larger neighbors in more central meadow locations. Even under favorable climatic conditions, a favorable growing season that contributes to growth, maintenance and reproduction; smaller *A. lasiocarpa* individuals can be outcompeted by larger neighbors. So under strained resources and on unfavorable sites, as found in more central meadow locations, then competition between different sized individuals is more fierce and larger trees will exclude their neighbors. Since *A. lasiocarpa* is a long-lived and hardy competitor, it dominates high elevation forests and influences successional dynamics over a longer period of time (Liguna et al. 2008, Watt 1947).

6.5 Abiotic Factors that Structure Subalpine Forests and Meadows

Environmental heterogeneity, specifically edaphic and topographic factors, may have a strong control on dynamic plant geography, which may especially be true in the high mountain environments (Cowles 1911, Whittaker 1960). Species composition and the growth of individual plants are considered to change along limiting resource gradients, such as light, moisture, and nutrient levels (Sarr et al. 2005).

Abies lasiocarpa dominant forests and meadows have a common genetic make-up, yet one may argue the spatial pattern and size structure of individuals established in meadows and ribbon forests is in response to resource patchiness of more unproductive habitats (Grime 2001). These individuals express the tradeoff in allocation of resources to either shoots or roots, between foraging for light, mineral nutrients, or water, which is reflected in the stature of individuals (Grime 1973, 1994, Huston and Smith 1987, Tilman 1988). In a drier climate scenario in the high mountain environment, the importance of moisture gradients to seedlings regeneration and spatial patterns become pronounced (Sarr et al. 2005). In tree islands and meadow "rims" organic matter is more plentiful and soil depth is greater. The accumulation of humus affects succession, and "humus accumulation occasions an increase in soil moisture on uplands and a decrease in soil moisture in depressions; hence it is probable that the changed water relation due to humus accumulation is the dominating factor in determining the mesophytic trend, both in hydrophytic and in xerophytic habitats" (Cowles 1911). In the more open meadows of Preston Park, especially in meadow interiors, these individuals are more sparse in density and are shorter statured. Butler et al. (2003a) found in Preston Park that meadow and ribbon forest "rims" had greater organic matter and alluvium present and central meadow interiors had less organic matter and colluvium present.

Field observations found two meadows which seem to serve as good examples of a wet meadow and a dry meadow. Based on the Ripley's K residual analysis, meadow 1, which exhibits characteristics of a wet meadow, shows an establishment pattern of spatial clustering across the entire range of the meadow above what is expected (Fig. 5.26). Meadow 1 is a good example that plentiful soil moisture facilitates invasion across the entire forest-meadow boundary. Meadow 2 seems to be a very dry meadow, and it shows spatial clustering at a lesser extent across the entire range of the neighborhood (Fig. 5.26). This meadow is a good example of the effects of limiting resources for soil moisture.

The effects of solar irradiance on seedlings are influential on seedling establishment patterns. In the high mountain environments more open areas experience greater light intensity, which increases temperatures during the summer months as well as creates moisture stress (Thomas et al. 2005). A dense stand buffers seedlings from the deleterious effects of light. Intraspecific differences in *A. lasiocarpa* age and size structure suggest seedlings require protective cover from bright sunlight and temperature, which are important factors in facilitating growth in germinated seedlings in high mountain environments (Germino & Smith 1999, 2000, Germino et al. 2002, Maher and Germino 2006). Maher et al. (2005) found tree cover increased photosynthesis and survivorship in conifer seedlings at the alpine treeline, especially in *A. lasiocarpa*. A greater stress tolerance, both photosynthetic tolerance and temperature extremes, imparts a greater competitive advantage to *A. lasiocarpa* thereby allowing it to remain dominant in Preston Park subalpine meadows.

Topographic influence may be a factor on seedling establishment pattern. For example a majority of the establishment occurs on the hotter, drier aspects positioned on the south, southwest, and west facing slopes. *Abies lasiocarpa* can grow as a pure stand in severe sites, and become the dominant species in such areas (Burns and Honokala 1990). Aspect and slope affect irradiance and soil temperatures, patterns of wind and has an effect on precipitation (Jones 1992). Other topographic and lithologic factors also control tree and seedling spatial patterns. Butler et al. (2003a) found strong geomorphic and topographic controls on tree spatial pattern. Meadows at lower elevation positions on the topography are found “between ridges where erosion along bedding plane strike was concentrated” (Butler et al. 2003a and b). Ribbon forests express a parallel to sub-parallel pattern in their position to one another, which follows the area stratigraphy. These forests are often found perpendicular in direction to prevailing winds (Billings 1969, Holtmeier and Broll 1992). Large trees are found on the higher ridges that are well drained sites both in meadows and Ribbon forests.

Seedling establishment is more concentrated on the slopes of meadows near forest edges (Fig. 5.28-Fig. A.19). Steep slopes have decreased establishment (Fig. A.20 and Fig. A.22) Slopes may benefit from deposition of humus downslope from the ridges, which may improve soil depth and soil quality on more less steep slopes. In the high mountain environment local topography is a strong control both in determining resource factors and microclimate (Jones 1992). Slope and soil factors contribute to water stress which can affect seedling mortality or growth in more open sites (Thomas et al. 2005). Based on the Ripley's K residual analysis, meadow 2 and the higher elevation, erosional meadows and ribbon forests exhibited similar spatial patterns of clustering below what is expected with dispersion at spatial associations greater than 4 m (Fig. 5.26). Meadow 2 did not have steep slopes as compared to the other meadows in this study. The dispersion pattern may reflect the influence of slope factors on seedling establishment patterns, which is more pronounced at higher elevation, erosional meadows. Steep slopes catch more snow in leeward edges of meadows and ribbon forests. Snowpack insulates the ground near the upper rooting zone buffering the soils from freezing, and once snowpack melts, soils temperatures reflect mean daily temperatures and soil moisture is increased (Evans and Fonda 1990, Woodward 1998). *Abies lasiocarpa* starts leaf and shoot expansion directly after snowmelt (Hansen-Bristow 1986, Peterson and Peterson 2001). *Abies lasiocarpa* has developed to take advantage of the snowmelt to have as productive a growing season as possible.

Resource constraints express a similar pattern for all meadows on the elevation and topographic gradient with the exception of meadows 5, 8, and 9; and the lack of individuals at lower meadow and forest boundaries may reflect sites with inadequate resources for germination and establishment of seedlings. These meadows are more eroded, and have steeper slopes than lower meadows, which may also reflect a greater depth of a “snow fence” effect where wind blown snow piles up, and persists on the landscape for a longer time and shortens the growing season in these specific locations. Limiting factors, such as soil moisture and high light, are strong controls on this establishment pattern.

6.6 Summary and Conclusions

Abies lasiocarpa invasion was initiated in forest boundaries directly after the end of the Little Ice Age in the 1850s, and this invasion is most pronounced in subalpine meadow interiors by the 1920s. There is a strong relationship between climate and seedling establishment in Preston Park, GNP. For total establishment the significant climate variable is fall mean temperature (r^2=0.35). There are significant relationships between residual establishment and fall mean temperature, fall mean minimum temperature and fall mean maximum temperatures in forests. There is also a significant, positive correlation between establishment and spring Pacific Decadal Oscillation for forests, which seems to indicate warmer, wetter conditions initiating establishment. For meadow establishment spring mean temperature is the significant climate variable (r^2=0.27). The relationship between establishment and negative PDO is inversely related in meadows indicating cooler, drier periods are favorable for establishment of *A. lasiocarpa*. The climate-establishment relationship does show a strong spatial and temporal lag effect between forests and meadows, which is pronounced along the elevation gradient.

Vegetation patterns in subalpine meadows and ribbon forests in Glacier National Park seem to reflect positive feedback effects (Wilson and Agnew 1992). The buffering of negative climate conditions is crucial for seedlings to survive during periods when climate is not optimal for further seedling advancement. Because data collection of smaller trees was restricted, it is difficult to discern if climate has had an effect on contemporary establishment patterns. There is a strong spatial association of large trees and seedlings in the subalpine meadows in Preston Park, GNP. The continued facilitation of seedlings by trees may "in-fill" and meadows will become more closed canopied in response to continuing climate change that is favorable for establishment.

Topography and influences the spatial patterns of soil nutrients moisture and temperature, as well as influences the amount and duration of snowpack within Preston Park meadows and ribbon forests. Establishment, especially tree patches or tree islands, tracks deeper soils resources closely. These factors in turn influence the spatial patterns of *A. lasiocarpa* in Preston Park meadows and forests. Climate has more indirect effects on environmental heterogeneity and the role of competitive hierarchical interaction between individuals of species *A. lasiocarpa*. Because *A. lasiocarpa* is an excellent competitor on severe sites under these climate conditions it may continue to dominate subalpine forests unless disturbance enters the basin. In the presence of a hotter, drier climate that reduce snowpacks and extend the growing season, then *A. lasiocarpa* recruitment in forests may increase, but this climate would maintain meadows. Periods of cooler, wetter climate may continue to destabilize the meadow-forest boundaries and recruit seedlings into meadow interiors where soil resources are available.

6.7 Future Research for Understanding *A. lasiocarpa* Establishment in Preston Park

The regional climate phenomenon of PDO had a significant effect on *A. lasiocarpa* establishment in Preston Park meadows, but the specific role total precipitation and snowpack plays in the establishment pattern is largely unknown in this area of the subalpine zone. Additional information on snowpack would be interesting for two reasons. First, data on snow water equivalence would allow a more detailed analysis on the timing of invasions in response to the start of the growing season. Second, water chemistry analysis might be interesting to infer effects from the moisture resource and how it affects vegetation pattern.

Finally, a more rigorous second order multi distance spatial analysis should be performed based on tree heights of individuals in close proximity to one another. The bivariate Ripley's K analysis would allow a more specific analysis of the effects canopy height on neighboring vegetation. This analysis would allow further exploration of relationship between vegetation pattern and competition and facilitation. Understanding these mechanisms of positive feedback would allow a greater understanding on how plant to plant interactions are controlling vegetation patterns on the landscape.

Finally, soils play an important role in subalpine meadow establishment. A more quantitative analysis of soil depth and density for the meadow belts is needed. Specifically, how the density numbers and soil depth changes with distance from forest edge into meadow interiors. The information would give greater insight into the role of soils influencing meadow establishment patterns.

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APPENDIX

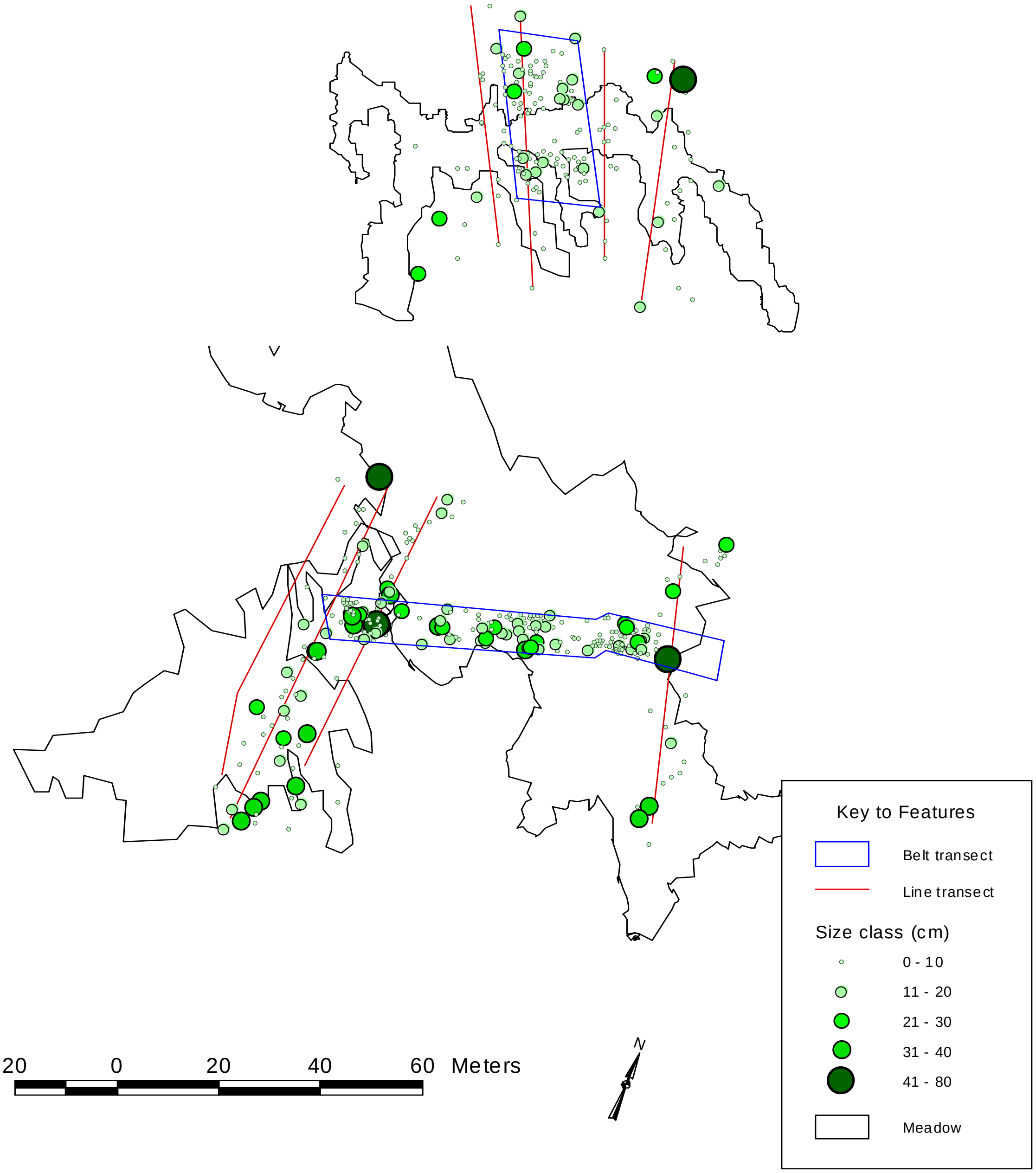

Fig. A.1. Size class maps of seedling and tree diameters (cm) in meadow/forest boundaries of meadows 3 and 4 in Preston Park.

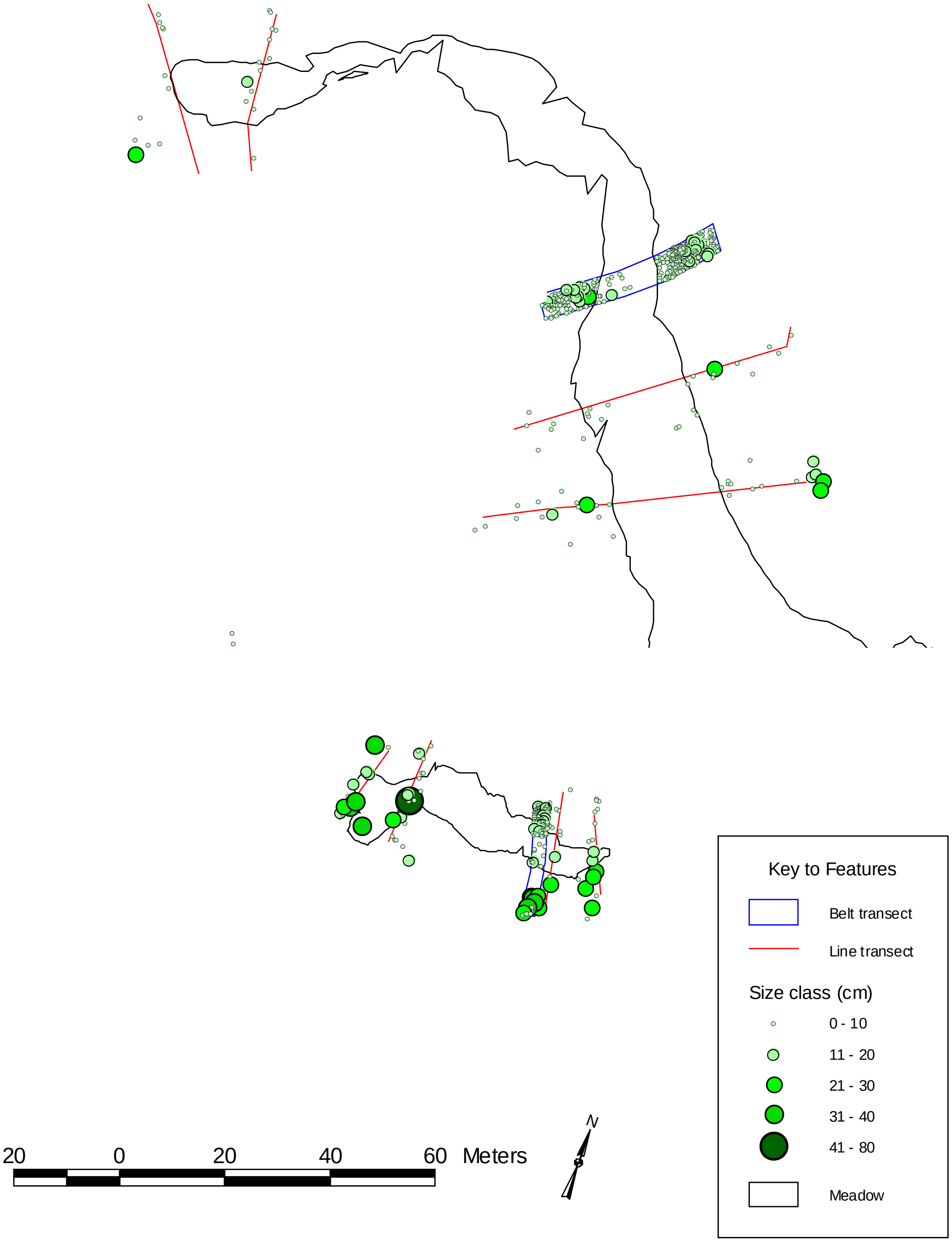

Fig. A.2. Size class maps of seedling and tree diameters (cm) in meadow/forest boundaries of meadows 5 and 6 in Preston Park.

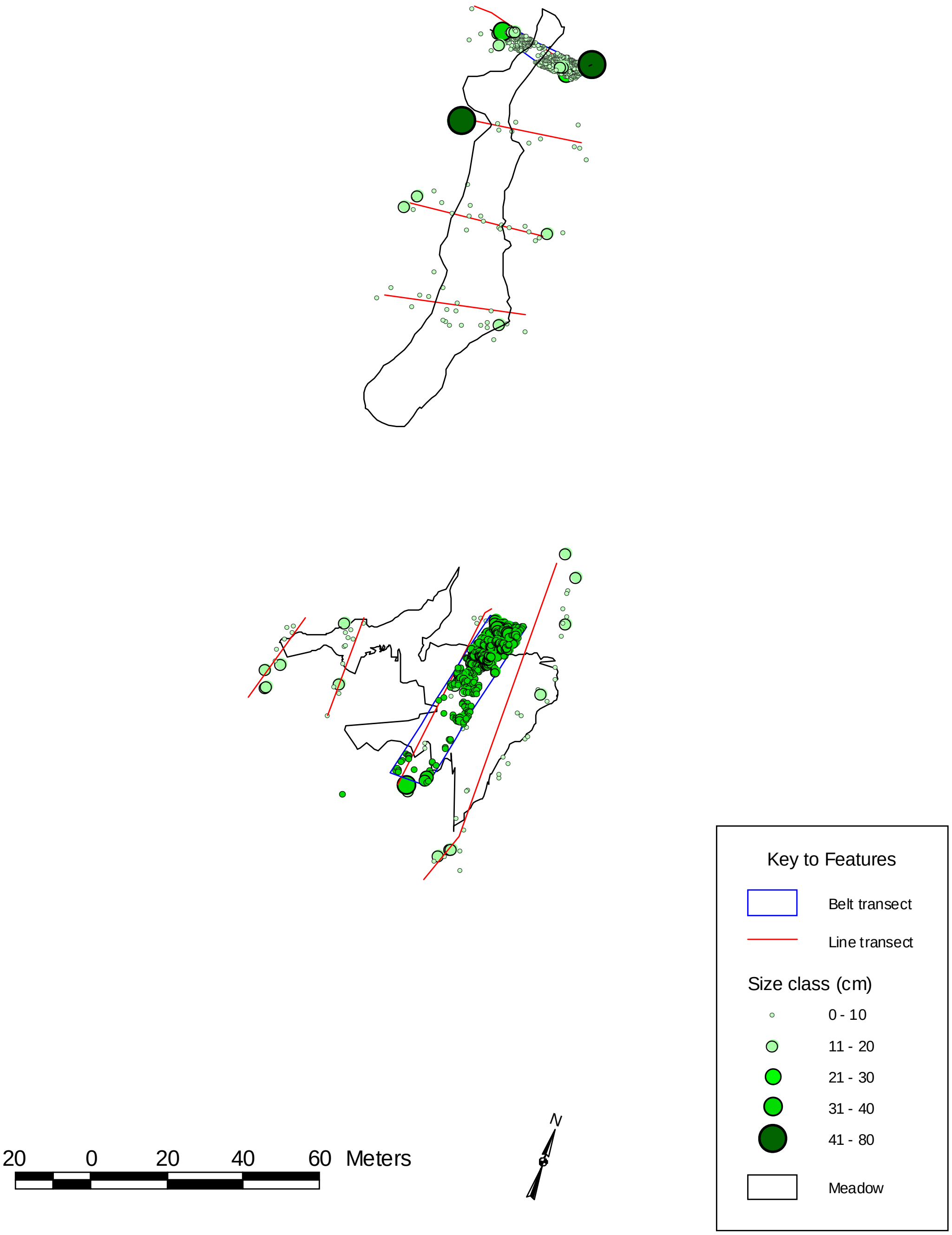

Fig. A.3. Size class maps of seedling and tree diameters (cm) in meadow/forest boundaries of meadows 7 and 8 in Preston Park.

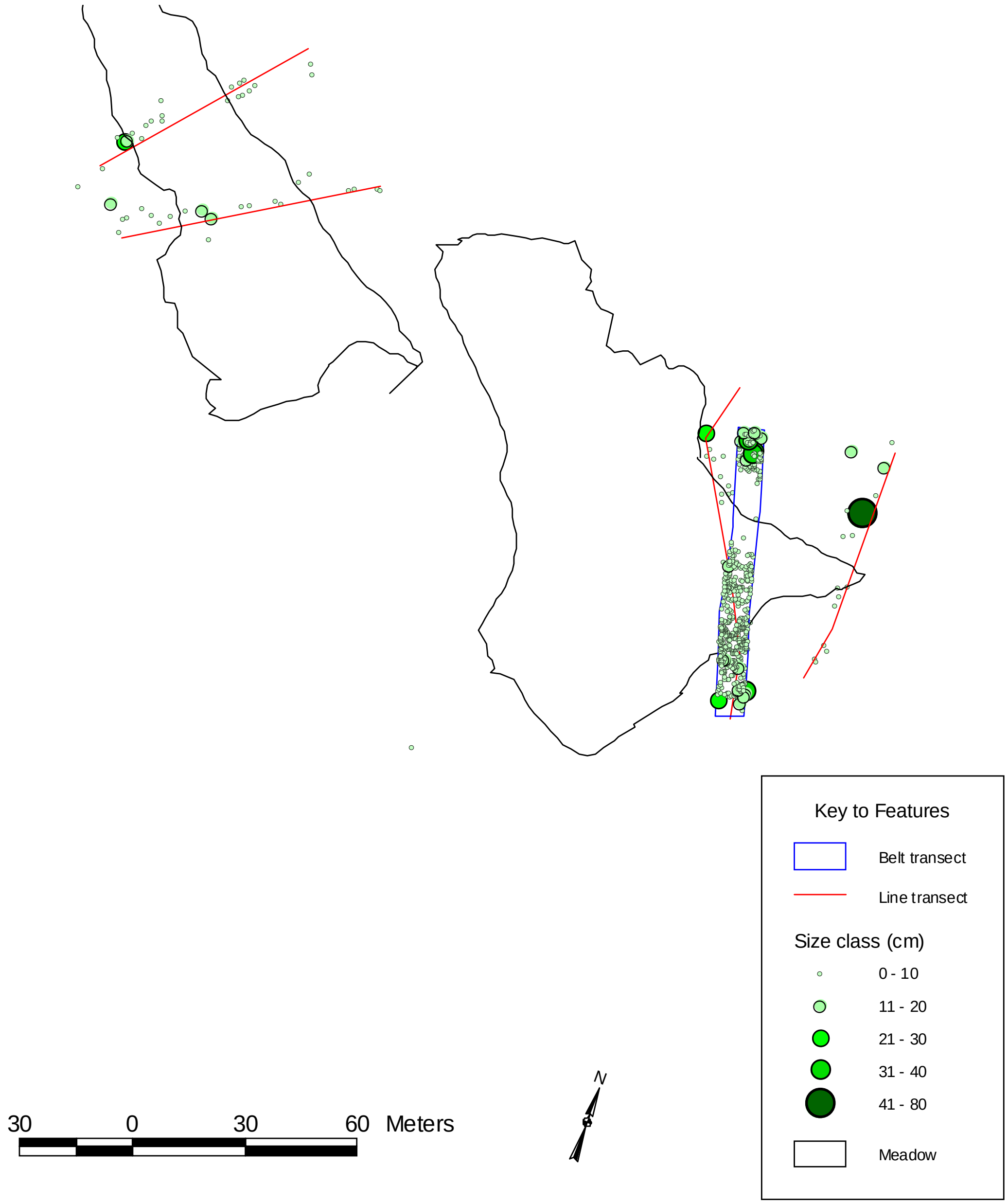

Fig. A.4. Size class maps of seedling and tree diameters (cm) in meadow/forest boundary of meadow 9 in Preston Park.

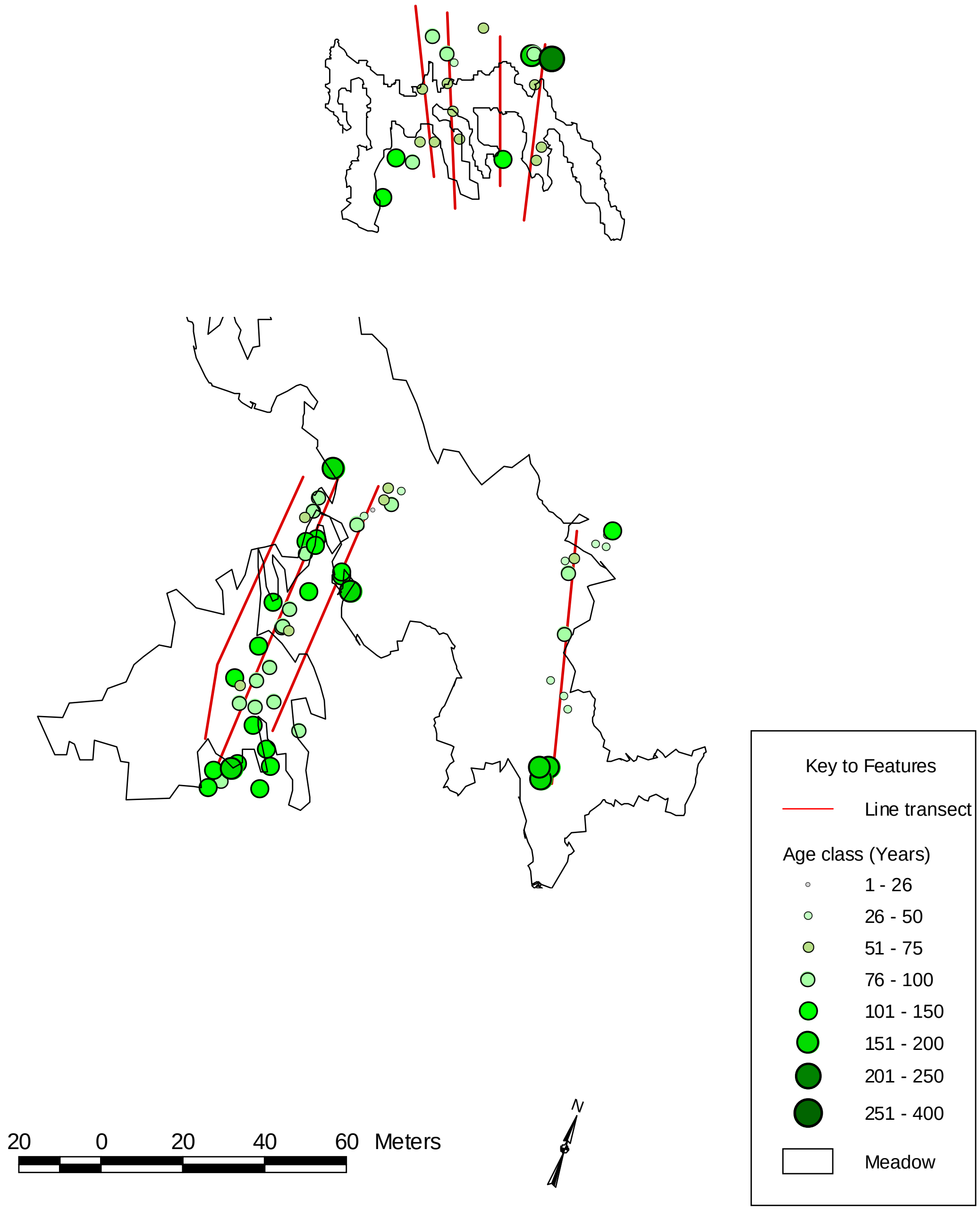

Fig. A.5. Age class maps of seedling and tree diameters (cm) in meadow/forest boundaries of meadows 3 and 4 in Preston Park.

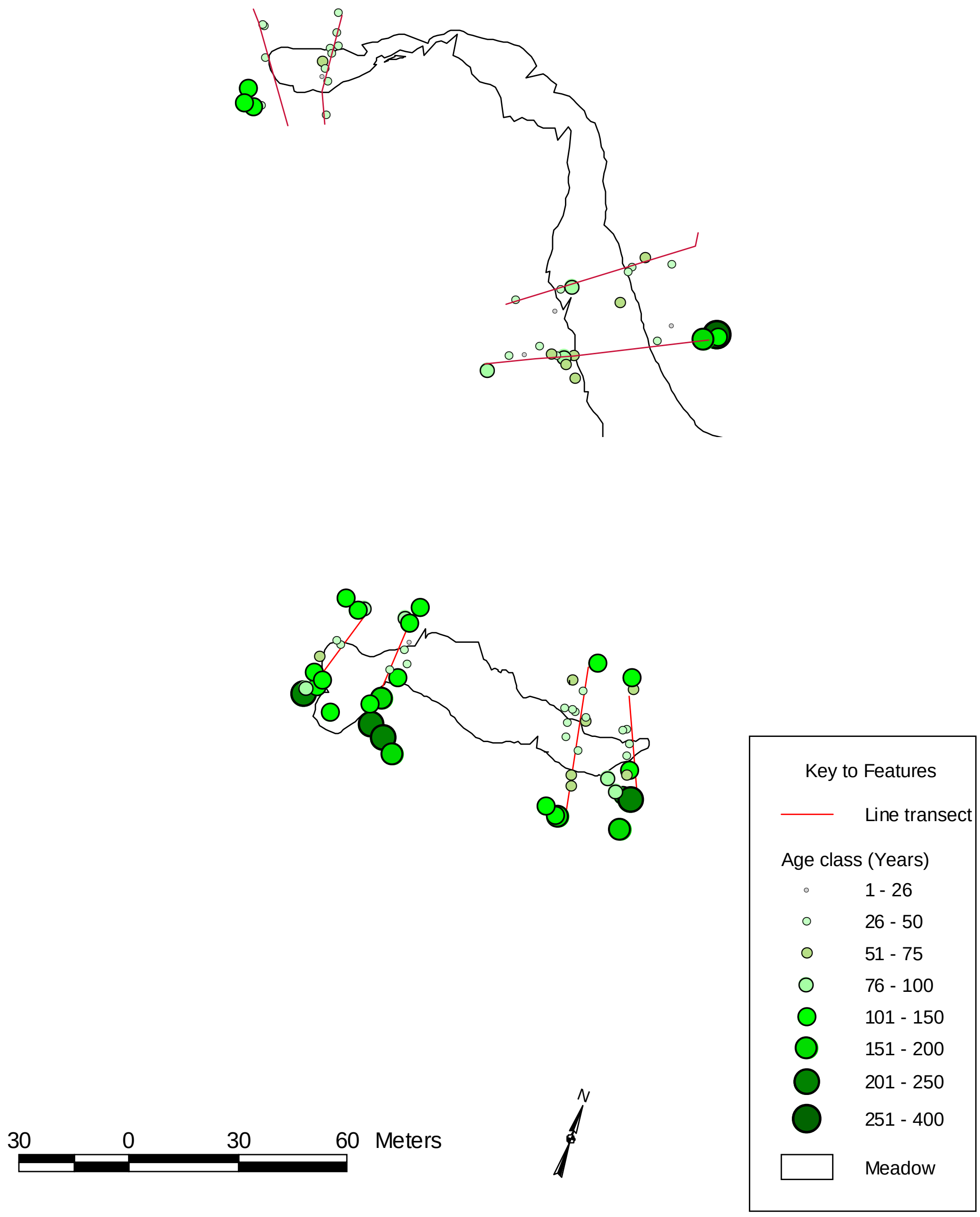

Fig. A.6. Age class maps of seedling and tree diameters (cm) in meadow/forest boundaries of meadows 5 and 6 in Preston Park.

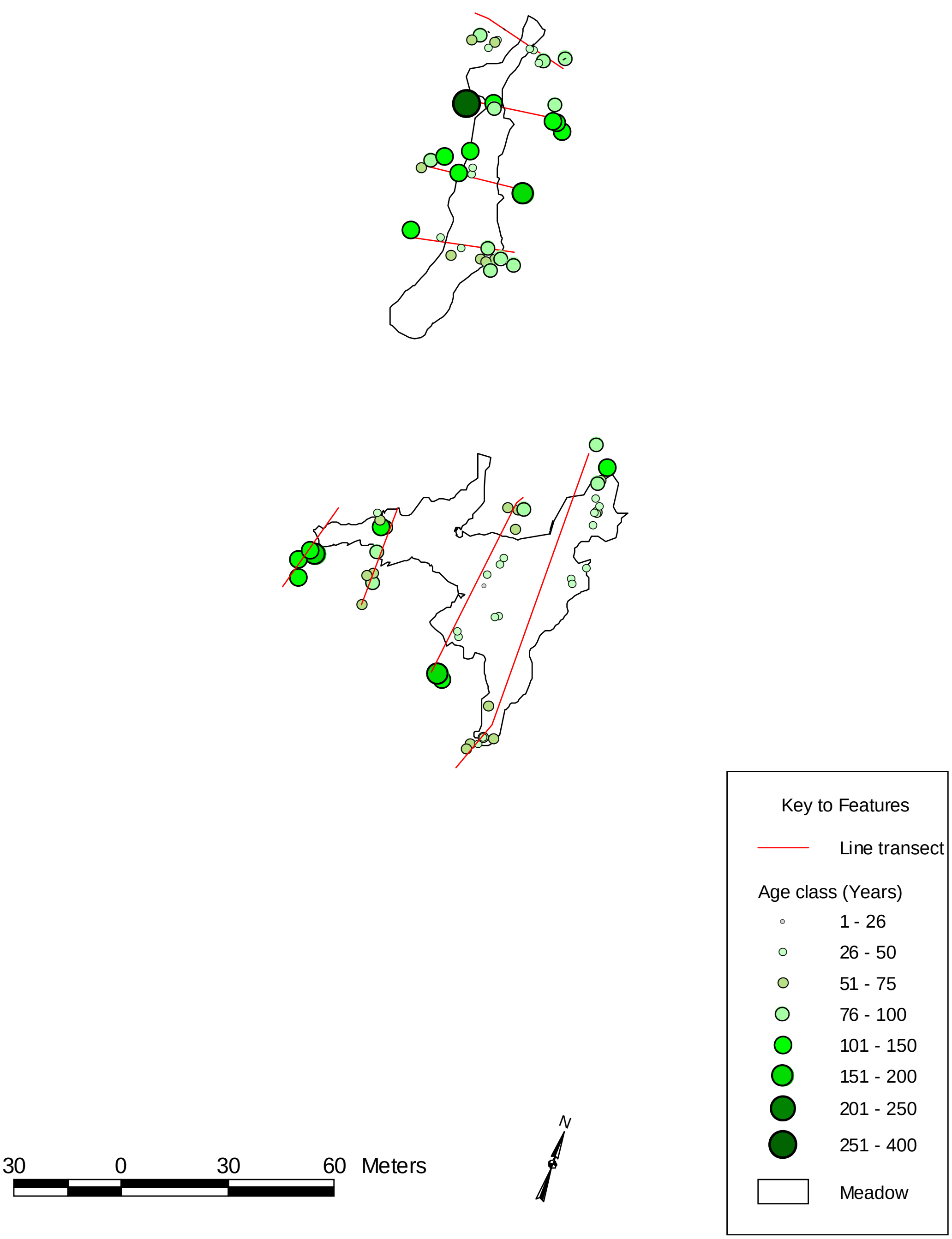

Fig. A.7. Age class maps of seedling and tree diameters (cm) in meadow/forest boundaries of meadows 7 and 8 in Preston Park.

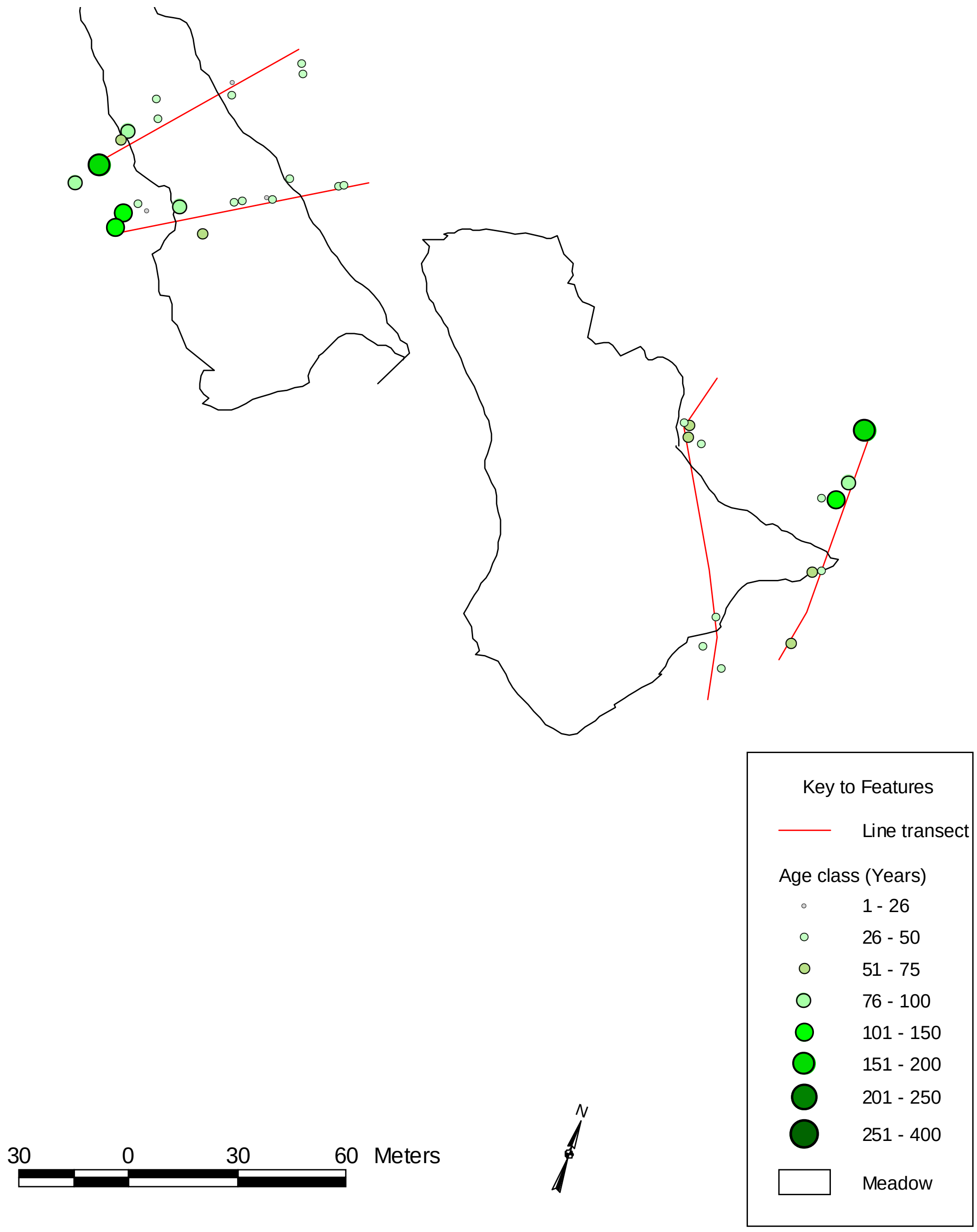

Fig. A.8. Age class maps of seedling and tree diameters (cm) in meadow/forest boundary of meadow 9 in Preston Park.

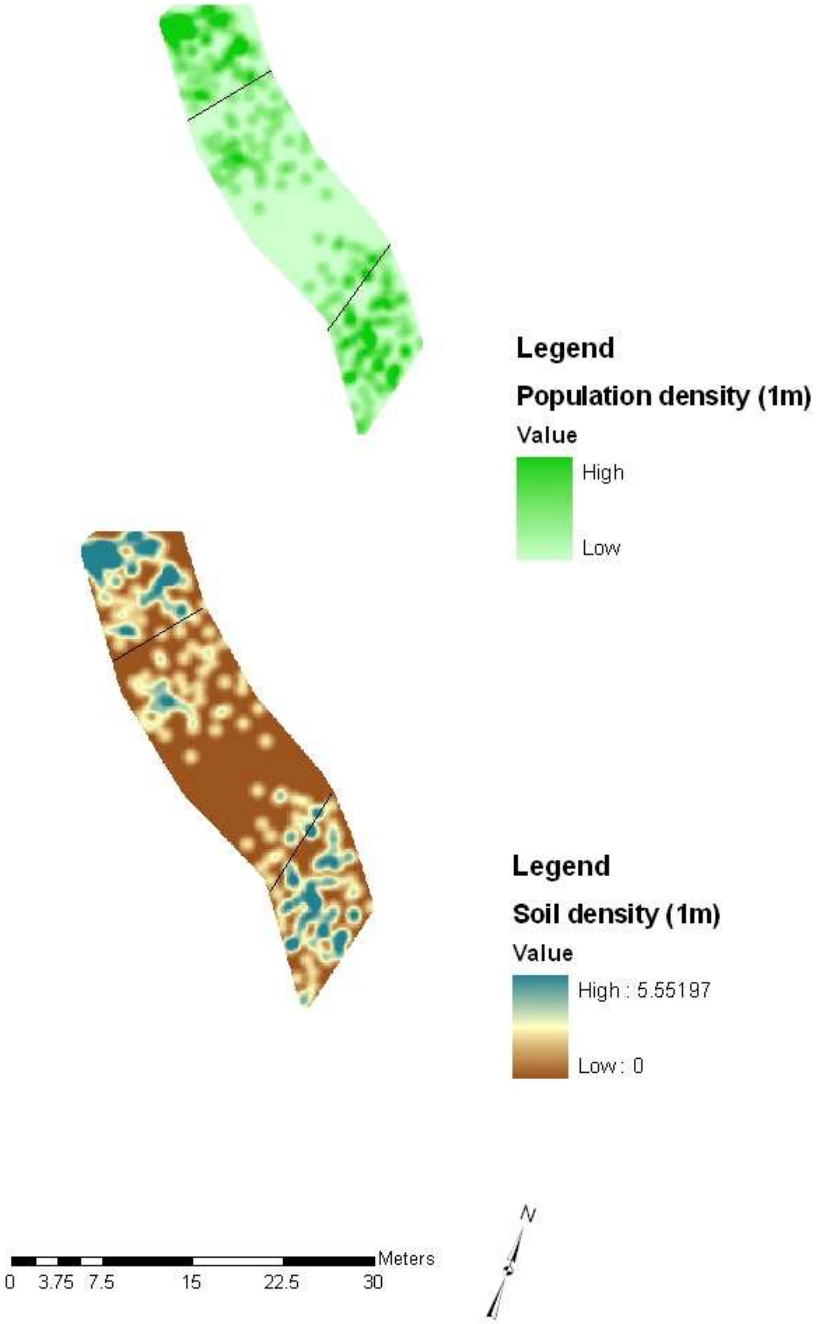

Fig. A.9. Tree and soil density maps in the meadow 2 belt transect in Preston Park. The back line indicates the meadow-forest boundary.

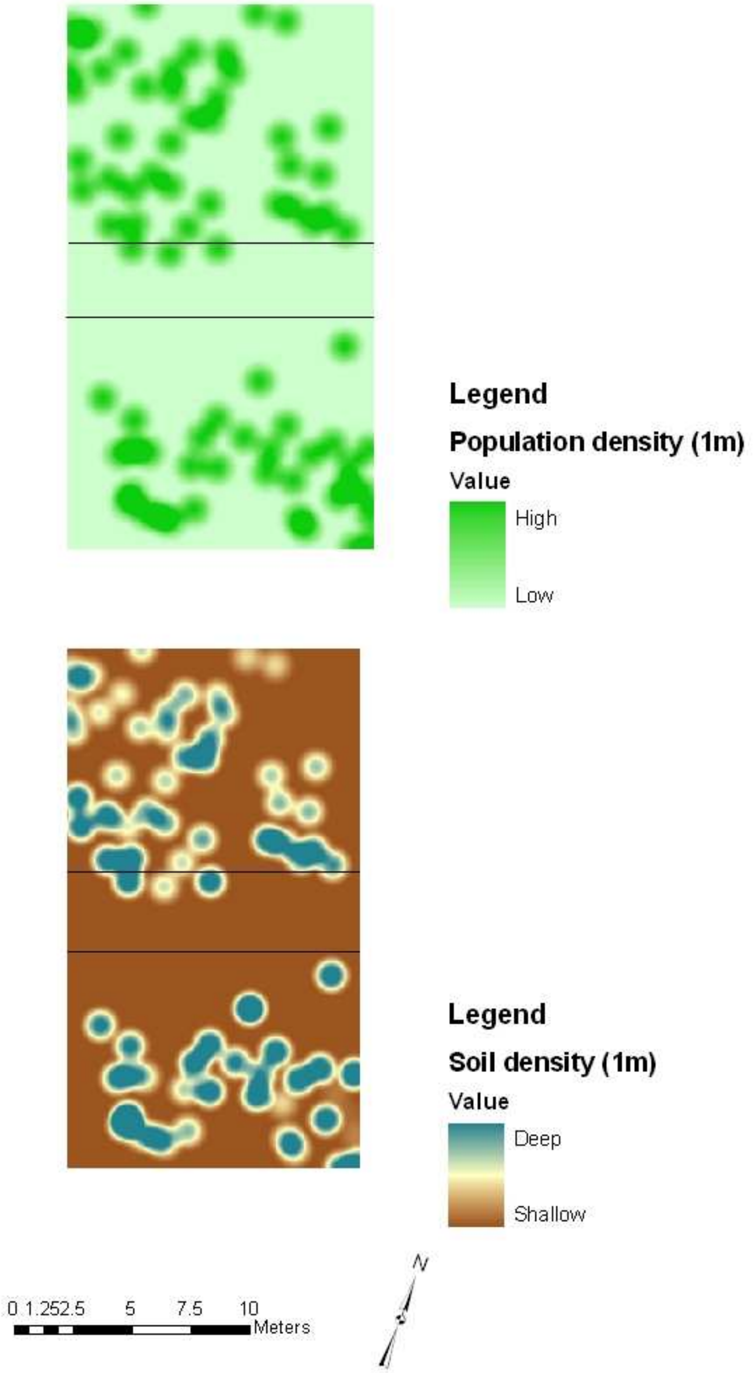

Fig. A.10. Tree and soil density maps in the meadow 3 belt transect in Preston Park. The back line indicates the meadow-forest boundary.

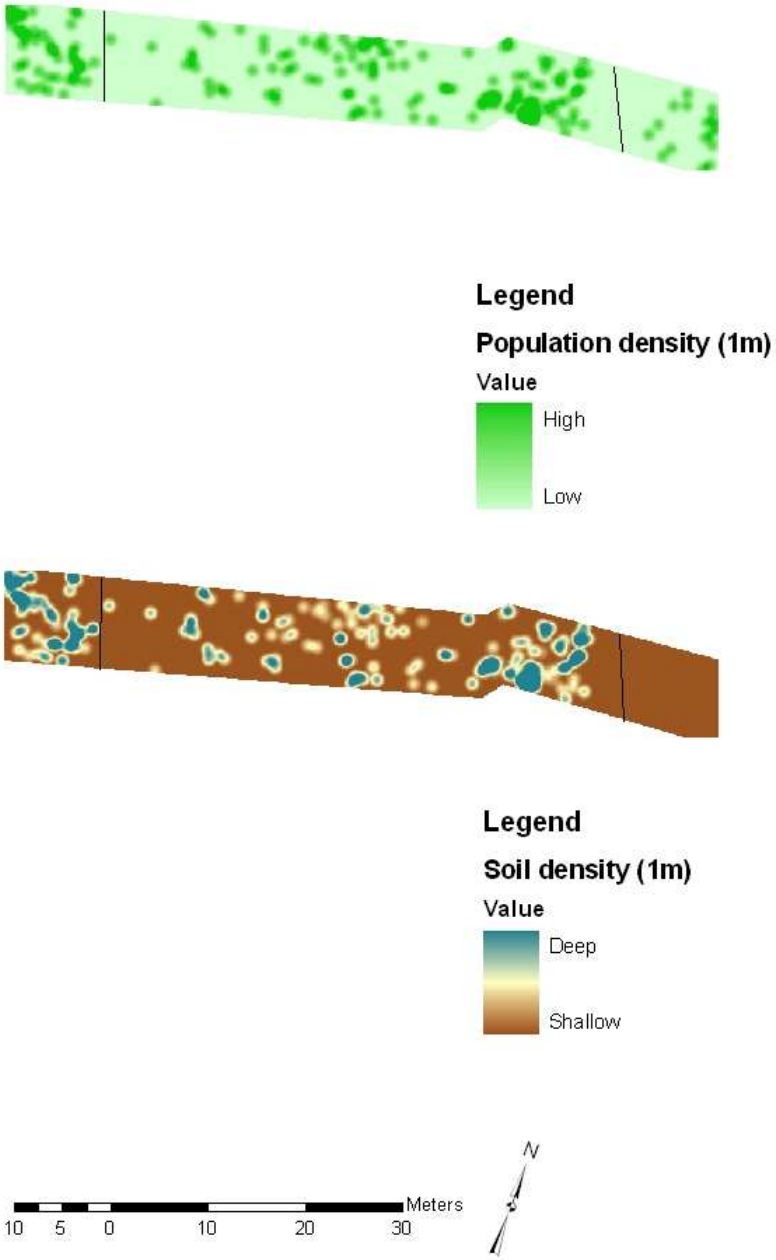

Fig. A.11. Tree and soil density maps in the meadow 4 belt transect in Preston Park. The back line indicates the meadow-forest boundary.

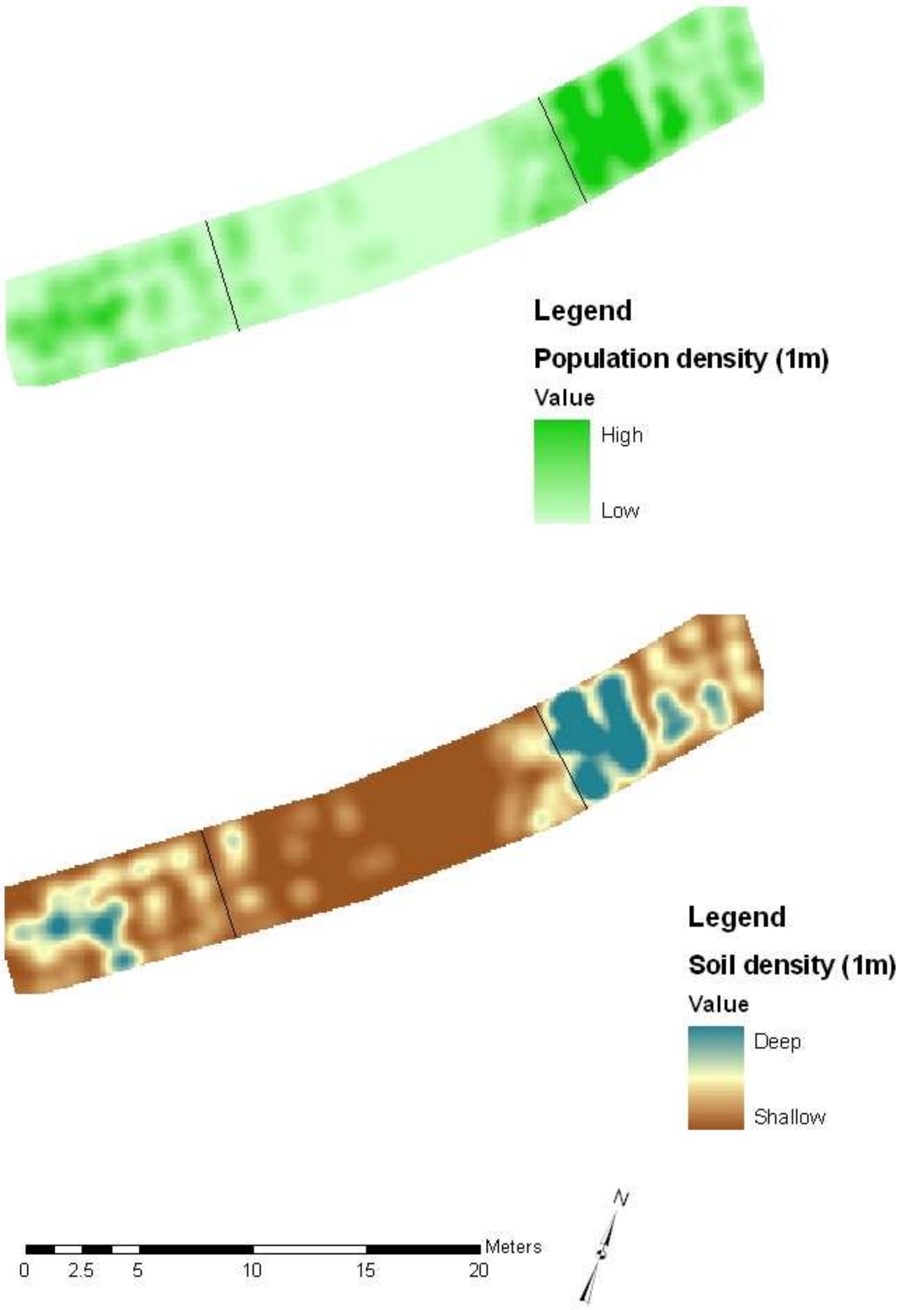

Fig. A.12. Tree and soil density maps in the meadow 5 belt transect in Preston Park. The back line indicates the meadow-forest boundary.

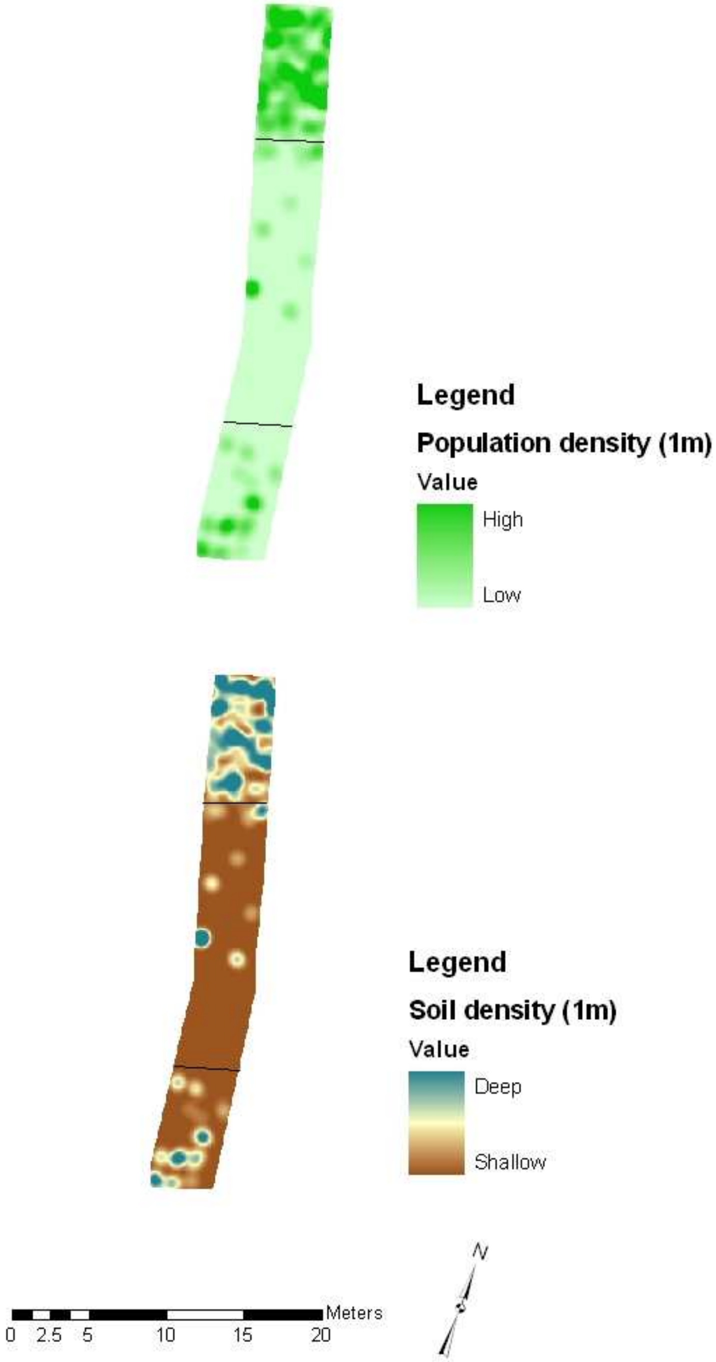

Fig. A.13. Tree and soil density maps in the meadow 6 belt transect in Preston Park. The back line indicates the meadow-forest boundary.

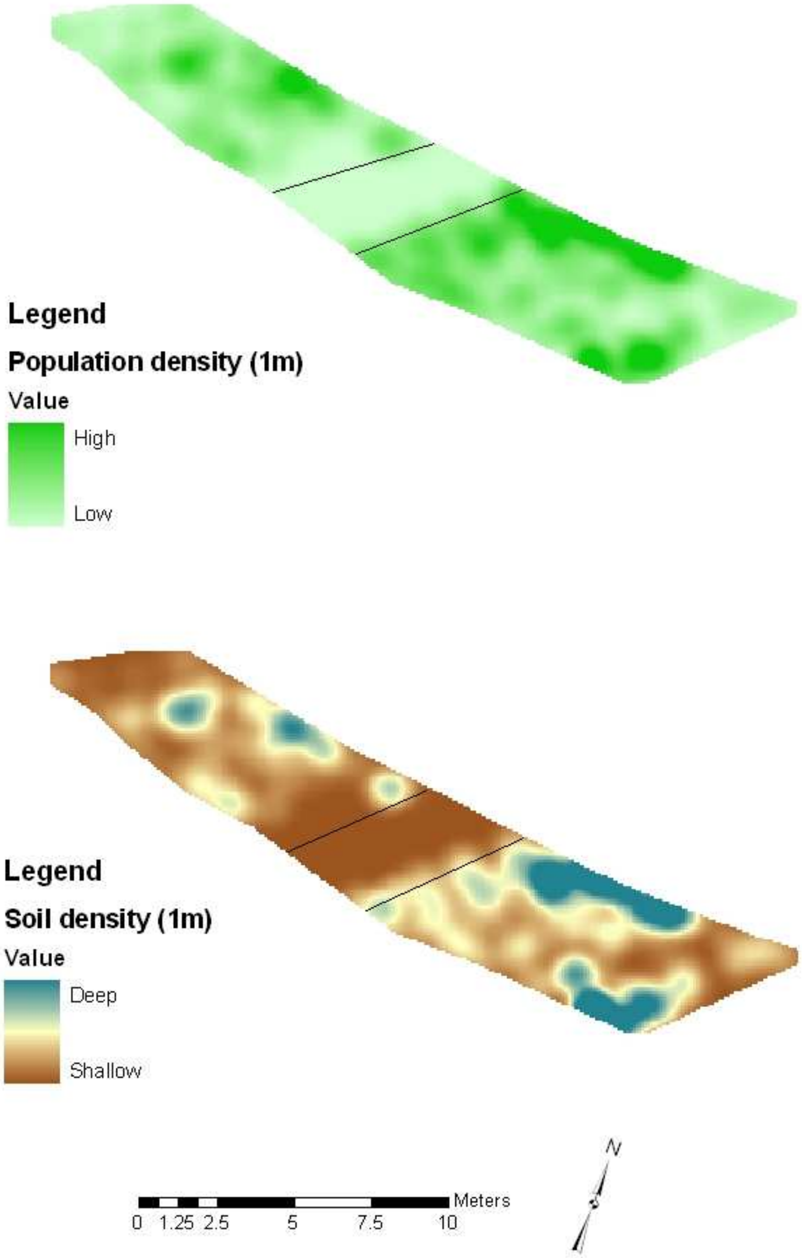

Fig. A.14. Tree and soil density maps in the meadow 7 belt transect in Preston Park. The back line indicates the meadow-forest boundary

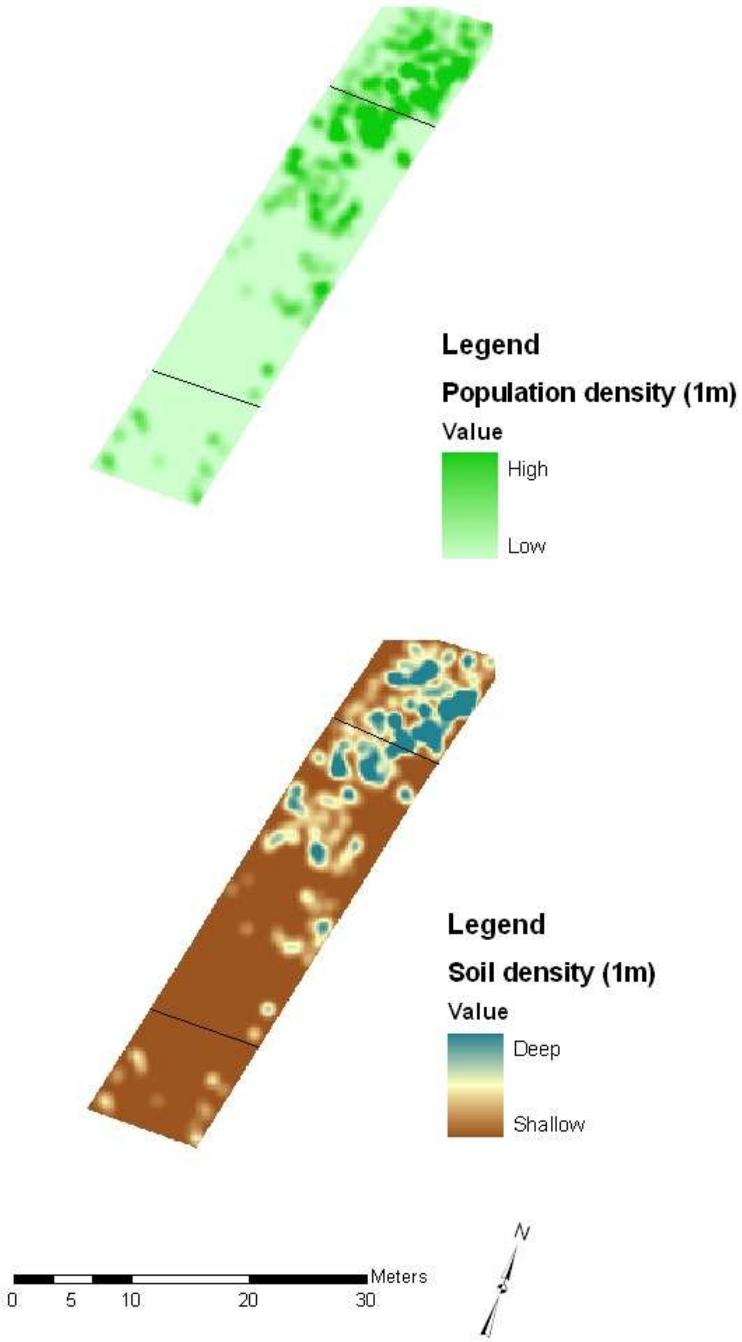

Fig. A.15. Tree and soil density maps in the meadow 8 belt transect in Preston Park. The back line indicates the meadow-forest boundary.

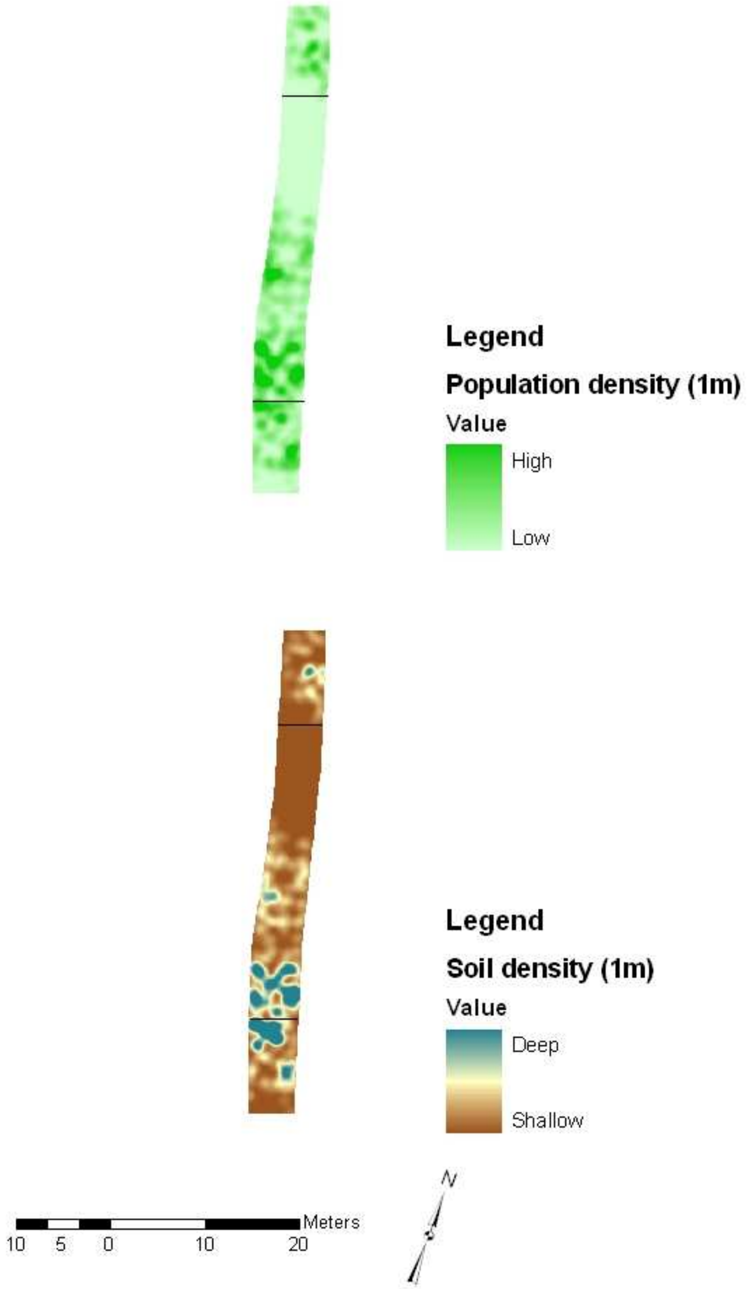

Fig. A.16. Tree and soil density maps in the meadow 9 belt transect in Preston Park. The back line indicates the meadow-forest boundary.

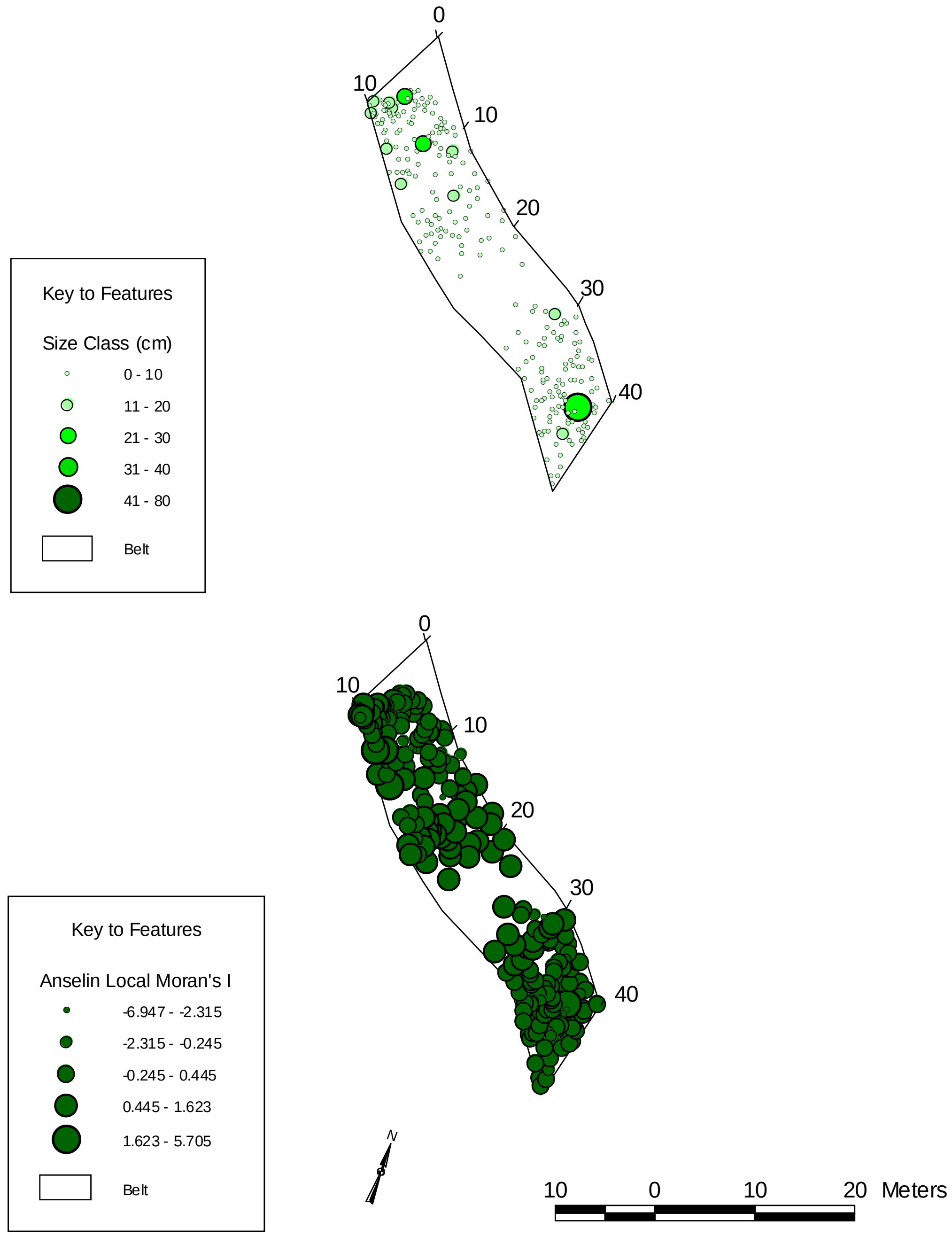

Fig. A.17. Meadow 2 size class (upper) and Anselin Local Moran's I analysis of clusters (lower).

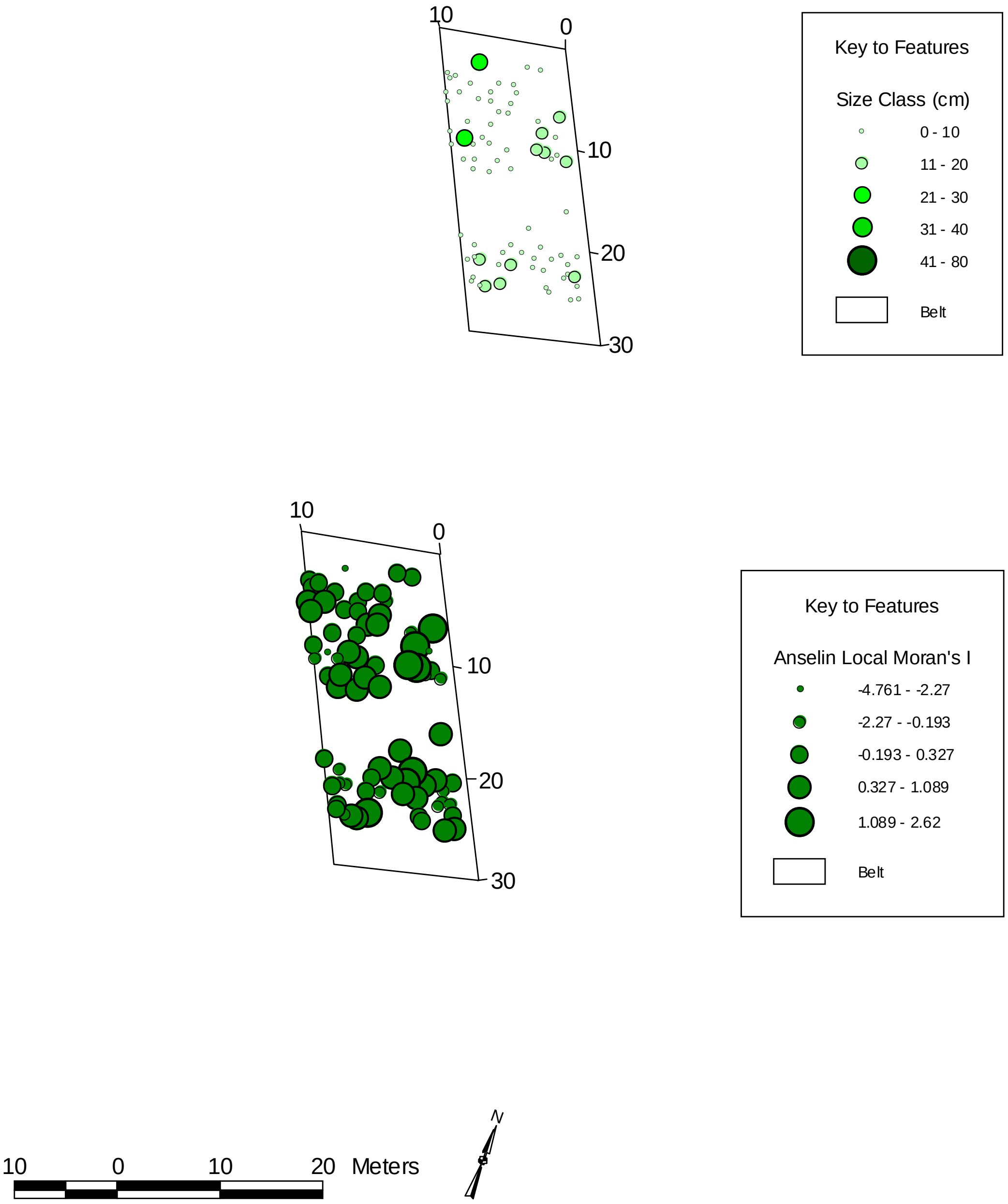

Fig. A.18. Meadow 3 size class (upper) and Anselin Local Moran's I analysis of clusters (lower).

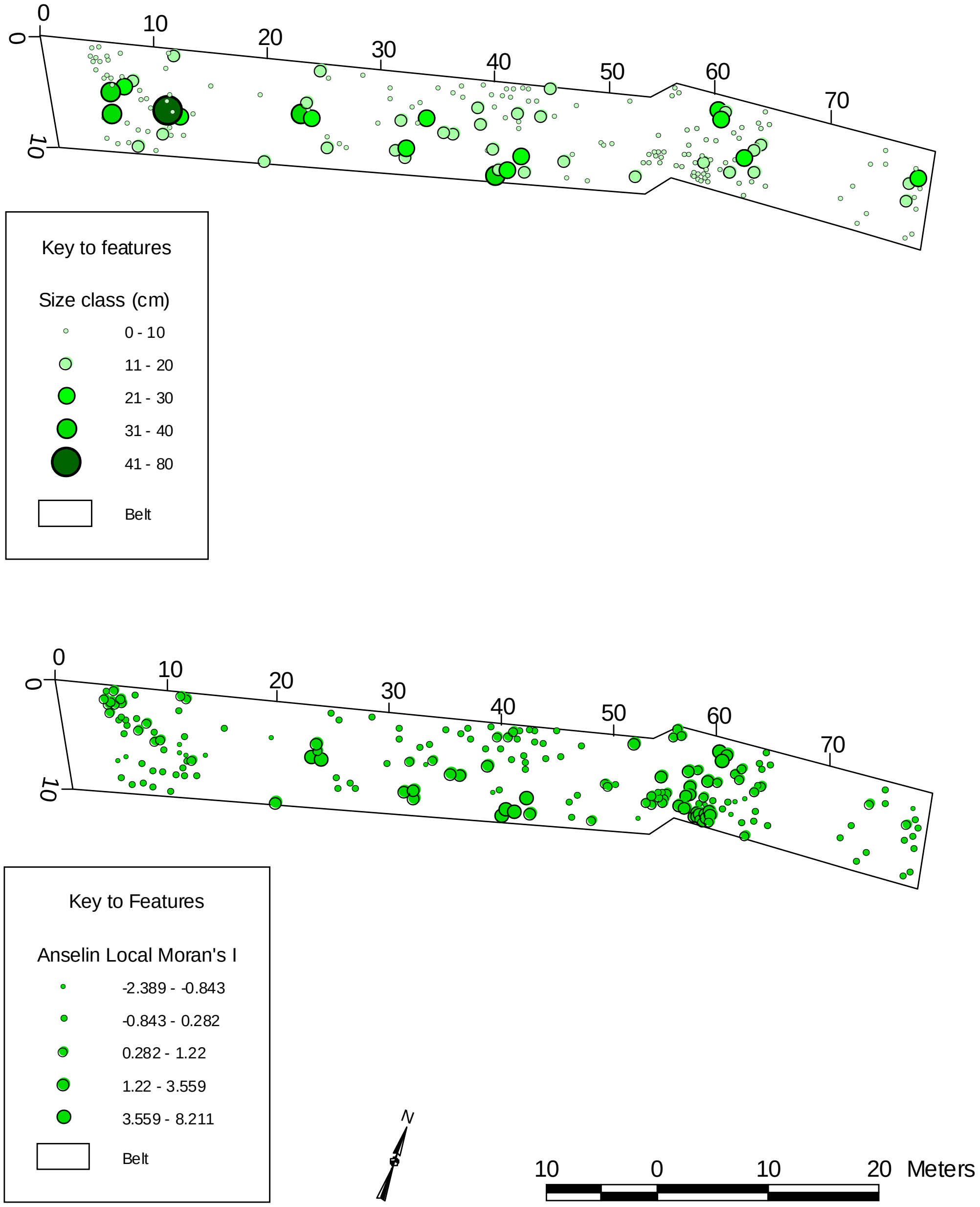

Fig. A.19. Meadow 4 size class (upper) and Anselin Local Moran's I analysis of clusters (lower).

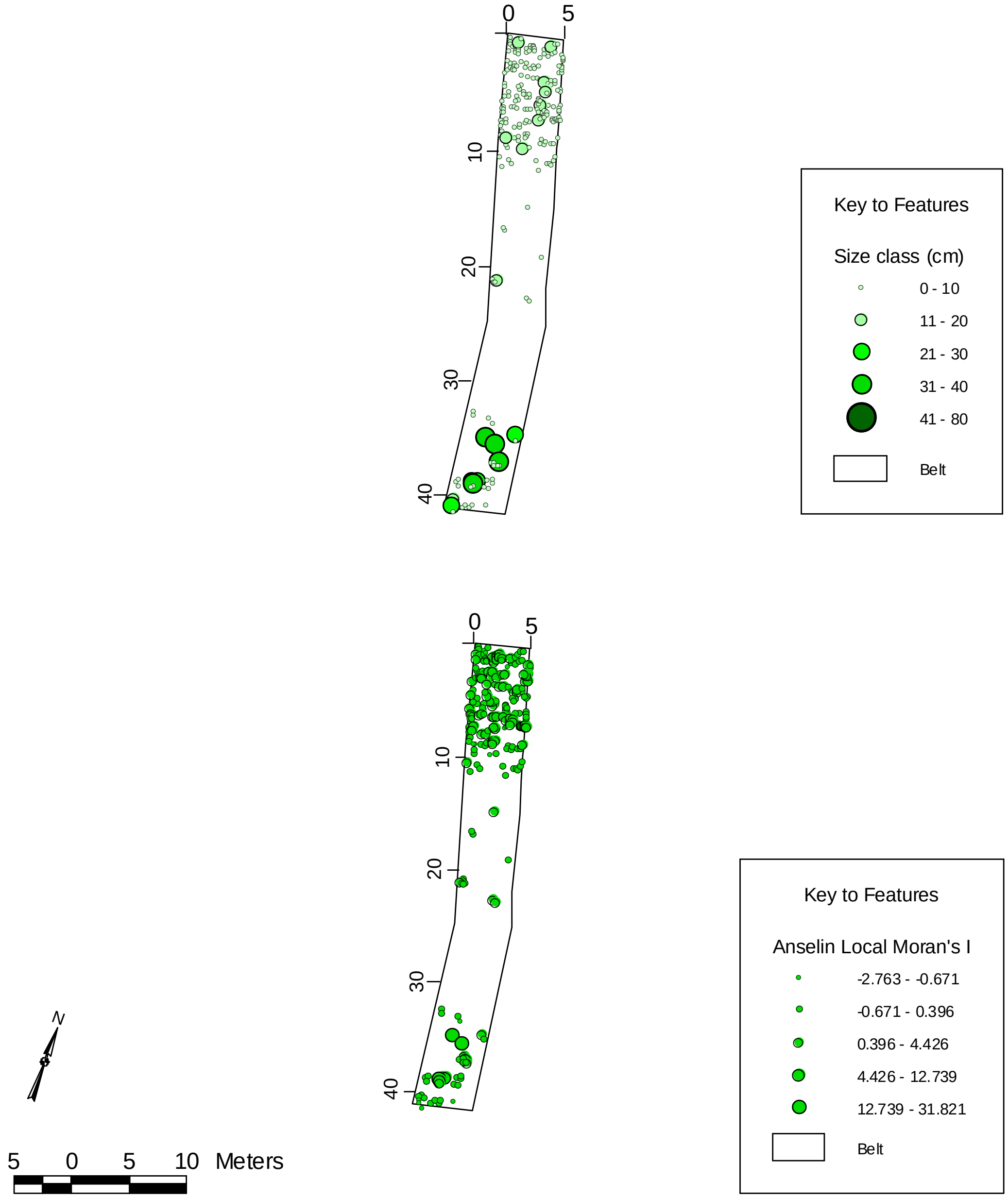

Fig. A.20. Meadow 6 size class (upper) and Anselin Local Moran's I analysis of clusters (lower).

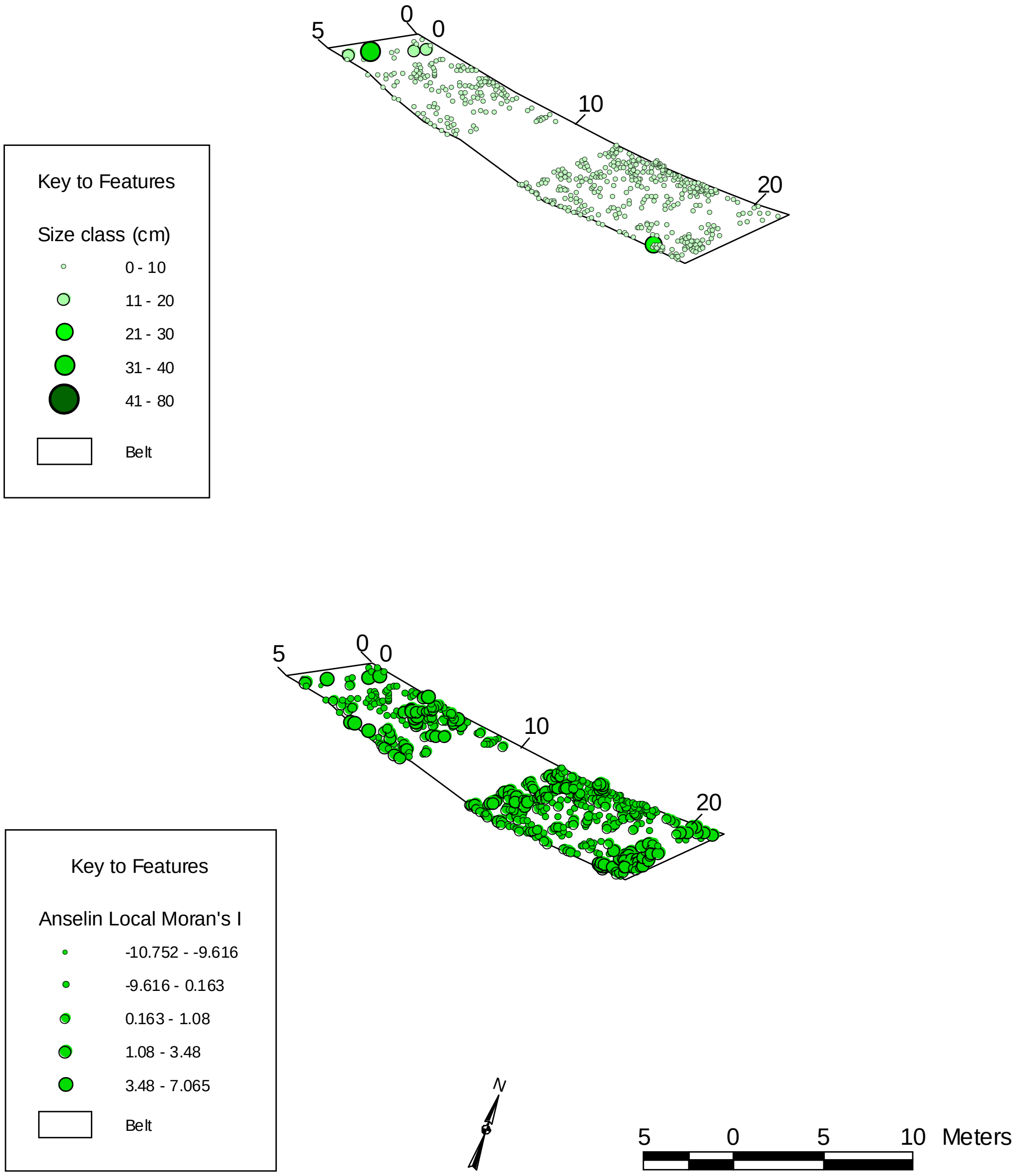

Fig. A.21. Meadow 7 size class (upper) and Anselin Local Moran's I analysis of clusters (lower).

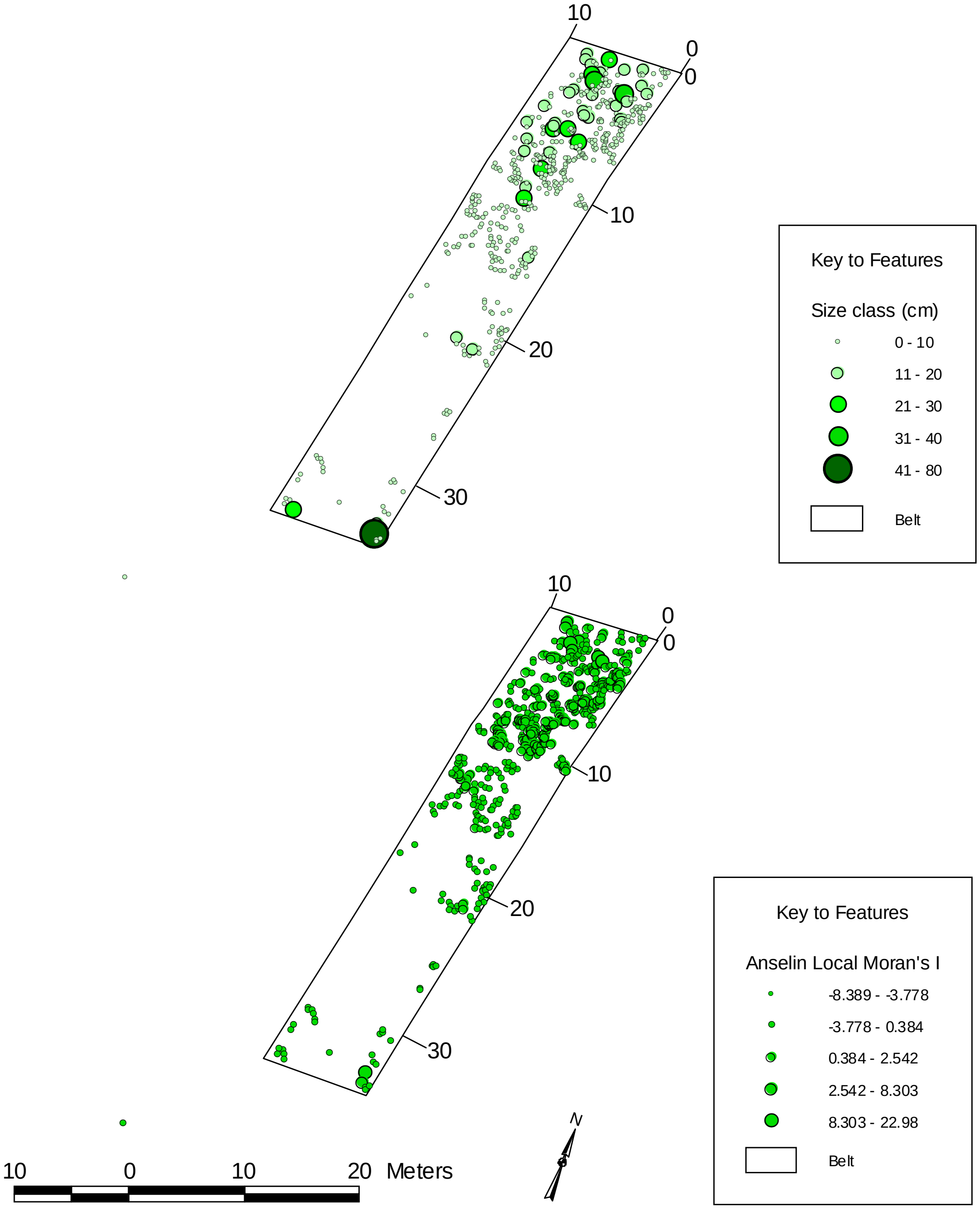

Fig. A.22. Meadow 8 size class (upper) and Anselin Local Moran's I analysis of clusters (lower).

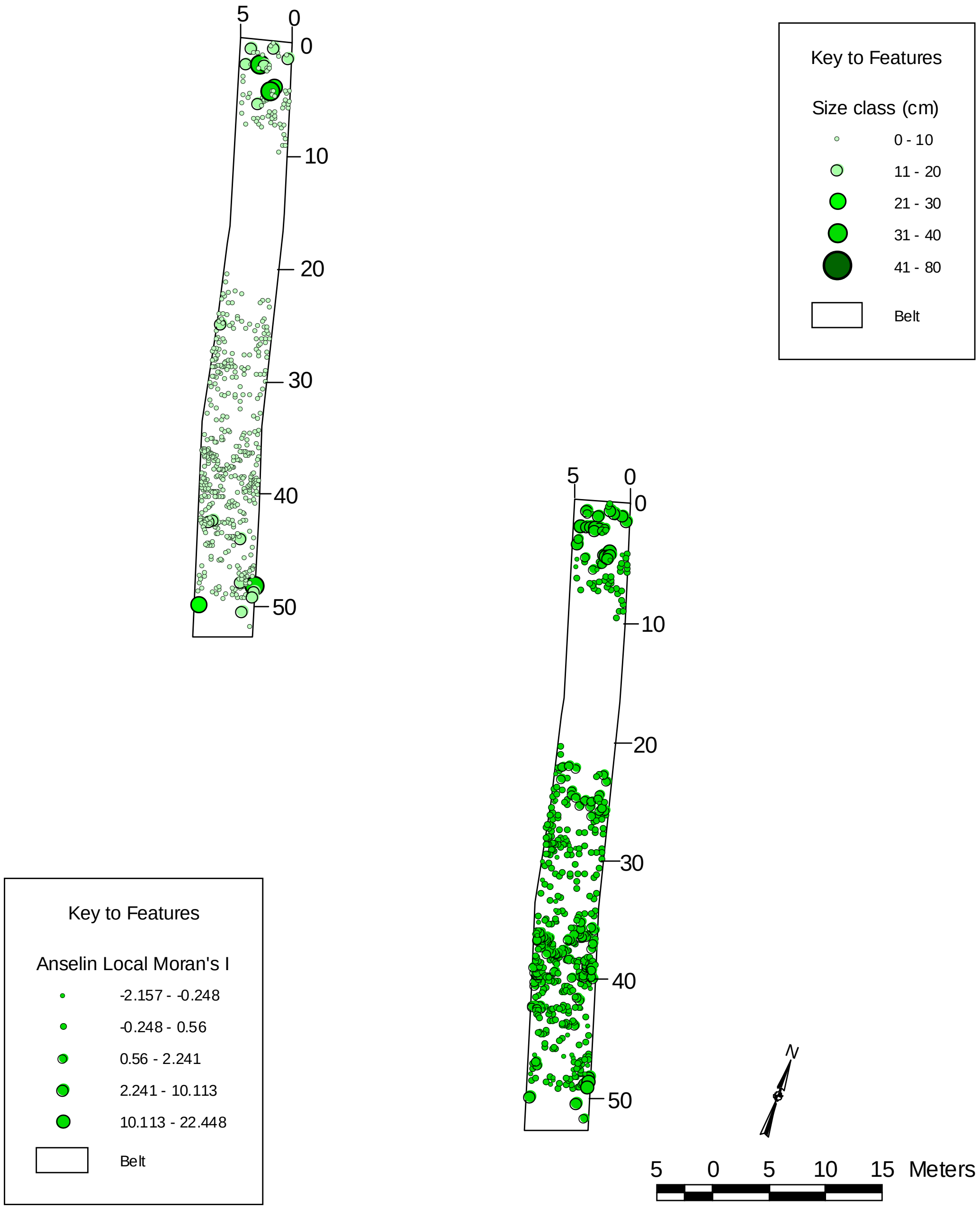

Fig. A.23. Meadow 9 size class (upper) and Anselin Local Moran's I analysis of clusters (lower).

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PUBLICATIONS

Gielstra, D., Runyon, C. and Waldron, J. 2007. Hydrochory and successional changes in abandoned rice fields, Georgetown County, South Carolina. *Southeastern Geographer* 47(2): 239-253.

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