

Structure, dynamics, and climate sensitivity of range-margin jack pine forests in
central Minnesota

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Dedication

This thesis is dedicated to James Adams and Topher Kazanski

Abstract

Species' ranges are expected to shift in response to changes in climate and disturbance regimes. Individuals and populations along the edge of their range are expected to be most affected because of their proximity to climatically limiting factors and the unique dynamics relative to non-marginal portions of their range. However, limited empirical knowledge exists concerning the historic range of ecological variability in range-margin populations and systems.

Jack pine (*Pinus banksiana*) reaches its southwestern range limit in central Minnesota where it displays traits, including low-levels of cone serotiny, that differ from other portions of its range. However, the stand dynamics (establishment, age structures, and disturbance regimes) and linkages with climate have never been documented for these populations. Our aim was to quantify the natural range of variability of stand dynamics and climate relationships to establish reference conditions for monitoring future climate impacts, informing refinement of forest ecosystem models, and assisting in the development of management decisions for conservation.

Our results indicate that jack pine stands in this region are structurally complex even and un-even aged systems that follow a variety of developmental pathways. These patterns are attributed to the non-serotinous cones of jack pine in this region, which allow for both episodic and extended recruitment patterns over time. Annual growth and recruitment were both significantly sensitive to moisture and temperature variables, especially during the winter-to-spring transition, yet the directionality of associations displayed much seasonal variation. Our results suggest that management and modeling practices should be broadened to account for the variety of structural conditions and developmental pathways that historically characterized these range-margin jack pine forests. Such changes will help to conserve jack pine forests for the short-term while promoting the propensity for long-term resilience and adaptability.

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Chapter 1:

Introduction

One of the preeminent questions currently being asked is: how will human and natural systems be affected by climate change? The projected changes in temperature, moisture, extreme events and their interactions have political, economic, and ecological consequences at all scales of life (IPCC 2013, 2014a, c, b). For ecological systems, climate change is expected to have major effects on above- and belowground temperature and moisture regimes, which, in association with other abiotic factors, impact all life histories stages of individual plants, communities, and biomes (Woodward 1987). Such changes to abiotic conditions are expected to significantly alter species distributions resulting in global and local plant extinctions and a reshuffling of known communities as plants migrate, persist, or expand into new areas (Davis and Shaw 2001, Chapin et al. 2004, Bellard et al. 2012, Blois et al. 2013). Models depicting the future distributions and dynamics of trees and forest communities under current and future climate change scenarios are a common tool for anticipating the impacts of climate change on forests; however, their usefulness is dependent on an ability to account for ecological complexities through statistical representations (Bugmann 2001, Iverson et al. 2008). Empirical studies of the natural range of variation in plant and community behaviors and dynamics in response to climate and other drivers are necessary for guiding, validating, and adding detail to these representations (Bugmann 2001). The accuracy of models and the empirical evidence used for their improvement are not only important for research but also for management in the face of uncertain future conditions (Millar et al. 2007, Puettmann 2009, D'Amato et al. 2011a).

Forest managers have always had to make decisions within the context of uncertainty. Current managers are not just addressing uncertain climatic conditions but also must balance this emerging issue with other current and traditional short and long-term goals such as maintaining species biodiversity and endangered species habitat, preserving recreation value, producing forest products, and mitigating atmospheric carbon

accumulation (Puettmann 2009). Current management guidelines for a particular forest type or species are typically based upon research performed in non-marginal portions of a species' range. However, individuals and populations near the edge of their distributional limit tend to display atypical individual behaviors and community dynamics (Hoffmann and Blows 1994, Kawecki 2008) and are expected to be the first affected by climate change (Allen and Breshears 1998, Woodall et al. 2013). These factors cause range-margin populations to be of high conservation value and valuable for quantifying the natural range of variability of forest dynamics (Lesica and Allendorf 1995, Hannah et al. 2002) but also create novel current and future issues for forest managers. Documentation of the behaviors and dynamics of these populations is necessary both for addressing the uncertainty of species' current and long-term climatic-suitability (Millar et al. 2007) and determining appropriate management goals.

For this thesis, we sought to contribute to the growing body of science addressing the impacts of climate on species and forest dynamics and distributions. We focused on the behavior, dynamics, and climate relationships of jack pine (*Pinus banksiana* Lamb.) in north-central Minnesota (Figure 1.1). We chose this species and study area for two primary reasons: 1) proximity to the natural distributional limit (range margin) of jack pine (issues outlined above) and 2) relevance to current management issues. Currently, managers are facing challenges in adequately maintaining and regenerating jack pine forests (Locke et al. 2007). One hypothesis for the current management challenges is that, similar to other marginal jack pine forests, the natural stand dynamics patterns of the region do not follow the expected dynamic for this species (Gauthier et al. 1993, Conkey et al. 1995, Barton and Grenier 2008), which is high density even-aged recruitment following stand-replacing fires (cf. Ellis 1911, Sterrett 1920, Heinselman 1973). A second hypothesis is that they are no longer suited to the local climate (Frelich and Reich 2009). This thesis addresses both of these hypotheses in two separate research chapters.

Chapter 2 of this thesis quantifies the natural range of variation in structural and dynamic attributes of extant range-margin jack pine forests in north-central Minnesota. We use

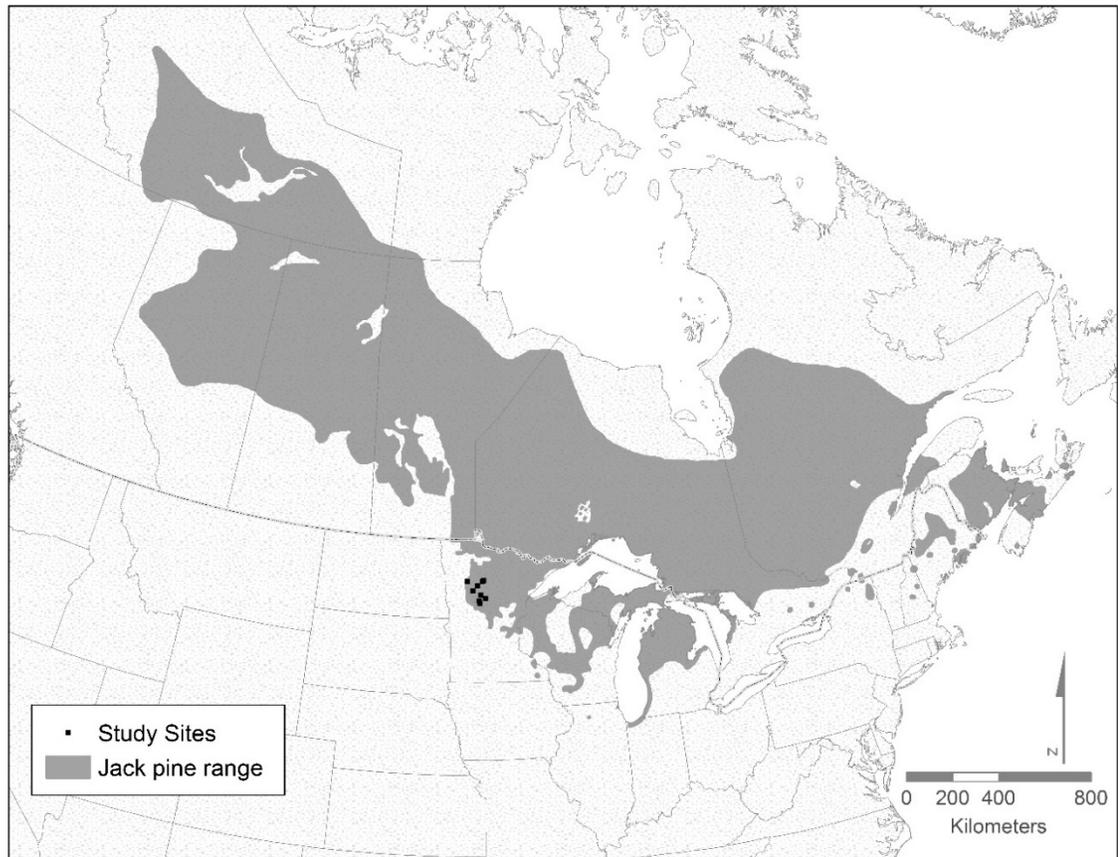
forest mensuration techniques to quantify above-ground structures and dendroecological techniques to gain a better understanding of the processes contributing to these structures. We find a range of structural attributes that suggest early-successional forest complexity (sensu Tappeiner et al. 1997, Donato et al. 2012). Both even- and uneven-aged structures were observed and are hypothesized to be resultant of a combination of disturbance (fire, insects, and wind) and climatic factors. One of the most interesting findings, although only prevalent at one site, is evidence of growth suppression and release in jack pine, something that has rarely, if ever, been observed in this shade-intolerant species. Our results suggest multiple developmental pathways have occurred and lead us to recommend both even- and uneven-aged management techniques that create spatially variable forest conditions, such as the individuals, clumps, openings (ICO) method (Plotkin et al. 2002, Churchill et al. 2013) and variable retention harvest systems (Franklin et al. 1997). When relying on natural regeneration, the protracted recruitment windows suggest that more than five years should be expected for full stocking; a period exceeding current recommendations.

The third chapter addresses the role of climate in both jack pine growth and recruitment. We use dendroclimatological techniques to quantify relationships between these factors. Seasonal correlation analysis (*seascorr*) demonstrated that growth was primarily indirectly associated with moisture budget (precipitation minus potential evapotranspiration [P-PET]), except during the peak of the growing season (June and July) when an opposite association was observed. As well, growth and temperature were primarily directly related with temperature. Together, these results suggest that the timing of release from winter-dormancy and the weather conditions during the peak period of active growth are key factors in the annual growth of jack pine. Seedling recruitment was primarily associated with growing season P-PET but the direction of the association varied among sites. A novel technique of using response function analysis between growing season climate and recruitment patterns indicated intra-season variation in this relationship. We found that recruitment success was favored by cool, wet June weather, which would help limit drought stress, but also dry Septembers, which would enhance the

degree of seedling hardening in preparation for winter. These results suggests that both growth and recruitment will not have a seasonally or regionally uniform response to increased moisture deficits in the future. The intra-region and intra-species variability observed underscores the need to account for fine-scale geographical differences in climate responses in the growth and recruitment of a species when modeling future species distributions and forest dynamics in response to projected climate change.

The final chapter of this thesis, Chapter 4, consolidates conclusions from both chapters, expands upon management implications, and recommends future research directions while discussing potential study limitations.

Figure 1.1. Natural range of jack pine (*Pinus banksiana*) in North America as delineated by (Little 1971) and locations of study sites along the southwest range margin in north-central Minnesota.



Chapter 2: Structure and dynamics of range-margin *Pinus banksiana*–dominated forests in Minnesota, USA

Introduction

Plant species meet their distributional limit due to a variety of factors (Woodward 1987, Almendinger 1992, Blois et al. 2013). At the broadest scales, abiotic factors, such as climate and soils, drive biome and landscape-level patterns of vegetation; at smaller scales, interactions between abiotic and biotic factors create a mosaic of communities and individuals (Gosz 1993). At all scales, disturbances, such as drought, fire, wind, and insects, play a role by affecting both abiotic and biotic components and, therefore, successional processes. In response to recent and future changes in climate, species distributions are expected to shift, but not necessarily in accordance with current community associates (Davis and Shaw 2001, Parmesan 2006). However, it is unknown whether the rate of change will outpace species' abilities to adequately migrate and potentially adapt in anthropogenically-impacted landscapes (Franklin 1993, Davis and Shaw 2001, Bellard et al. 2012, Reyer et al. 2013). Plant populations at their biotic margins (geographic and/or ecological) are expected to be indicators of change given their proximity and vulnerability to abiotic conditions that limit key demographic processes related to establishment and persistence (Kawecki 2008, IPCC 2014a).

Marginal populations tend to display atypical species traits and population-level dynamics due to their proximity to sub-optimal abiotic conditions and novel community associations (Griggs 1914, Schoenike 1976, Chapin et al. 2004). These populations are the dynamic edges of a species' larger central population because their expansion or contraction is an indication of species range or elevation shifts (Hoffmann and Blows 1994, Kawecki 2008). Conservation of marginal populations, their connectivity with central populations, and the biologically diverse ecotones in which they converge with other marginal populations (Gosz 1993) is seen as a way to maintain migratory, adaptive and evolutionary potential in the face of uncertain future conditions (Franklin 1993, Lesica and Allendorf 1995, Puettmann 2011). Given their uniqueness, as well as their

vulnerability to change, there is a great need to quantify the natural structures and dynamics of these communities as baselines for assessing long-term climate impacts and setting conservation priorities (Swetnam et al. 1999, Frelich and Reich 2009, Stephens et al. 2013, IPCC 2014a).

Many studies have addressed the natural range of variability in forest conditions for numerous forest types (Landres et al. 1999, Swetnam et al. 1999). However, most have focused on non-marginal old-growth stands (e.g., Fule et al. 2002, D'Amato et al. 2008, Fraver and Palik 2012). This focus has left key knowledge gaps regarding the variety of conditions associated with potentially distinct and early-successional forests (Swanson et al. 2011). Particularly important in this regard is the natural range of variability in forest structure and developmental pathways for these communities (Oliver and Larson 1996, Franklin et al. 2002, Donato et al. 2012). Quantifying this range of variability would provide the context for appropriate management to enhance climate-change adaptation or mitigation (Puettmann 2009, D'Amato et al. 2011), and it is critical to our understanding of future response.

The jack pine (*Pinus banksiana* Lamb.)-dominated forests within the prairie-forest border in Minnesota constitute one such marginal population in need of benchmark documentation. The natural range for this species extends from the Northwest Territories to the Maritime Provinces of Canada and south to the Great Lakes region of the USA. A nearly disjunct marginal population of this typically boreal species exists along the southern range margin in north-central Minnesota, USA (Iverson et al. 2008, Landscape Change Research Group 2014) as part of the prairie-forest border (cf. Ewing 1924, Davis 1977). Jack pine migrated to its current landscape position as recently as 5000 years before present by displacing, and now associating with, species of the tallgrass prairie and eastern deciduous forest biomes. Individuals and stands within this population are thought to be more closely related to other southern range-margin populations than to the more proximate populations of northeastern Minnesota (Critchfield 1985). For example, although jack pine has primarily serotinous cones in northeastern Minnesota and

throughout a majority of its range, serotiny is reduced or absent in populations in north-central Minnesota and others along the southern range margin (Ellis 1911, Marttila 1958, Schoenike 1976). The low levels of serotiny may suggest that these populations do not adhere to the often assumed paradigm of single-cohort stands that originate following stand-replacing fires (Heinselman 1973, Despons and Payette 1992, Gauthier et al. 1996).

Although the natural regeneration and stand dynamics of southern range-margin populations have been investigated elsewhere (Abrams et al. 1985, Gauthier et al. 1993, Conkey et al. 1995, Barton and Grenier 2008) the prairie-forest border population of Minnesota has yet to be investigated. Several of these previous studies have used reliable techniques for generating age structures and characterizations of stand dynamics, yet none have quantified the physical structures or tree spatial arrangements. This topic has timely and important management implications because both natural and artificial regeneration difficulties in central Minnesota jack pine stands (Locke et al. 2007) are contributing to a reduction of this forest type (Almendinger 2011). Potential causes of regeneration difficulties may be incongruity between the historic dynamics and contemporary use of even-aged management (Almendinger 2011), or perhaps a shift towards unsuitable climatic conditions (Frelich and Reich 2009).

We investigated the natural range of variability in structure and stand dynamics of marginal jack pine dominated forests in north-central Minnesota to document reference conditions used to assess change and inform current regional forest management guidelines. More specifically, we aimed to 1) quantify the natural range of variability of stand and age structure in representative stands; and 2) characterize historic stand dynamics that have shaped the forests we see today. The short-lived nature of jack pine precluded the use of stands that originated prior to European settlement. However, we feel we were able meet these objectives using primary forest stands that were initiated and developed outside of active management.

Methods

Study Area

Our study sites (Figure 2.1) all fall within the western half of the Northern Minnesota Drift and Lake Plains (MDL) ecological subsection of the Laurentian Mixed Forest Province (Aaseng et al. 2003). The cold-temperate continental climate of the area is characterized by short cool summers and long cold winters with periods of extremes in both seasons. The mean annual temperature for this region over the past century has been 3.9 °C; mean annual precipitation is 632 mm, with over 80% of this precipitation occurring between April and October (NCDC 2014). The MDL has complex surface geology due to a patchy distribution of glacial deposits such as outwash plains, lake plains, till plains, outwash channels, moraines, and drumlin fields (Aaseng et al. 2003). The flat, nutrient and moisture poor sandy outwash plains tend to support jack and red pine (*Pinus resinosa*) woodlands and forests without other canopy associates and are thought to be an edaphic climax (Rudolf 1965, Aaseng et al. 2003). Morainal deposits in these areas have a higher soil nutrient and moisture status, and canopy tree species on these sites often include quaking and big-tooth aspen (*Populus tremuloides* and *P. grandidentata*), paper birch (*Betula papyrifera*), bur and northern red oak (*Quercus macrocarpa* and *Q. rubra*), and eastern white pine (*Pinus strobus*). These higher quality sites can be dominated by jack pine, especially after a stand-replacing disturbance, but typically succeed to longer-lived species (Kittredge Jr. 1934, Spurr 1954, Silver et al. 2013). Correspondingly, old-growth red and white pine dominated the pre-settlement forests (Spurr 1954, Frissell 1973), especially on sites of relatively higher quality, while jack pine dominated stands were commonly found on xeric outwash plains (Almendinger 1992).

The relatively level terrain in close proximity to the headwaters of the Mississippi river system made the area a focus of widespread timber harvesting in the late 19th and early 20th centuries (Sargent 1884). The creation of open conditions via clearcut harvesting in conjunction with large-scale slash fires during this period led to an increase in the abundance of jack pine by the 1920s relative to pre-settlement eras (Eyre 1938). Heavy

utilization of jack pine for pulp and paper products began around this time (cf. Ellis 1911, Sterrett 1920) and continued, along with sawlogs and other products, through World War II (Rudolf 1958). More sustainable harvests for the same products, with the addition of energy-wood harvests, continues today (VanderSchaaf 2013). On both high and low quality sites, vigorous fire-suppression efforts, management for other species, successional patterns, and agricultural conversion have resulted in a reduction in the abundance of jack pine forests when compared with pre-settlement and early twentieth-century forests (Frissell 1973, Almendinger 2011). Where actively managed for forest products, jack pine stands are typically managed using even-aged regeneration methods, namely clearcutting-based systems, on rotation lengths between 40 - 60 years (Benzie 1977) and are generally expected to be fully regenerated five years following harvest.

Site Selection

Because of the aforementioned history and comparatively short lifespan of jack pine, finding old-growth stands dominated by this species was not possible (sensu Heinselman 1973, D'Amato et al. 2008). Instead, we focused on primary stands of natural origin that were older than the recommended rotation length (cf. Reinikainen et al. 2012). We sought out stands with no or minimal signs of management such as cut stumps, uniform tree spacing, or logging roads. In addition, given our suspicion that multi-aged jack pine systems existed in this portion of the species range (cf. Abrams 1984), we sought out stands that included jack pine snags and a variety of crown and diameter classes. Potential stands were identified from a Geographic Information System (GIS) provided by the Minnesota Department of Natural Resources, along with input from area professionals. Together, these sources identified 128 potential stands, which were further evaluated via historic aerial photographs (1939 – present) to screen for past logging activities. From this pool, 76 stands were inspected on the ground. Ten ultimately met our criteria and were selected for this study (Figure 2.1, Table 2.1).

Field Sampling

Within each selected stand, one 50 x 50 m study plot was established along cardinal directions (cf. Fraver and White 2005). For two relatively small stands (~4 ha), we placed plots in the geographic center of the stand to avoid edge bias. For larger stands, a point was randomly selected in a GIS and established as plot center. From plot center, the four corners were established, ten 5 x 50 m transects laid out, and all trees ≥ 10 cm diameter at breast height (DBH, 1.37 m) within the plot were sampled. Each tree was given a unique number and sampled for species, DBH, crown class, mortality class (living or snag), and *x*- and *y*-coordinates. Crown class was assigned to living individuals using the Kraft classification system (Oliver and Larson 1996), as dominant, codominant, intermediate, or suppressed. Saplings, defined as any tree species taller than breast height and < 10 cm DBH, were tallied by species and diameter class (four 2.5 cm classes) in three predetermined within-plot transects.

To characterize past tree regeneration and growth patterns, increment cores were collected at 30 cm above the forest floor from all living trees and, when possible, dead individuals. To ensure age accuracy, efforts were made to obtain cores that were at least within five rings of pith. If trees displayed fire scars, cores were collected to obtain fire history following the methods of Barrett and Arno (1988).

Downed woody debris (DWD) ≥ 10 cm in diameter at line-intersection point was sampled along eight equiangular line-intercept transects (Van Wagner 1968) radiating from plot center, for a total of 241 m of transect per plot. Each piece was sampled for species (unless precluded by advanced decay), diameter at intersection, decay class (Sollins 1982), and base-to-tip orientation azimuth (except Midge Lake East and Midge Lake West). DWD volume per hectare was calculated using published equations (Van Wagner 1968, D'Amato et al. 2008) and reduced to account for collapse of decay class IV and V pieces (Fraver et al. 2013). The directionality of DWD was assessed for the eight sites for which orientation azimuths were collected using Rayleigh's Uniformity Test (Zar 1999) in Oriana 4.02 (Kovach 2013).

Laboratory and Statistical Analyses

Increment cores were affixed to wooden mounts in the laboratory and sanded using progressively finer grits (up to 800 grit) in order to clearly display ring anatomy. A Velmex sliding-stage micrometer (Velmex Inc., Bloomfield, NY) was used to measure annual growth rings to the nearest 0.001 mm. If the core had not passed directly through the pith, the number of missing years to pith was estimated using a visual estimator (Applequist 1958). All cores were cross-dated visually (Yamaguchi 1991) and statistically confirmed with COFECHA (Holmes 1983). Cores from dead trees were cross-dated against the living-tree chronologies using marker years and statistically confirmed with COFECHA. Intact cores from both living and dead trees with estimated pith adjustments ≤ 10 yr were used for developing stand age distributions and recruitment windows. Jack pine recruitment windows for each site were assessed at each site using the innermost annual ring dates, adjusted if necessary, in order to quantify the number of years it took for a strong majority (middle 90%) of individuals to establish. Recruitment windows were quantified by finding the difference between 95th and 5th percentiles of year of recruitment and adding one year; these were standardized by the median year of recruitment for display.

Spatial arrangement of jack pine locations at each plot were assessed to elucidate patterns of tree establishment and stem arrangement using Ripley's K -function (Ripley 1976). $K(t)$ was transformed to $L(t)$ in order to set the expectation to zero as well as to stabilize the variance (Haase 1995). The transformation was calculated based on Kenkel (1988), for which positive values outside of the confidence intervals (see below) indicate uniformity and negative values indicate clumping. Confidence intervals (95%) were produced using 100 Monte Carlo simulations. All analyses were done using the SPATIAL macro (Moser 1987) in SAS 9.4 (SAS Institute Inc., Cary, NC). Additionally, sites that demonstrated protracted recruitment were further examined by grouping stems at each site into two age groups. Groups were separated based upon cohorts, when present, or at or near the median year of recruitment to provide relatively balanced sample sizes per group.

Results

Composition and Structure

Pines dominated the canopies at each study site, with jack pine importance values ranging from 32 – 89% (Table 2.2). Total live tree densities ranged from 376 – 904 stems ha⁻¹ (species pooled) and from 128 – 696 stems ha⁻¹ for living jack pine (Table 2.2). The basal area of living stems ranged from 16.4 – 32.5 m² ha⁻¹ (species pooled) and from 7.1 – 19.0 m² ha⁻¹ for living jack pine (Table 3). The representation of red pine was smaller and more variable than jack pine as evidenced by its live tree importance values, which ranged from 0 – 72%. Paper birch was absent or a minor component at most sites, but at Bladder Lake its importance value and basal area exceeded those for living jack pine (Tables 2.2 and 2.3). Stand-level diameter distributions varied in shape across sites from unimodal (Midge Lake West), bimodal (Nimrod Range), to negative exponential (Midge Lake East) (Figure 2.2). A focus on jack pine within the distributions shows primarily unimodal shapes centered about the mean diameter; this shape was more protracted (e.g., Lake George), or absent (Midge Lake East), in stands with extended recruitment windows. Quadratic mean diameters for jack pine at each site ranged from 18.7 – 29.3cm ($Mean \pm SE = 24.0 \pm 1.0$). Total sapling densities (species pooled) ranged from 560 – 2187 stems ha⁻¹ (Table 2.2). Very few jack pines were found in the sapling layer; oak saplings, 84% of which were red oaks, were the most well represented sapling species group.

Standing and downed deadwood were abundant structural components across sites. Jack pine snags ($N = 670$) occurred nearly as often as living jack pine ($N = 674$), while snags of other species were rare ($N = 15$). The diameters of jack pine snags tended to be smaller than those of living jack pines (Figure 2.2). The quadratic mean diameter of snags per site ranged from 14.3 – 23.8 cm ($Mean \pm SE = 19.9 \pm 1.0$), which was significantly smaller than those for living stems of this species ($p = 0.01$). The total DWD volume per site ranged from 18.8 – 125.6 m³ ha⁻¹ (Table 2), of which 43 – 99% ($Mean \pm SE = 83.2 \pm 5.3\%$) was jack pine. A majority of DWD at each site was in decay classes II and III, yet distribution among decay classes varied by site (Appendix 1). DWD had significant

uniform directionality at five of the eight sites assessed (p values < 0.05). The mean fall direction for these sites ranged from $40 - 106^\circ$.

Age and Recruitment Patterns

Age distributions indicate primarily uneven-aged patterns across sites when considering all species (Figure 2.3). Sites tended to have one primary pulse of jack pine recruitment (age at coring height), although this pulse was often protracted (see below), with recruitment of additional jack pine and other species prior, during, and/or after this period. Most sites displayed varied, but usually low, levels of non-jack pine recruitment concurrent with the primary jack pine cohort (e.g., Straight River). A few older red pines were observed at several sites (e.g., Lake George and Beaver Dam), with these sites also tending to have further red pine recruitment concurrent with, or slightly delayed from, the primary jack pine pulse (e.g., Roy Lake Creek). At Bladder Lake and Lake George cohorts of paper birch and red pine, respectively, occurred after the establishment of most jack pines that, at the time of sampling and when only considering live trees, were of greater importance value than jack pine (Table 2.2). Dated fires at Lake George and Roy Creek do not appear to have coincided with initiation of any individuals sampled at these sites; at Nimrod Range the earliest cohort of red pine regenerated shortly after an autumn 1894 or spring 1895 fire (Figure 2.3).

Jack pine age distributions (Figure 2.3, black bars) and recruitment windows (Figure 2.4) indicate both even-aged and uneven-aged structures but typically display one primary pulse with no or varying levels of additional recruitment surrounding the pulse. The duration of recruitment pulses for even-aged jack pine ranged from five-year recruitment windows (1946-1950 at Nimrod Range) to up to 15 years (1930 – 1944 at Bladder Lake). Other sites had extended jack pine recruitment windows and age structures that followed three primary patterns. At Straight River, two cohorts were separated by just under a decade of no recruitment. At Midge Lake East, Midge Lake West, and Wolf Lake, varying levels of low to nearly continuous recruitment either preceded or followed a five- to ten-year window for the primary cohort. A similar trend was observed at Lyons Forest

and Lake George but with primary cohorts spanning 10 - 15 yr. These results include recruitment data for jack pine snags, the ages of which were not significantly different from living trees ($p > 0.05$).

Radial growth patterns of jack pine typically displayed rapid initial growth following recruitment (Appendix 2a); however, the first-recruited jack pine trees on the Midge Lake West site showed an uncharacteristic period of slow growth (ca. 20 yr) followed by an abrupt and sustained growth increase beginning ca. 1967 (Figure 2.5), at which time a new jack pine cohort recruited. False rings were common in early growth stages and used as marker years when they occurred in later growth stages. Years with sharply below average ring width (Appendix 2b) or severely reduced latewood width also supplied marker years.

The spatial arrangement of jack pine stems (living and dead combined) across sites was primarily random; however, several sites showed significant clumping at various spatial scales (Appendix 3) and when assessed by age group (Appendix 4). At Lake George and Nimrod Range, all jack pine stems were clumped at distances > 5 m. At Straight River a consistent trend towards clumping of all jack pines was seen at most distances, but the trend was only rarely significant. Results from jack pine age-group spatial analysis indicate significant clumping of the first group at five out of six plots (Appendix 4). Three of these plots also show significant clumping of the second group. Tree locations indicate that these groups generally did not overlap in space (Figure 2.6).

Discussion

Our results indicate that these early successional marginal populations have a range of structural characteristics that are more often associated with late-successional stands (Tappeiner et al. 1997, Donato et al. 2012). Most poignant in this regard are the ranges in diameter and age structures, high volumes of standing and downed deadwood, canopy and sub-canopy species diversity, and stand decadence. Catastrophic and intermediate disturbance, demographic transition of shorter-lived canopy trees, as well as seed

available from non-serotinous cones has contributed to this complexity. These findings are similar to the early successional complexity observed in other jack pine forests in Michigan, USA (Abrams et al. 1985), as well as *Pinus contorta* forests of a variety of western USA montane regions (e.g., Nyland 1998, Pierce and Taylor 2011) and *Pseudotsuga menziesii* communities in the Pacific Northwest, USA (Donato et al. 2012). Conservation and promotion of these types of forests is key, as their role in larger ecosystem function has only recently been appreciated (Swanson et al. 2011, Donato et al. 2012). In addition, their ephemeral nature and ability to develop along multiple successional pathways may provide for adaptability and resiliency as climate and disturbance regimes change (Millar et al. 2007)

Composition and Structure

The dominance of jack pine in the canopy at most sites and the abundance and stature of associated species were within the ranges of earlier descriptions of these communities for the region (Kittredge Jr. 1934, Frissell 1973, Almendinger 1992). Basal areas and trees per hectare were within, but towards the lower end, of ranges recommended in management guides for this species (Benzie 1977, Archibald and Bowling 1995) and reported from other naturally regenerated jack pine stands (e.g., Schoenike 1976, Beland and Bergeron 1993, Conkey et al. 1995, Barton and Grenier 2008, Hoffer and Tardif 2009); this was also the case when living and dead jack pines were pooled. The low densities typical of these stands often led to interrupted canopies (Figure 2.7). Mean jack pine diameters were higher than most reported ranges, but the unimodal diameter distributions observed (Figure 2.2, black bars), along with the trend towards flattened and protracted distributions in less age-uniform populations, were similar to those observed in northern Quebec, Canada (Parisien et al. 2004).

The abundant standing and downed deadwood observed across sites reflected historic disturbances, as well as developmental dynamics related to the limited longevity of jack pine. Jack pine budworm (*Choristoneura pinus*) outbreaks have been periodic in the region (2012 Forest Health Annual Report, www.dnr.state.mn.edu) and sharp decreases

in radial increment patterns (cf. Kulman et al. 1963) suggest that many of our sites were affected by these outbreaks (Appendix 2b). The advanced age of these populations may have contributed to a higher canopy tree mortality during these outbreaks (Kulman 1971, Kouki et al. 1997). Wind-related mortality was also evident at several sites, as evidenced by the consistent alignment of DWD with prevailing winds and recent (summer 2012) straight-line wind events. The high volumes of less-decayed DWD at some sites are likely the result of wind storms, but all sites also had considerable volume of DWD in advanced decay classes indicating earlier mortality events in these stands. In association with disturbance, age, rather than stem density seemed to be driving mortality (Archibald and Bowling 1995, Sharma and Zhang 2007). Nevertheless, self-thinning mortality was likely also an important developmental process in these populations, as jack pine snags were smaller in DBH than their living counterparts, which has been inferred as evidence of self-thinning mortality from jack pine stands in Ontario (Yarranton and Yarranton 1975) and Manitoba, Canada (Kenkel et al. 1997). The collective influence of these mortality processes has resulted in a high degree of structural complexity in these early-successional forests (sensu Donato et al. 2012).

Age and Recruitment Patterns

The variety of age structures observed for these populations is consistent with previous work that has examined marginal jack pine, and it is likely closely linked with low degree of cone serotiny in these populations (Bergeron and Brisson 1990, Gauthier et al. 1993, Conkey et al. 1995, Barton and Grenier 2008). Jack pine forests developing following stand-replacing disturbance are generally expected to display strongly even-aged populations, short recruitment windows, and high stand densities (Heinselman 1973, Gauthier et al. 1993). Several sites we examined displayed these characteristics (Nimrod Range, Beaver Dam, and Roy Creek), although older cohorts predating the jack pine at these sites indicate these recruitment events were not from truly stand replacing disturbances. The trend more often observed in our stands was towards protracted recruitment windows extending beyond those typically associated with jack pine populations with a high degree of cone serotiny.

Protracted recruitment windows are likely related to low initial stand densities and moderate severity disturbance events during the course of stand development. Densities of mature jack pine were quite low in these populations, even when dead trees were included. Although density-dependent mortality likely reduced these densities during some stages of stand development, age and spatial structures, as well as radial growth patterns, suggest that initial stand densities at some sites were relatively low (cf. Tappeiner 1997), as can be the case even after high-severity fire events (Pinno et al. 2013). These open stand conditions presumably allowed for opportunistic seeding and recruitment in the absence of major disturbances, which has been observed in other portions of jack pine's range (Sutton 1979, Bergeron and Brisson 1994, Conkey et al. 1995, Barton and Grenier 2008). Extended stand initiation stages (*sensu* Oliver and Larson 1996) have been observed in Douglas-fir systems in the Pacific Northwest, USA and contribute to the creation of structural complexity in early-successional forests (Tappeiner et al. 1997, Donato et al. 2012). Additionally, low densities and community associations with prairie species could also reduce the risk of tree mortality during fire events due to a lower propensity for crown-fires and promotion of higher frequency, but lower intensity and severity, surface fires, which played a major role in these systems historically (Spurr 1954, Frissell 1973, Almendinger 1992). Disturbance and its relationship with stand development is discussed further below.

Climatic patterns or events could also aid in this opportunistic recruitment (Zackrisson et al. 1995, Swetnam and Betancourt 1998, Elliott and Kipfmueller 2011). Chapter 3 of this thesis, which directly investigated recruitment and climate relationships, finds strong, but seasonally variable, associations between jack pine recruitment and moisture budget. Wet periods in the region were shown to be correlated with regional recruitment success, as has been documented in other arid-margin ecotones (Villalba and Veblen 1997) as well as arid landscapes (e.g., Brown and Wu 2005, Brown 2006). Both early summer low temperatures with high moisture and late growing-season high temperatures with low moisture were found to be beneficial for recruitment success. Given the study area is at

the arid margin for these forests and moisture budget is thought to be the major climatic driver within the prairie-forest ecotone (Danz et al. 2011) and limitation of seed germination (Nyland 1996), the early summer relationship can be easily understood. However, the late growing-season relationship is less clear. Earlier studies of jack pine recruitment have suggested that germination after August might result in elevated winter mortality due to tissues having insufficient time to harden for winter (Zehngraff 1943). One hypothesis of the late growing-season recruitment relationship is that warm, dry conditions promote cold-hardening in preparation for winter, as is the case with mature trees (Fritts 1976). An additional hypothesis, as has been suggested by managers in the study area, is that late growing-season dry conditions on sandy soils may reduce densities of associated prairie species, thereby exposing mineral soil and creating micro-sites for jack pine germination. Regardless of the specific mechanism responsible, evidence strongly suggests that climate, along with periodic disturbance, contributes to regional jack pine recruitment success.

The spatial patterns observed provide evidence for multiple potential developmental pathways for these jack pine communities. Spatial patterns in several stands suggest that randomly arranged stems recruited into unoccupied, or open, sites, while clumped stems recruited into sizeable gaps between mature trees. Evidence for recruitment into open conditions was corroborated by aerial photographs of Bladder Lake and Roy Lake Creek from 1939 and of Midge Lake West from 1969, times which coincide with spatially random cohort recruitment at these sites. Similar randomly arranged recruitment into open sites has been demonstrated in high-density post-fire jack pine recruitment (Kenkel 1988) and in low densities above the tree line in mixed-conifer montane forests (Elliott 2011). Sites with clumped stem arrangements (usually at distances > 5 m) suggest jack pine recruitment in gaps (> 100m²) between pre-established mature trees; this pattern is best demonstrated by the second grouping of jack pines at Midge Lake East (Figure 2.6) and the jack pines establishing following the red pine cohort at Nimrod Range (Figure 2.8). Similar significant clumping of pine recruitment in gaps between surviving trees has been documented in fire-prone *Pinus palustris* systems (Platt et al. 1988) and in a variety

of other conifer forests (as reviewed by, Larson and Churchill 2012). Collectively, these findings illustrate that jack pine systems in this region may follow classic even-aged (Oliver and Larson 1996), two- or multi-aged gap-phase (e.g., White 1979, Platt et al. 1988), or early-successional precocious multi-aged (Tappeiner et al. 1997, Donato et al. 2012) developmental pathways.

Although jack pine is generally thought to require open conditions for recruitment, one site, Midge Lake West, contained surprising evidence of growth suppression prior to release. The site showed continuous recruitment for ca. 20 years beginning in 1948 (Figure 2.3). These first established trees showed an uncharacteristic period of slow growth followed by an abrupt and sustained growth release beginning in 1967 (Figure 2.5) and a new, randomly arranged, jack pine cohort recruited. Aerial photos from 1969 corroborate open conditions at the site but do not provide further evidence of the particular disturbance that promoted the growth release and subsequent recruitment. This potential for sustained suppressed growth followed by release has rarely, if ever, been observed for jack pine (but see Copenheaver and Abrams 2003) and suggests an additional developmental pathway within range margin populations.

Disturbance Effects on Stand Development

As eluded to above, disturbance has played a major role in the dynamics of these stands, affecting structural and compositional conditions and recruitment pathways. Although there was no physical evidence of logging in these sites, it is very likely turn-of-the-20th-century logging activities had a profound impact on the early development of these stands. Historic photographs and rapid early-growth in jack pines at most sites indicate that many of these sites initiated under relatively open growing conditions. Though we cannot determine the cause of these conditions, the broader regional land use history suggests they were most likely initiated through logging and fire disturbance, the combination of which was prevalent in the region through the 1910s and early 1920s (Mitchell 1927, Eyre 1938) before fire suppression efforts became effective (Frissell 1973). Given the limited longevity of jack pine, it is unclear if surviving individuals from

pre-disturbance stands served as the seed source for the populations we examined, as red pine was the only species with individuals predating post-disturbance cohorts. Presumably, the seed source for colonizing jack pine on these sites was from adjacent stands or scattered surviving individuals, as the arboreal seed bank in these open-coned populations is smaller than in closed-cone populations.

Fire is put forth as the primary disturbance agent shaping the development of jack pine stands (e.g., Heinselman 1973, Simard and Blank 1982); however, its importance is generally emphasized during stand initiation. Other work documenting multi-cohort jack and red pine populations in this region have suggested that patchy or moderate severity fires are important for recruiting additional cohorts over the course of stand development (Gauthier et al. 1993, Fraver and Palik 2012), as is also the case for pines in other regions (e.g. Platt et al. 1988). Further suggestive evidence of the historic role surface-fires, as opposed to stand-replacing crown fires, is reflected by the non-serotinous cones on these sites, which have been shown to be correlated with historic fire regimes (Gauthier et al. 1996, Radeloff et al. 2004) and above average bark thickness in these jack pines (Schoenike 1976). Although we documented uneven-aged structures at several sites, there was little direct evidence linking cohort establishment with low to moderate severity surface fires. However, record of such fires is not always evident (Piha et al. 2013). In such cases, it is quite possible that age structures displaying clear cohort recruitment (Bergeron and Brisson 1990, Fraver and Palik 2012), rather than low levels of extended recruitment (e.g., Bergeron and Brisson 1994, Conkey et al. 1995), are sufficient evidence of past surface fires (but see Gauthier et al. 1993). If so, there is a high likelihood that the second cohort at Straight River was generated by a surface fire that left no record other than its age structure. In contrast, the extended recruitment periods observed in other sites in the absence surface fires may be related to wind, insects (see above), or periods of disturbance quiescence with favorable climatic conditions for seedling establishment (Chapter 3).

Wind storms, although known to be common in this region, are not expected to play a large role in the recruitment dynamics of jack pine because these events generally accelerate successional development by releasing advance regeneration of later-successional species (Canham and Loucks 1984, Woods 2004, Rich et al. 2007, D'Amato et al. 2011b). We found little evidence of jack pine recruitment in response to wind disturbance at the sites we examined, thus successional trajectories, in the absence of surface fires, appear to follow expectations based on other descriptions of these and related communities (Kittredge Jr. 1934, Webb 1989, Webb and Scanga 2001, D'Amato et al. 2011b). In particular, canopy mortality of jack pine, both through wind and other disturbance agents, is contributing to demographic transitions away from jack pine.

Demographic Transition

Many of the populations we sampled are displaying a demographic transition towards hardwood dominance, particularly paper birch and potentially oaks, as the jack pine canopy breaks up. Historically, red and white pine often increased in dominance during this transition (Kittredge Jr. 1934, Spurr 1954, Frissell 1973, Zenner and Peck 2009, Silver et al. 2013); however, only one site, Lake George, showed this type of transition. Most of the age and diameter distributions confirm the high abundance of young, non-jack pine individuals in the smaller diameter classes, especially oaks. Few oaks were observed in the canopy (data not shown) and are not expected to attain canopy heights (Webb and Scanga 2001). These short-statured trees in combination with high densities of shrubs, such as American and beaked hazelnut (*Corylus americana* and *C. cornuta*), create a dense understory ill-suited to shade-intolerant pine regeneration. This pattern is consistent with other woodland systems dominated by intolerant pine species in which frequent fire is required to reduce hardwood abundance and create conditions for maintaining conspecifics in the understory (Platt et al. 1988, Palik and Pederson 1996, Gilliam and Platt 1999). Additionally, preferential browsing by white-tailed deer (cf. Webb and Scanga 2001, Zenner and Peck 2009) is likely to eliminate any pine individuals that are able to regenerate under these conditions. In the absence of surface fire or targeted management actions that create suitable seedbed conditions for

recruitment (Eyre 1938, LeBarron and Eyre 1938, Zehngraff 1943, Chrosiewicz 1988) and protect seedlings from browse damage, it is highly unlikely that any pine species will germinate, persist, and attain canopy positions in these transitioning stands (Tester et al. 1997). Similar transition effects caused by removing fire from fire-prone systems have been observed across North America (see Wright Jr and Heinselman 1973). Without significant intervention focused on restoring historic disturbances that facilitate pine recruitment, these conditions will lead to a continued regional decline in a once-important forest type (cf. Platt et al. 1988, Gilliam and Platt 1999).

Management Implications and Conclusions

The wide range of reference conditions and developmental pathways documented here indicate that a variety of silvicultural techniques can be employed to manage stands within these range-margin populations. Many stands showed evidence of minimal competition for light in early stages of development that resulted in both even and uneven-aged stands. This finding suggests that when traditional even-aged harvesting systems are used, a range of initial densities and recruitment windows should be expected. This range will likely be relative to the amount of passive or active site preparation (Eyre 1938, LeBarron and Eyre 1938), presence of herbaceous ground competition, and herbivory reduction efforts. Our findings also suggest that establishment of new seedlings can supplement the initial tree density (Sutton 1979). Seed tree systems have been effective in other portions of jack pine's range (Chrosiewicz 1988) and could be an effective alternate even-aged silvicultural system in this region. Additionally, the observed two-aged and other uneven-aged stands suggest that multi-aged techniques, such as seed tree with reserves or variable density thinning, could also be used. Variable density thinning regimes, such as the individuals, clumps, and openings (ICO) method (Churchill et al. 2013), or variable retention harvest systems (Franklin et al. 1997, Franklin et al. 2007) that utilize a variety of gap sizes ($>100\text{m}^2$) and clumps ($25 - 400\text{m}^2$) could be used. These prescriptions would promote structural complexity while providing adequate harvest volumes and space for natural regeneration, especially with sufficient site preparation. Multi-aged silvicultural systems should especially be considered on

medium to lower quality sites where understory shrub competition is less limiting. However, they could also be considered on higher quality sites as long as understory competition is minimized. In such cases, if late-successional jack pine is not desired, an alternate longer-term goal could be to facilitate succession to old-growth red or white pine (Tester et al. 1997, Zenner and Peck 2009).

Regionally, it is unlikely that the frequency of harvests and natural fires observed at the beginning of the twentieth century that were beneficial for jack pine recruitment will be recreated. However, given that current models predict only a slight decrease in jack pine importance within north central Minnesota over the next century (Iverson et al. 2008) prescribed fire, or other management techniques that reduce canopy and understory competition and expose mineral soil, should be used to mimic historic regimes and promote jack pine recruitment. Such efforts will conserve extant forests and promote future resilience in these structurally complex and ephemeral communities.

Tables

Table 2.1. Stand characteristics for range-margin jack pine study stands. Native plant communities were assessed with plant survey and dichotomous key found in Aaseng et al. (2003). Geomorphic descriptions, soil textures, and stand sizes were obtained using a GIS with data from SSURGO (NRCS 2014) and Cummings and Grigal (1980), and forest inventory data provided by the Minnesota Department of Natural Resources, respectively.

Site Name	Site Code	Native Plant Community ¹	Geomorphic Description ²	Soil Texture ³	Stand Size (ha)
Beaver Dam	BD	Northern Dry-Sand Pine Woodland	Hillslopes on moraines	Coarse-loamy	4
Bladder Lake	BL	Central Rich Dry Pine Woodland	Outwash plains	Sandy	13
Lyons Forest	LF	Central Dry Pine Woodland	Outwash plains	Coarse-loamy	40
Lake George	LG	Central Poor Dry Pine Woodland	Flats on outwash plains, Rises on outwash plains	Sandy	15
Midge Lake East	ME	Central Dry Pine Woodland	Outwash plains, valley trains	Sandy	59
Midge Lake West	MW	Central Dry Pine Woodland	Outwash plains, valley trains	Sandy	59
Nimrod Range	NR	Central Rich Dry Pine Woodland	Hillslopes on outwash plains	Sandy	10
Roy Creek	RC	Central Rich Dry Pine Woodland	Hillslopes on outwash plains	Fine-loamy	4
Straight River	SR	Central Rich Dry Pine Woodland	Hillslopes on moraines	Sandy	28
Wolf Lake	WL	Central Rich Dry Pine Woodland	Hillslopes on outwash plains	Sandy	31

¹ Aaseng (2003)

² SSURGO (NRCS 2014)

³ Cummins and Grigal (1980)

Table 2.2. Structural characteristics of range-margin jack pine study stands including density (Den), importance value (IV, $[Relative\ basal\ area + Relative\ Den] / 2$) for live trees, jack pine snag density, density for jack pine (JP) saplings and saplings of all species (Total), and downed woody debris (DWD) volume. Jack pine had the highest IV in the plot, unless otherwise noted. For Bladder Lake and Lake George, mature tree structure values indicate that jack pine is not currently the dominant tree species. However, age distributions (Figure 2.3) suggest that this is due to demographic transition and that jack pine was the dominant species throughout much of earlier stand history.

Site	Live trees	Jack Pine Living		Jack Pine Snags	Saplings		DWD
	Den ha ⁻¹	Den ha ⁻¹	IV %	Den ha ⁻¹	JP ha ⁻¹	Total ha ⁻¹	m ³ ha ⁻¹
BD	800	292	40.5	284	.	1253	72.3
BL	528	128	32.3 [†]	212	.	1573	67.2
LF	516	348	64.8	196	27	987	13.9
LG	904	232	27.3 [‡]	276	.	560	21.3
ME	376	224	57.4	276	67	2187	29.9
MW	780	696	89.1	308	13	1053	18.8
NR	448	236	44.7 [∞]	208	.	1373	39.8
RC	444	184	45.5	288	.	1227	125.6
SR	408	144	47.2	168	.	1027	60.3
WL	476	212	49.6	464	.	1147	54.6
<i>Mean</i>	568	270	49.8	268	11	1239	50.4
<i>(SE)</i>	(59.3)	(51.6)	(5.6)	(26.4)	(6.8)	(135)	(10.7)

[†] Paper Birch IV = 56.9%
[‡] Red pine IV = 72%
[∞] Red Pine IV = 47.5%

Table 2.3. Basal areas (m² ha⁻¹) for each species or species group and mortality class by site. The *Populus* species group includes *P. grandidentata* and *P. tremuloides*. The *Quercus* species group includes *Q. macrocarpa* and *Q. rubra*. The Other Conifers group includes *Abies balsamea*, *Picea glauca*, *Picea mariana*, and *Pinus strobus*). The Other Deciduous group includes *Prunus serotina*, *Acer rubrum*, *Ulmus americana*, *Alnus incana*, and *Fraxinus pennsylvanica*. Basal areas for jack pine snags and stand totals with snags, which are thought to have died within 10 - 15 yr prior to sampling, are included as representation of stand structure prior to this mortality.

Group	Species	BD	BL	LF	LG	ME	MW	NR	RC	SR	WL	Mean (SE)
Live Trees	<i>Pinus banksiana</i>	14.5	7.1	11.9	8.7	8.7	19.0	11.1	10.8	9.7	9.3	11.1 (1.1)
	<i>Pinus resinosa</i>	11.5	0.0	6.5	21.3	5.3	1.1	18.1	6.9	0.9	1.8	7.4 (2.4)
	<i>Betula papyrifera</i>	2.0	9.2	0.7	0.0	0.3	0.0	0.1	0.2	0.6	2.0	1.5 (0.9)
	<i>Populus</i> spp.	4.1	0.6	0.0	0.0	0.0	0.0	0.3	2.2	2.4	3.0	1.3 (0.5)
	<i>Quercus</i> spp.	0.0	0.6	0.0	0.0	0.8	0.2	0.6	0.7	1.9	0.3	0.5 (0.2)
	Other Conifers	0.5	0.0	0.0	0.2	0.6	1.0	0.0	0.5	0.0	0.5	0.3 (0.1)
	Other Deciduous	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.5	0.9	0.1	0.2 (0.1)
	Total	32.5	17.5	19.1	30.2	15.8	21.4	30.1	21.8	16.4	17.0	22.2 (2.0)
Snags	<i>Pinus banksiana</i>	9.9	9.4	4.9	5.5	8.7	5.0	6.2	12.5	6.9	15.2	8.4 (1.1)
Live + Snags	Total	42.4	26.9	24.0	35.8	24.5	26.4	36.2	34.3	23.3	32.2	30.6 (2.1)

Figures Legend

Figure 2.1. Location of study area and sites within a southern range-margin *Pinus banksiana* population in north-central Minnesota, USA. Jack pine range (grey shading) based on Little (1971). The Midge Lake sites are on opposite sides of the same larger stand (Table 1).

Figure 2.2. Diameter at breast height (DBH) distributions of living trees (n_{living} below site name) and snags (inset) for ten range-margin jack pine stands ($N = 2105$). DBH classes are labeled by the low end of the 5cm range (i.e. '15' includes stems $15\text{cm} \leq \text{DBH} < 20\text{cm}$).

Figure 2.3. Age distributions for ten range-margin jack pine sites. Ages for trees correspond with their age at recruitment and are grouped into five-year bins. Triangles indicate fire-scar dates; note that except at Nimrod Range, the recruitment of current canopy trees and snags does not seem to closely follow these fires.

Figure 2.4. Jack pine recruitment windows at ten range-margin jack pine sites. Recruitment windows are the number of years it took for the middle 90% of trees to establish. The total window length is listed in parentheses next to the site code (codes found in Table 2.1). Year of recruitment for each site is standardized and displayed by the median year of recruitment.

Figure 2.5. Mean growth chronology (black line) of raw ring width from all jack pine increment cores ($n = 176$), as well as the raw tree-ring series (grey lines) from 19 trees recruited prior to 1960 at Midge Lake West. These 19 series demonstrate an uncharacteristically lengthy period of slow radial growth prior to a growth release that began circa 1967.

Figure 2.6. Tree locations for six sites that had protracted recruitment windows. At each site, jack pine trees are separated into first and second groupings of recruitment based upon cohorts or near the median recruitment date; the date in parentheses is the earliest year of recruitment for the second group. The locations of jack pines with no age data (mostly snags), and other species are included to provide reference of where gaps are unoccupied.

Figure 2.7. Plate of the *Pinus banksiana* forest at the Lyons Forest study site showing an interrupted low density canopy, significant stem clumping (background left), a range of diameter and canopy sizes in *P. banksiana* (three foreground stems, as well as others with scaly bark), and *P. resinosa* in both mature (middle-ground left, in front of *P. banksiana* clump) and immature (foreground center) age classes. Patchy understory clumps of *Corylus americana* (middle-ground right) are also evident on this site of medium moisture and nutrient quality. Literature evidence (Andrews 1906) indicates 1905 as the last major year of fire in adjacent areas, which corresponds with the earliest recruitment of both *P. banksiana* and *P. resinosa*. The majority of recruitment happened in an extended period between 1930 and 1960.

Figure 2.8. Tree locations at Nimrod Range showing even-aged jack pine recruitment in ~100 – 400 m² groups between red pines that were around 50 years old at the time of jack pine recruitment. Circles indicate the location of jack pine stems, which are significantly grouped at distances between 5 and 20m, and squares indicate the locations of red pine stems, which were spatially no different from random. Light and dark grey coloring indicates whether a tree recruited before or after 1945, respectively. The black outlines are sized to represent five DBH classes. Outlines with no coloration indicate locations and sizes of trees with no age data available, which were included to provide reference of where gaps are unoccupied.

Figure 2.1.

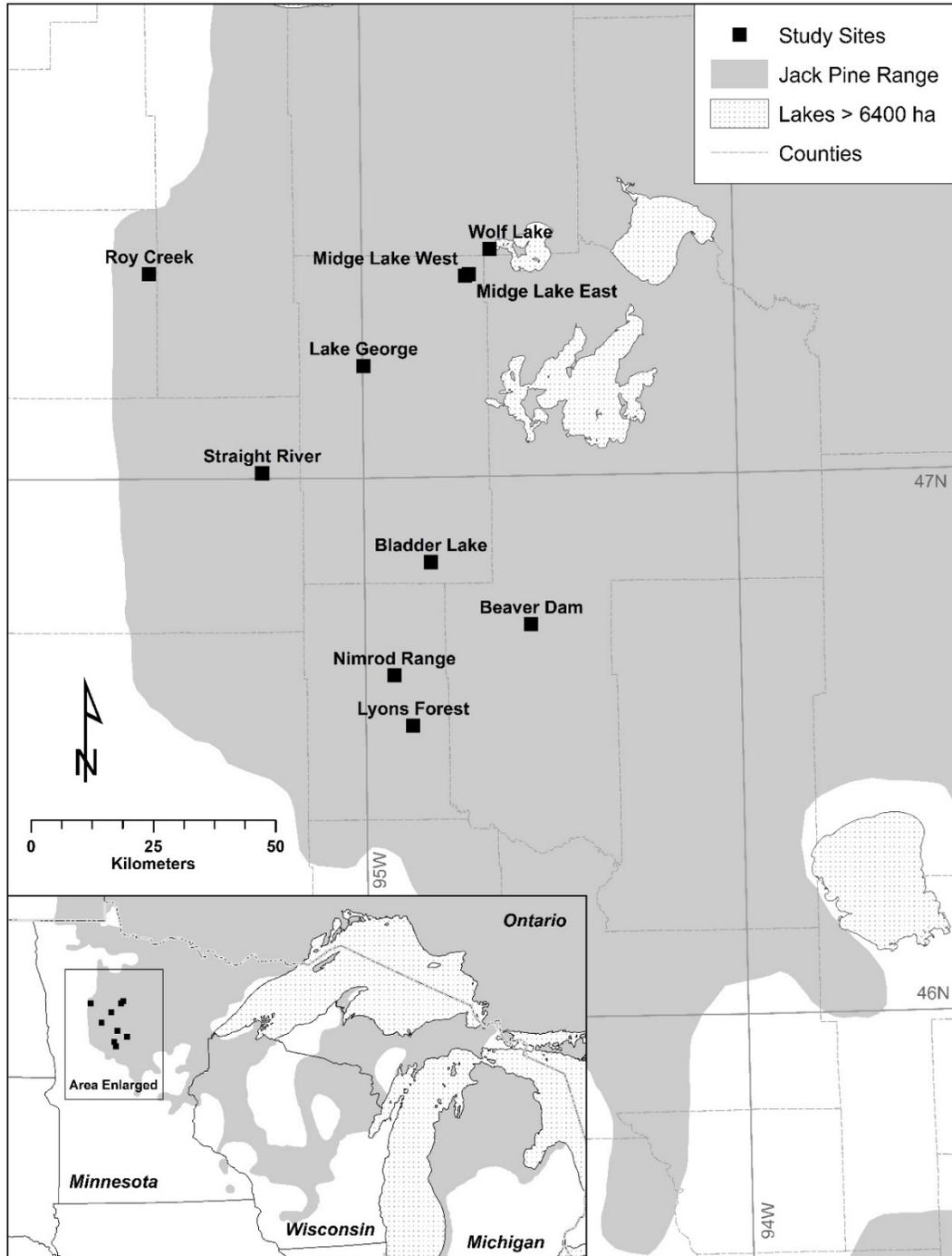


Figure 2.2.

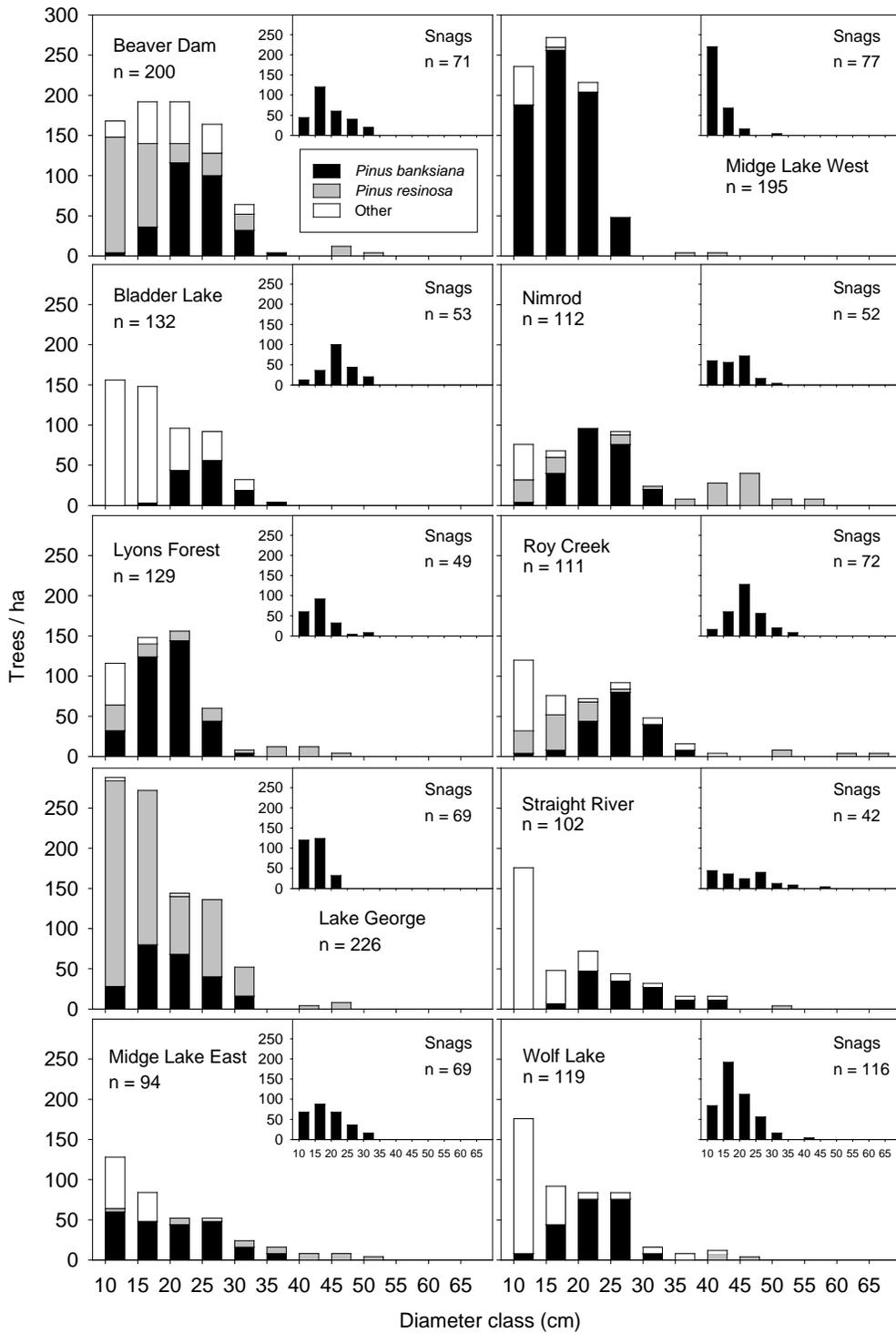


Figure 2.3.

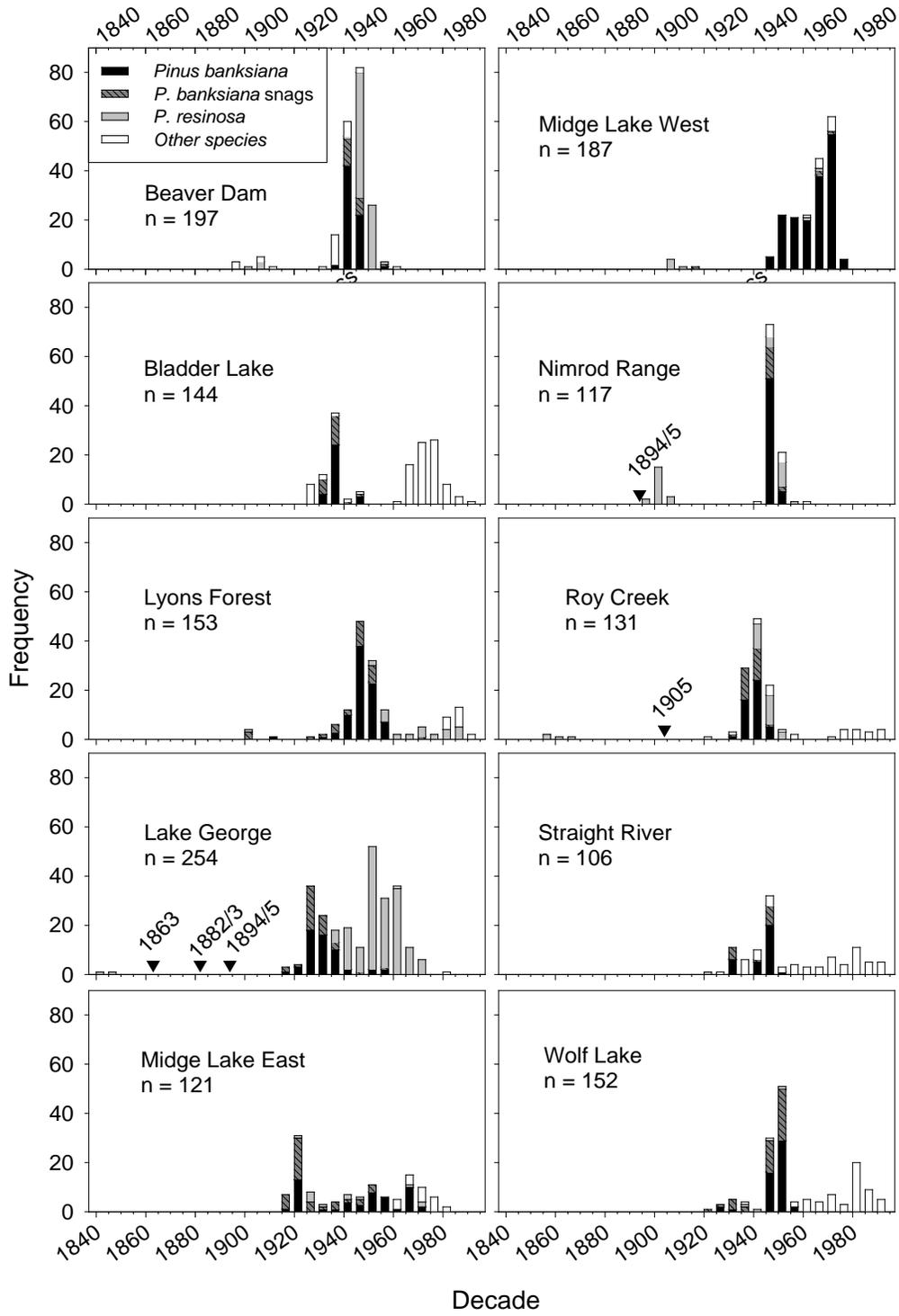


Figure 2.4.

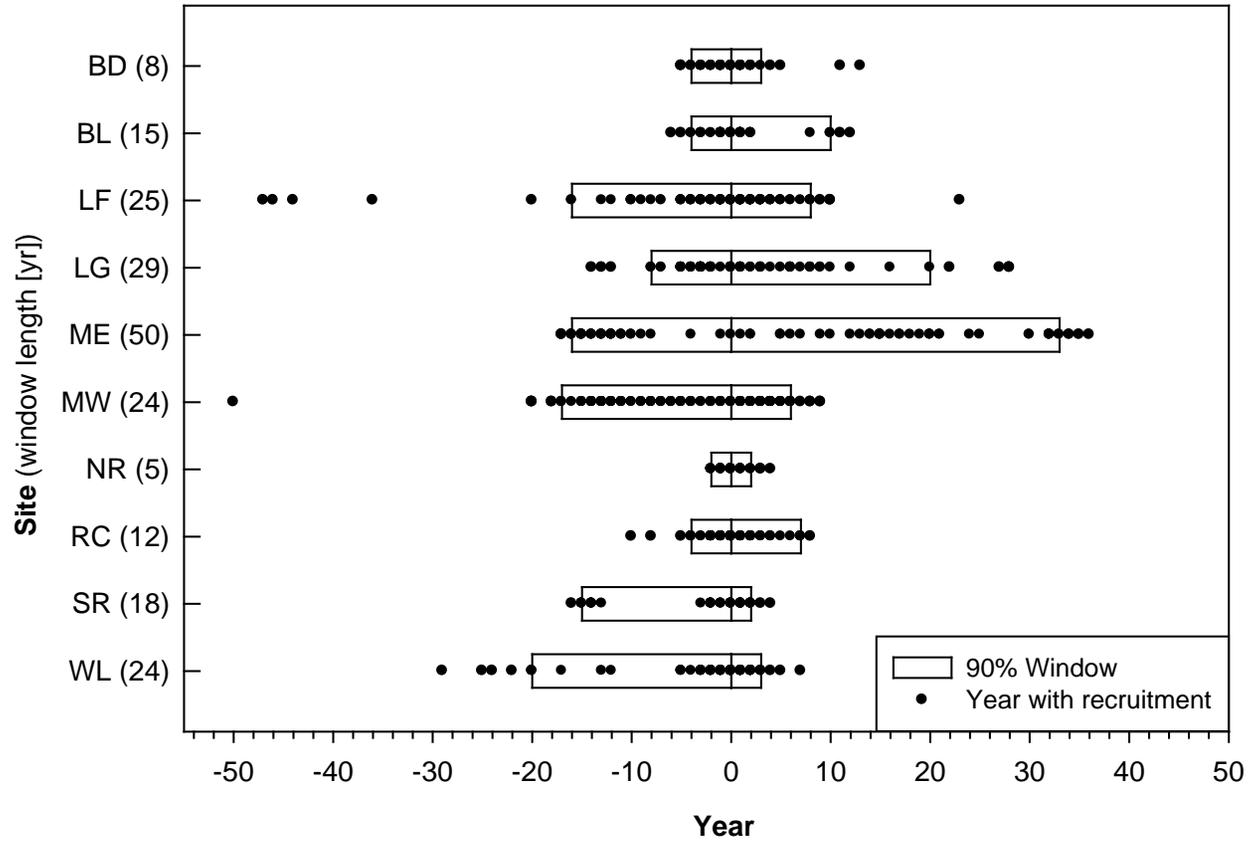


Figure 2.5.

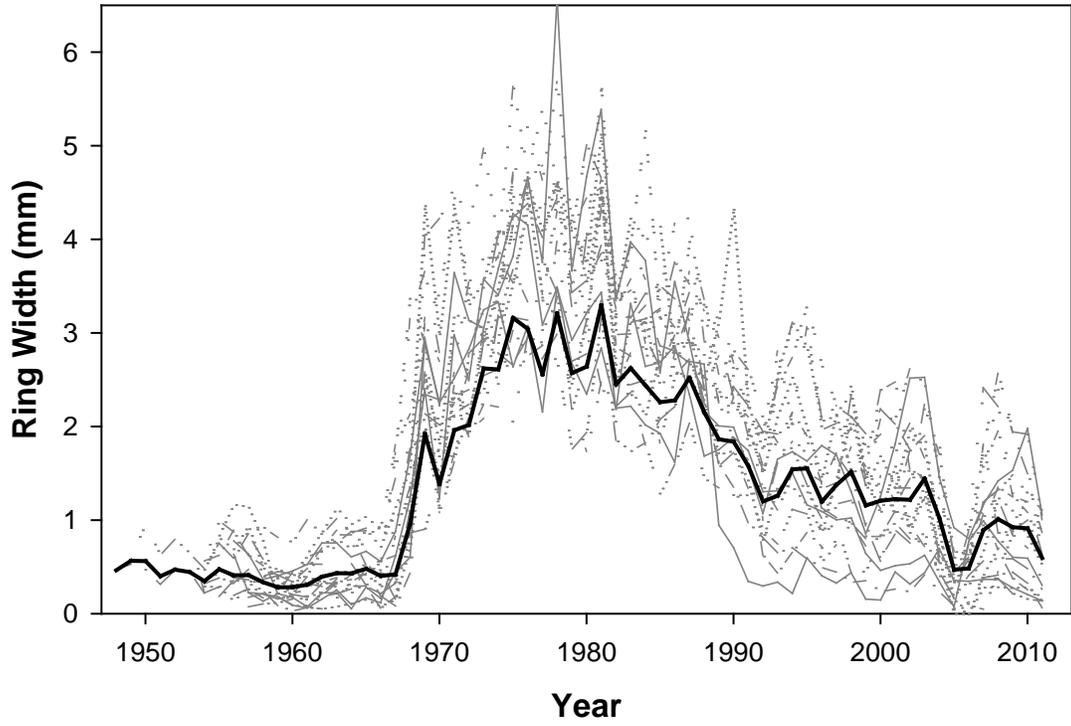


Figure 2.6.

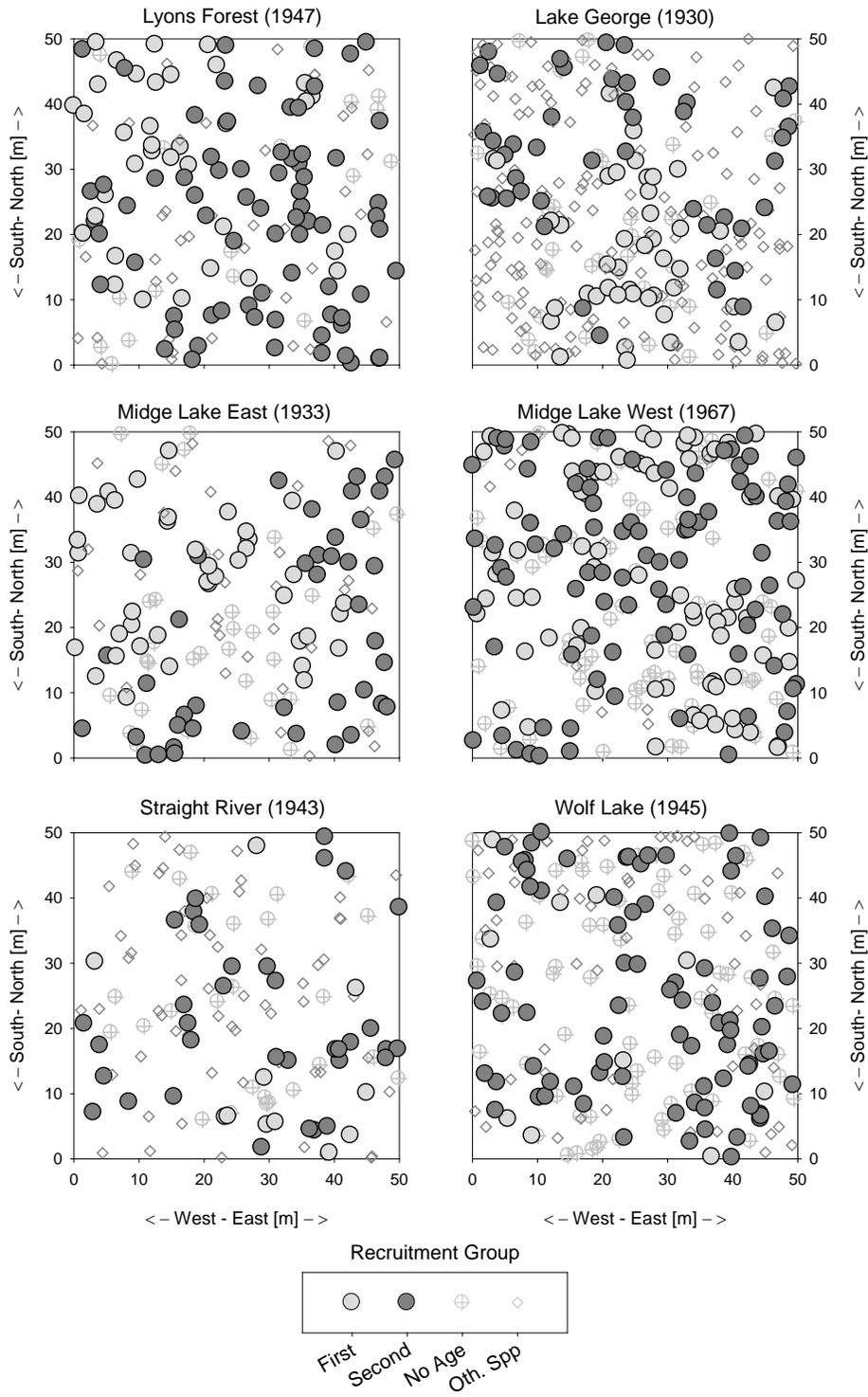
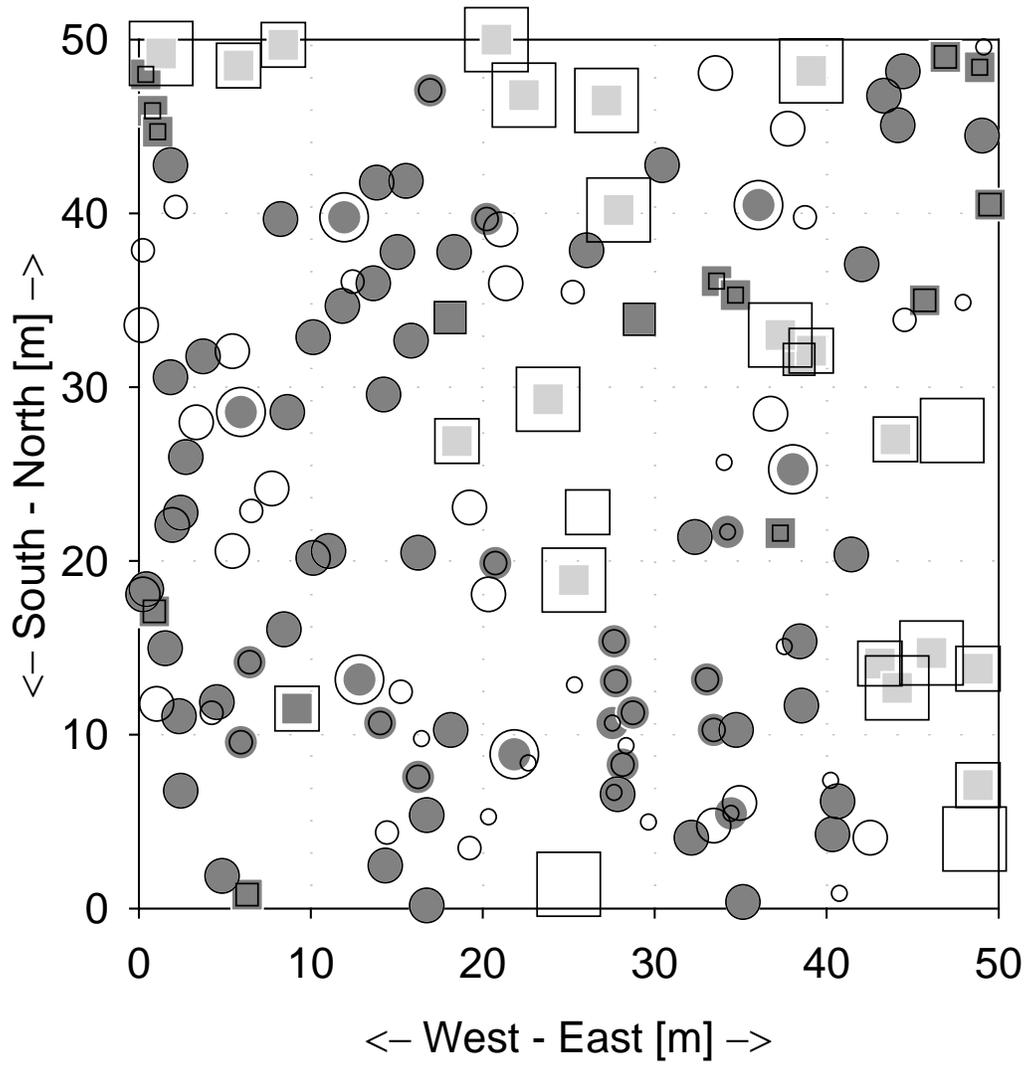


Figure 2.7.



Figure 2.8.



Chapter 3: Variation in *Pinus banksiana* climate-growth and -recruitment relationships at its southern range margin in Minnesota, USA

Introduction

Climate strongly influences the natural range and distribution of plant species (Woodward 1987, Davis and Shaw 2001). The general expectation under a warming climate is that species in the northern hemisphere will shift their ranges northward (Parmesan 2006). However, this expectation is more complicated than often suggested by models that assume intra-species homogeneity of climate-response, genetics, and forest dynamics (Alberto et al. 2013). Further empirical data collection and refinement of forest dynamics models by incorporating intra-species variability are seen as necessary factors for conservation of marginal populations and improving predictions of future range shifts (Hannah et al. 2002, Hampe and Petit 2005).

The intimate linkages between climate and tree growth have long been established (Fritts 1976). The non-uniformity of this relationship across a species' range has been increasingly demonstrated (e.g., Wilmking et al. 2004, Carrer et al. 2010, Huang et al. 2010, Herrero et al. 2013). Individuals and populations at the margins of their range, especially their rear edge (Hampe and Petit 2005), are particularly useful for establishing the range of climate-growth relationships for a species given these populations may already be at their biological limit (Allen and Breshears 1998, Danz et al. 2011, Fisichelli et al. 2013) and highly sensitive to climatic fluctuations (Fritts 1976). These populations also tend to be characterized by atypical individual and community dynamics (Hoffmann and Blows 1994, Kawecki and Ebert 2004, Hampe and Petit 2005) and should be an area of focus for detecting potential range shifts.

The establishment and survival of tree seedlings (recruitment) is likely more sensitive to climate and site factors than established, mature trees (Brubaker 1986, Bugmann 2001, Woodall et al. 2009), yet these relationships are less well understood and more

challenging to predict and model due to the complexity of factors involved (Agee and Smith 1984, Clark et al. 1998, Price et al. 2001, Ibanez et al. 2007). Typically, recruitment is linked with episodic canopy disturbances of varying intensities. Such disturbances open growing space for seedlings (e.g., Heinselman 1973, Henry and Swan 1974, Lorimer 1980, Bergeron and Brisson 1990, Frelich and Lorimer 1991, Fraver and White 2005, D'Amato et al. 2008), which is especially key for shade intolerant species. These events clearly play a vital role in creating conditions required for recruitment. However, prolonged (Bergeron and Brisson 1994, Svoboda et al. 2012) or irregular (Agee and Smith 1984, Tappeiner et al. 1997, Donato et al. 2012) patterns of post-disturbance recruitment, as well as non-disturbance-related recruitment in forests assumed to be governed by disturbance (Conkey et al. 1995, Barton and Grenier 2008) suggest the importance of other in- and ex-situ factors. In arid forests and at forest-non-forest ecotones, episodic tree recruitment has been aided by both limitation of frequent disturbance and promotion of recruitment by pluvial climatic periods (Woodward et al. 1995, Villalba and Veblen 1997, Swetnam and Betancourt 1998, Brown and Wu 2005, Brown 2006). Given the central role environmental conditions, such as temperature, precipitation, and available soil moisture, have in seed germination and seedling establishment (Brubaker 1986, Nyland 1996), the relationship between climate conditions and tree recruitment is paramount for approximating how tree demographics might be affected by climate change (Price et al. 2001, Dullinger et al. 2004, Ibanez et al. 2007).

Jack pine (*Pinus banksiana* Lamb.) exhibits significant phenotypic, genotypic, and ecological variation across its native range, especially along the southern range margin (Schoenike 1976, Huang et al. 2010, Genries et al. 2012, Subedi and Sharma 2013). It is a dominant component of the boreal forest biome in North America (Iverson et al. 2008, Huang et al. 2010) that reaches its southwestern range margin in the prairie–forest ecotone (cf. Davis 1977) in Minnesota. Along this ecotone, which exhibits an abrupt dry-mesic moisture gradient (Danz et al. 2011), jack pine is often found in relatively low density, even- and multi-aged stands on dry, nutrient poor sandy outwash plains

(Almendinger 1992, Aaseng et al. 2003, This thesis Chapter 2). The proximity to its range margin, as well as the xeric soil on which it is often found, likely contribute to climate sensitivity in these populations. Natural disturbance, particularly fire, is expected to control recruitment across much of jack pine's range (Heinselman 1973, Despons and Payette 1992, Frelich and Reich 1995). However, the fact that these range-margin populations – unlike the typical populations – have mostly non-serotinous cones (Rudolf 1958, Schoenike 1976), coupled with the observed protracted recruitment windows (Chapter 2) suggest that successful jack pine recruitment might rely not only on disturbance, but also on climate. These factors provide an ideal location to further study the relationships of tree growth and recruitment to climate.

The primary objective of this study was to determine the effect of climatic factors on growth and recruitment of range-margin jack pine populations. More specifically, we aimed to 1) quantify the relationship between climate and radial growth in mature trees; and 2) quantify the relationship between climate and tree recruitment. Previous work suggests that a combination of temperature, precipitation, and evapotranspiration demand, henceforth moisture budget, will be the primary climatic factor at this dry–mesic margin (Villalba and Veblen 1997, Danz et al. 2011).

Methods

Study Area

The range-margin population of jack pine in north-central Minnesota, USA (Figure 3.1) is found within the western half of the Northern Minnesota Drift and Lake Plains (MDL) ecological subsection of the Laurentian Mixed Forest Province (Aaseng et al. 2003). The MDL is characterized by complex surface geology due to a patchy distribution of glacial deposits such as outwash plains, lake plains, till plains, outwash channels, moraines, and drumlin fields (Aaseng et al. 2003). Jack pine most often dominates xeric outwash plains along with red pine (*Pinus resinosa*); on less xeric sites, deciduous species, such as quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and northern red

oak (*Quercus rubra*), are common associates. The climate of the region is cold-temperate continental with short cool summers and long cold winters. The mean annual temperature for the study area over the last century, as calculated using climate data for each study site (see below), ranges from 1.7 – 6.8 °C with a mean of 4.1 ± 0.1 °C and the total annual precipitation, a majority of which falls between April and October, ranges from 347 – 851 mm with a mean of 632 ± 10 mm. Both climate variables show considerable annual and seasonal variability (Figure 3.2).

In order to obtain the longest possible age records in this short-lived species, we sought stands of natural origin that were older than the recommended management rotation length (cf. Reinikainen et al. 2012). Using a Geographic Information System (GIS) provided by the Minnesota Department of Natural Resources and recommendations by natural resource professionals working in the study area, 128 potential study sites were identified. These sites were evaluated via historic aerial imagery (1939 – 2012) to screen out sites with obvious anthropogenic influence during stand history. The remaining 76 sites were inspected on the ground for representation of jack pine, indications of advanced age, such as ample standing and downed deadwood, and signs of past management, such as cut stumps, uniform spacing, or logging roads. Nine sites ultimately met our criteria and were sampled (Table 3.1, Figure 3.1).

Field and Laboratory Techniques

One 0.25 ha square study plot was established along cardinal directions at each site from a randomly selected point in a GIS or at the geographic center of the site. Within each plot, each tree ≥ 10 cm diameter at breast height (DBH, 1.37 m) was given a unique number and sampled for species, DBH, crown class (Kraft classification system, Oliver and Larson 1996), and mortality class (living or snag). One increment core was extracted at 30 cm above the ground from all living trees and, when possible, dead trees to be used for developing jack pine tree-ring chronologies for each site (Table 3.2). Additional

variables were sampled at each site, as well as an additional plot at Midge Lake (Midge Lake West), for a concurrent dendroecological study (This thesis Chapter 2).

In the laboratory, increment cores were affixed to wooden mounts and sanded using progressively finer grits (up to 800-grit) in order to clearly display yearly growth boundaries. All annual growth rings on each core were measured to the nearest 0.001 mm using a Velmex sliding-stage micrometer (Velmex, Inc., Bloomfield, NY). If the pith was not included in the core, the number of missing rings to pith was estimated using a visual pith estimator (Applequist 1958); cores > 10 years from pith were excluded from recruitment analyses. All cores were visually cross-dated using marker years (Yamaguchi 1991) and statistically confirmed with COFECHA (Holmes 1983). Cores from dead jack pine trees at each site were cross-dated against their respective living-tree chronologies using marker years and statistical confirmation.

Chronology Development and Statistical Analyses

Master growth chronologies for jack pine at each site were developed to be used for climate-growth analyses. In order to remove non-climatically related growth trends, some series were manually excluded and the remaining were standardized using established techniques. To assess non-climatic growth trends, each raw ring-width series was visually inspected for periods of unique growth, such as periods of sustained suppression or release (Frelich 2002). Series that displayed these characteristics, as well as those from trees classified as being in intermediate or suppressed crown positions, were excluded from chronology development. The radial growth of each remaining series was standardized using a cubic spline that preserved 50% of the variance at a wavelength of 33% of the series length. A bi-weight robust mean was used to combine standardized series (Cook and Peters 1981, Kipfmüller et al. 2010) into a master chronology for each site. Temporal autocorrelation was accounted for by using residual chronologies for analyses. Chronology development was done in ARSTAN v.44h3 (Lamont-Doherty Earth Observatory 2014, Cook 1985).

Total monthly precipitation (P) and monthly mean high and low temperature values were collected for each site using the parameter-elevation regressions on independent slopes model (PRISM, PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>, Daly et al. 2002), which utilizes data from Global Historic Climatology Network (GHCN) weather stations. With these, the monthly mean temperature (T), monthly total potential-evapotranspiration (PET, Hargreaves and Samani 1982), and the monthly moisture budget (P-PET) were calculated. Site-level monthly climate data were averaged to create regional climate data used in region-wide analyses.

Correlations between annual ring-width variance in each chronology and monthly climatic variables were assessed to discover the relationship between jack pine growth and climate. The *seascorr* function in the *treeclim* package (Zang 2014) in R 3.0.2 (R Foundation for Statistical Computing, Vienna, Austria) was used to calculate the simple (Pearson) correlations and partial correlations between growth and P-PET, as the primary variable, and T, as the secondary variable (Meko et al. 2011). P-PET was chosen to represent moisture conditions rather than precipitation (P) alone given the strong correlation between these two variables, as well as based on the findings of previous work which documented the overall importance of P-PET in driving growth and vegetation patterns in this ecotone (Danz et al. 2011). Individual months of a 14-month window from the previous year August ($t - 1$) through September in the year of growth (t) were analyzed. One-thousand bootstrap iterations were run to assess the statistical significance ($\alpha = 0.05$) of correlations.

Annual recruitment chronologies were developed for each site and for the region (all plots pooled) to assess the relationship between jack pine recruitment and climate. The earliest calendar year in each tree-ring series (after pith adjustment, if necessary) was considered the recruitment year. All recruitment chronologies were transformed with a five-year running mean in order to account for age-to-coring-height uncertainty (cf.

Bergeron and Brisson 1994); for consistency, each climate variable was also transformed with a five-year running mean. The relationship between recruitment chronologies and growing-season (April – October) T, P, and P-PET was assessed using Pearson’s correlation coefficients in SAS 9.4 (SAS Institute Inc., Cary, NC, USA). Although climatic factors outside of the growing-season, especially in the winter following germination, may impact recruitment success or failure, we focused on growing-season climate because jack pine seeds do not require climatic preconditioning to germinate (Rudolf 1965) and are expected to be able to germinate at any point between April and October if climate and seedbed conditions allow (Eyre and LeBarron 1944). Additionally, intra-annual effects on annual recruitment were assessed by regressing the regional recruitment chronology against principle components of monthly growing-season T and P-PET (P was excluded due to its significant correlation with P-PET, $p < 0.001$; growing-season T was not significantly correlated with P-PET [$p = 0.14$] or P [$p = 0.71$]). The *response* method of the *dcc* function in the *treeclim* package in R was used for these analyses, with the same significance determination as above.

Results and Discussion

Growth Chronologies

The total time period covered by at least one jack pine tree-ring series for the study area (N = 644) was from 1906 – 2012 (Table 3.2); however, the common time-period containing adequate sample depth ($n \geq 10$ series) and expressed populations signal (EPS, Wigley et al. 1984) ≥ 0.85 for each site was 1949 - 2011 (Table 3.2, Figure 3.3b), which was the time-period used for climate-growth analyses. For this time-period, residual chronologies were significantly correlated ($\alpha = 0.05$) with each other ($mean \pm SE = 0.51 \pm 0.02$). As such, chronologies displayed general agreement in years of above and below average growth (Figure 3.3a) with lowest growth across the region in 1956, 1967, 1979, 1995, and 2011 and highest growth in 1959 and 1973. Inter-series correlation ($mean = 0.34 \pm 0.02$) and mean sensitivity ($mean = 0.30 \pm 0.01$) values for site-level chronologies (Table 3.2) were within and above, respectively, the ranges of reported values in similar

studies (Hofgaard et al. 1999, Girardin and Tardif 2005, Huang et al. 2010, Genries et al. 2012). Taken together, these correlations and sensitivities indicate that jack pine growth has been influenced by both regional variables (i.e. climate) and stand-level variables (i.e. competition) for the common time-period.

Climate-growth Relationships

Significant relationships between jack pine radial growth and P-PET and T were observed across all sites and months (Figure 3.4, Appendix 5). Assessing both the higher and lower consistency trends between climate and growth indicates that growth was primarily indirectly related with moisture budget (P-PET), except during the growing season (year t), and directly related with mean temperature (T), except during the growing season prior to growth (year $t - 1$). Although there was considerable variation across sites in terms of significant climate-growth relationships, the following results and discussion will focus primarily on trends that were seen at three or more sites.

The timing of spring thaw was critical in the annual jack pine growth cycle. Indirect significant relationships between jack pine growth and P-PET were found to occur at each site (Figure 3.4) and in nearly every month prior to the current growing season. This trend was prevalent across the region during winter months (all sites except Wolf Lake), especially in the late winter (February and March) through early spring (April), when moisture can often be unavailable in the form of snow and ice. In addition, a majority sites had a significant direct relationship with temperature at some point during the spring shoulder season (February – May). These sensitivities to shoulder season climate suggest that the commencement of the active growing season might either be delayed by a persistent snowpack, as has been found in more northerly jack pine (Brooks et al. 1998) and montane conifer systems (Peterson and Peterson 2001), or hastened by above-average temperature, as is the case elsewhere in the boreal forest (Tanja et al. 2003). Direct relationships between jack pine growth and growing season length has also been reported along the Ontario – Quebec border (Hofgaard et al. 1999, Tardif and Conciatori

2001, Huang et al. 2010, Genries et al. 2012) and in Manitoba (Girardin and Tardif 2005). However, this relationship has primarily been reported to be driven by April temperature and only once has spring moisture been significant (Brooks et al. 1998). These results add further evidence to the general relationship between jack pine growth and growing season length but also highlight the intra-range variation of specific drivers.

Relationships between growth and growing season moisture and temperature were also significant. Direct relationships between growth and moisture were observed at a majority of sites during the peak of the growing season, June or July, in the year of growth (Figure 3.4). This suggests that growth was better during years with above average moisture or limited when moisture was low. Given the sandy, and potentially droughty soil of the study sites and proximity to the dry-margin of jack pine's range, direct sensitivity to summer moisture was expected (Waring and Schlesinger 1985, Tardif and Conciatori 2001, Girardin and Tardif 2005, Savva et al. 2008, Danz et al. 2011). Growth was also directly associated with growing season temperature at seven sites. Warmer than average temperatures likely encouraged extended periods of active foliar and, subsequent, diameter growth, especially given this species has been shown to be able produce multiple flushes of foliage if conditions are favorable (Rudolph 1964). However, above average temperatures, especially when later in the growing season, may have inhibited growth the following year, as suggested by the indirect relationships with prior year August through October temperatures (Figure 3.4). This has been documented in other studies of temperate conifer species and has been related to limited resource allocation to bud formation (Hofgaard et al. 1999, Huang et al. 2010, Genries et al. 2012) or carbohydrate storage in roots (Fritts 1976, Genries et al. 2012), both of which would limit following season growth potential. These conditions also may promote desiccation and loss of needles that would otherwise be retained and utilized the following growing season (O'Neil 1962).

Overall, the variation in jack pine climate-growth response observed within our study area, as well as across the range of jack pine (Brooks et al. 1998, Hofgaard et al. 1999, Savva et al. 2008, Huang et al. 2010, Genries et al. 2012, Subedi and Sharma 2013), support the notion of non-uniformity in a species response to climate across its range. This variation is thought to depend more on local and regional environmental factors than on genetics (Savva et al. 2008). Similar range-wide variation in climate-growth relationships has been reported, albeit in montane regions, in *Tsuga mertensiana* in the Pacific Northwest, USA (Peterson and Peterson 2001) and in multiple European species (e.g., Jump et al. 2006, Macias et al. 2006, de Luis et al. 2013).

Climate-recruitment Relationships

Peaks in annual recruitment surrounded by additional recruitment were observed at both site and regional scales. All site-level recruitment chronologies displayed at least one major peak in recruitment (Figure 3.5a). Most also showed low to high levels of additional recruitment, or had protracted peaks, over the period examined; at only one site (Nimrod Range) was there no additional recruitment surrounding this peak. These patterns led to a range of age structures (Chapter 2). Similar episodic and sustained recruitment has been observed in other portions of jack pine's range. Typically these patterns are attributed to disturbance events (Carleton 1982, Bergeron and Brisson 1990, Despons and Payette 1992, Gauthier et al. 1993), the absence of disturbance (Conkey et al. 1995, Parisien et al. 2004, Barton and Grenier 2008), or a combination of the two (Bergeron and Brisson 1994). Such patterns have also been documented in other forests dominated by shade-intolerant species in relation to climate (e.g., Zackrisson et al. 1995), patchy disturbance (e.g., Platt et al. 1988, Pederson et al. 2008, Fraver and Palik 2012, Reinikainen et al. 2012, Svoboda et al. 2012), or a combination of these factors (e.g., Swetnam and Betancourt 1998, Brown and Wu 2005). The regional recruitment chronology (plots pooled) had a pronounced peak between 1945 and 1955 (Figure 3.5b). Recruitment gradually increased throughout the 1920s and 1930s prior to peaking. It dropped off sharply after the peak but was sustained at a low level until 1975. As with

patterns in tree growth, patterns of recruitment suggest both regional and site-level factors have influenced jack pine recruitment. Site-level factors have been discussed earlier (Chapter 2), so here we will focus on the influence of regional factors, primarily climate.

Significant correlations between tree recruitment and growing-season climate, primarily precipitation and P-PET, were seen at most sites but were not of consistent direction (Table 3.3). At three sites, Beaver Dam, Lyons Forest, and Wolf Lake, recruitment was positively associated with moisture suggesting that recruitment is promoted during growing seasons with relatively high available moisture. However, indirect associations were observed at Lake George and Nimrod Range, suggesting that recruitment was better during times of low moisture. The former results support the findings of Bergeron and Brisson (1994), who investigated this relationship using jack pine on rocky outcrops in Quebec using similar techniques. The latter result, however, was unexpected. We offer two hypotheses for these indirect associations, both related to the effect of climate on seedbed conditions. First, hot and dry conditions are known to promote drought and, given ignition and fuel, fire (Swetnam and Betancourt 1998). It could very well be that the indirect relationship with moisture is indicative of conditions just prior to recruitment that promoted a fire, which would have reduced ground-layer competition and created favorable seedbed conditions for jack pine germination. A short and strong pulse of recruitment, as seen at Nimrod Range, would be expected after such an event (Gauthier et al. 1993). A second hypothesis, which is a more likely a driver of the protracted recruitment at Lake George, is that the hot and dry conditions may have limited the abundance of ground-layer species thus reducing the levels of competition experienced by seedlings originating from non-serotinous cones. In addition to these hypotheses for indirect associations, the opposing directionality at different sites suggests that intra-season variability, unaccounted for by lumping climate variables across the growing season, may be impacting these correlations.

Within-season variability in the relationship between regional jack pine recruitment and monthly growing season climate was demonstrated in the results from the response function analysis. Interacting effects of significant temperature and moisture associations in June and an indirect relationship with September moisture were significantly related to recruitment (Figure 3.6). In June, the indirect and direct associations with temperature and moisture budget, respectively, suggests that cool, moist weather during early summer was favorable for recruitment in a given year. These conditions would positively affect the available moisture and limit drought stress during the early stages of seedling development, a period during which individuals are most vulnerable to heat and drought-related mortality (Nyland 1996). In contrast to June, tree recruitment was indirectly related to moisture in September, suggesting that seedling success may be positively influenced by below-average moisture levels later in the growing season. Such low moisture conditions promote a transition to frost-hardiness prior to winter in mature trees (Fritts 1976). It is likely that the observed relationship confirms the importance of climatic conditions that promote this transition in seedlings as well. Taken together, these results highlight intra-season variability in the relationship between climate and recruitment, which if accounted for could improve predictions of forest dynamics (Price et al. 2001) and species ranges (Iverson et al. 2008) in different climatic scenarios.

The broader role of longer-term climatic conditions is important to consider as well. Even though correlation analysis between regional climate and recruitment yielded no significant results (Table 3.3), the peak in regional recruitment between roughly 1945 and 1955 (Figure 3.5b) appears to coincide with a post-drought, pluvial period across the region (Figure 3.2, smoothed precipitation). Investigations in other coniferous forests, *Austrocedrus chilensis* along arid-margin ecotones (e.g., Villalba and Veblen 1997), arid *Pinus ponderosa* forests (e.g., Brown and Wu 2005, Brown 2006), and arid forests of mixed species (Swetnam and Betancourt 1998), conclude that recruitment was favored during post-drought, pluvial periods with limited fire activity. Our data suggest this

relationship may be occurring in this region as well, although the recruitment chronology used is not long enough to confirm.

Variability in growth and recruitment relationships with climate at many scales is important to incorporate into vegetation modeling efforts. Climate models for time period 2041 - 2070 suggest increases in temperature of approximately 3.0, 2.5, 4.5, and 3.5 °C during winter, spring, summer, and autumn, respectively, for north-central Minnesota (Liu et al. 2013). Precipitation predictions are less uniform, suggesting slight increases for winter (December – February) and autumn (September – November) and slight decreases for spring (March – May) and summer (June – August). Given that even potential increases in precipitation are not predicted keep up with evapotranspirational demand, these changes are expected to increase moisture deficit in all seasons, and most substantially during summer and autumn (Liu et al. 2013). With such changes, current models predict the importance of jack pine in the region to be slightly decreased over the next century (Iverson et al. 2008). Our results show growth and recruitment to be sensitive primarily to moisture budget and generally support these predictions. However, our results also highlight the intra-season and regional variability of relationships of climate with growth and recruitment. We suggest that incorporating such variability into forest dynamic and landscape simulation models with empirical data, such as those outlined in this study, could improve predictive capabilities. This is especially true for climate-recruitment relationships, for which a lack of empirical data is thought to be a major limitation in current models (Bugmann 2001, Price et al. 2001).

Conclusions

Climate strongly influenced jack pine growth and recruitment in these range-margin populations but exhibited variability at a variety of scales. In general, a primary sensitivity to moisture budget in growth and recruitment processes was confirmed (Danz et al. 2011), yet there was also additional sensitivity with temperature. Ring growth was related to patterns in these climate factors in the spring and were presumably reflective of

the timing of winter-dormancy release and its effect on the duration and magnitude of annual growth. In addition, growth was sensitive to summer climate and was favored by warm, wet conditions. However, high temperatures without adequate moisture were potentially limiting to growth during the following year. There was variability in the specifics of these general trends both within the region and when comparing results with jack pine populations in other portions of its range. Similar intra-annual and regional variability was observed in climate-recruitment relationships. Response-function analysis demonstrated intra-season climate variability in the association between recruitment and moisture. While cool and wet conditions at the beginning of the growing season were beneficial for recruitment, an opposite relationship was seen for the end of the growing season, likely due to the need for seedlings to develop frost-hardiness prior to winter. When generalizing climate across the growing season, some sites showed direct relationships with moisture, which was expected, yet others showed indirect relationships. This and other findings provide further evidence of the high degree of variability in growth and recruitment response to climate that may exist for a given species. These results underscore the need to account for temporal and spatial variation in the climatic effect on tree growth and seedling establishment probabilities, particularly in forest gap and bioclimatic envelope models widely applied for projecting future forest conditions and species distributions.

Table 3.1. Stand characteristics for nine range-margin jack pine study sites. Basal Area and density calculated for live trees of all species within study plot.

Site Name	Site Code	Geomorphic Description ¹	Soil Texture ²	Stand Size (ha)	Basal Area (m ² ha ⁻¹)	Density (trees ha ⁻¹)
Beaver Dam	BD	Hillslopes on moraines	Coarse-loamy	4	32.5	800
Bladder Lake	BL	Outwash plains	Sandy	13	17.5	528
Lyons Forest	LF	Outwash plains	Coarse-loamy	40	19.1	516
Lake George	LG	Flats on outwash plains, rises on outwash plains	Sandy	15	30.2	904
Midge Lake East	ME	Outwash plains, valley trains	Sandy	59	15.8	376
Nimrod Range	NR	Hillslopes on outwash plains	Sandy	10	30.1	448
Roy Lake Creek	RC	Hillslopes on outwash plains	Fine-loamy	4	21.8	444
Straight River	SR	Hillslopes on moraines	Sandy	28	16.4	408
Wolf Lake	WL	Hillslopes on outwash plains	Sandy	31	17.0	476

¹ SSURGO (NRCS 2014)

² Cummins and Grigal (1980)

Table 3.2. Jack pine residual tree-ring chronology characteristics from each study site (codes provided in Table 3.1). Tree-ring series from both living and dead jack pines were included in analysis (N = 644). A minimum of ten series were required for site-level master chronologies used for analyses (Y10); expressed population signals (Wigley et al. 1984) were all > 0.85 where n > 10. Inter-series correlation (ISC), mean sensitivity (AMS), and mean segment length (MSL) for residual tree-ring chronologies were all calculated in ARSTAN. The common time-period used for climate-growth assessment was 1949 – 2011.

Site	Series (n)	Time Period	Y10	ISC	MS	MSL
BD	85	1940 - 2012	1943	0.283	0.255	64
BL	48	1932 - 2012	1936	0.440	0.331	64
LF	97	1906 - 2012	1937	0.420	0.364	60
LG	84	1918 - 2012	1927	0.291	0.271	68
ME	77	1919 - 2011	1921	0.283	0.285	66
NR	59	1947 - 2012	1949	0.331	0.296	59
RC	66	1933 - 2012	1939	0.347	0.316	63
SR	47	1932 - 2012	1936	0.348	0.319	59
WL	81	1926 - 2012	1939	0.344	0.288	56

Table 3.3. Pearson’s correlation coefficients between recruitment chronologies (Figure 3.5) and growing-season (April – October) mean temperature (T), total precipitation (P), and moisture budget (P-PET) for each site and for the region (sites pooled). Regional recruitment was assessed for time period 1918 - 1976. The number of years (*n*) from the commencement to completion of recruitment is given. (Site codes provided in Table 3.1).

Site	<i>n</i>	Growing Season		
		T	P	P/PET
BD	19	-0.22	0.56*	0.54*
BL	19	0.31	-0.44	-0.45
LF	44	-0.1	0.3*	0.33*
LG	41	-0.26	-0.64***	-0.57***
ME	54	0.07	-0.11	-0.09
NR	7	0.96***	-0.91**	-0.92**
RC	19	0.31	0.47*	0.45
SR	21	-0.27	0.36	0.37
WL	37	-0.21	0.6***	0.58***
Region	58	0.01	0.11	0.15

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; + $p < 0.1$

Figure Legends

Figure 3.1. Study area map displaying the natural range of jack pine (Little 1971) and the locations of nine study sites and area Global Historical Climatology Network (GHCN) weather stations. Site elevations across the study ranged from 405 – 462 m a.s.l.; topography at each site is flat.

Figure 3.2. Annual (a) and monthly (b) trends in total precipitation (grey lines and bars) and average temperature (black lines) of the study area for period 1913 – 2012. In panel (a), solid lines are the annual values and dotted lines are 5-yr running mean values. Values displayed are study area means calculated from PRISM climate data downloaded for each site.

Figure 3.3. Annual mean residual chronologies (a) and sample depth (b) for jack pine series from each study sites. The raw ring-width series at each site were standardized and combined using a bi-weight robust mean to create residual chronologies. The common time-period used for analyses, where each chronology was calculated from at least ten series, was 1949 – 2011.

Figure 3.4. Summary of the number of significant ($\alpha = 0.05$) correlations and partial correlations between jack pine growth and two climate variables across nine sites. The primary climate variable is the monthly total moisture budget (P-PET) and the secondary variable is the mean monthly temperature (T). Monthly correlation values for significant and non-significant relationships can be found in Appendix 5.

Figure 3.5. Jack pine recruitment chronologies for each site (a) and the region (b). Data were smoothed using a 5-yr running mean in order to account for uncertainty of age to coring height; values were expanded by five for visualization. The number of individuals included in each chronology development (n) is given below the site name.

Figure 3.6. Response function coefficients between regional jack pine recruitment and growing season (Apr – Oct) monthly mean temperature and total moisture budget (P-PET). Black bars indicate significant relationships ($\alpha = 0.05$). Both recruitment and climate data were smoothed with a five-year running mean prior to analysis.

Figure 3.1.

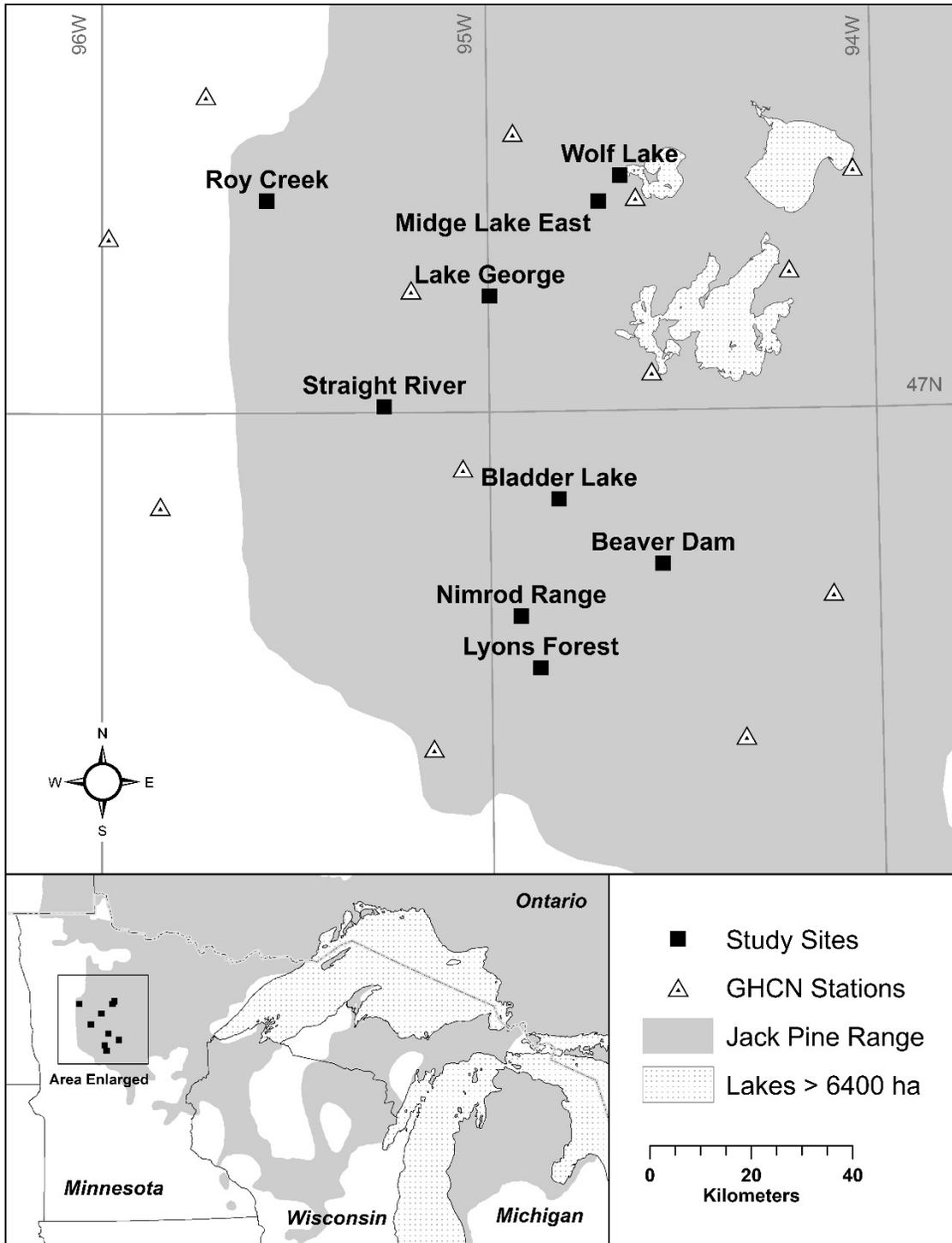


Figure 3.2.

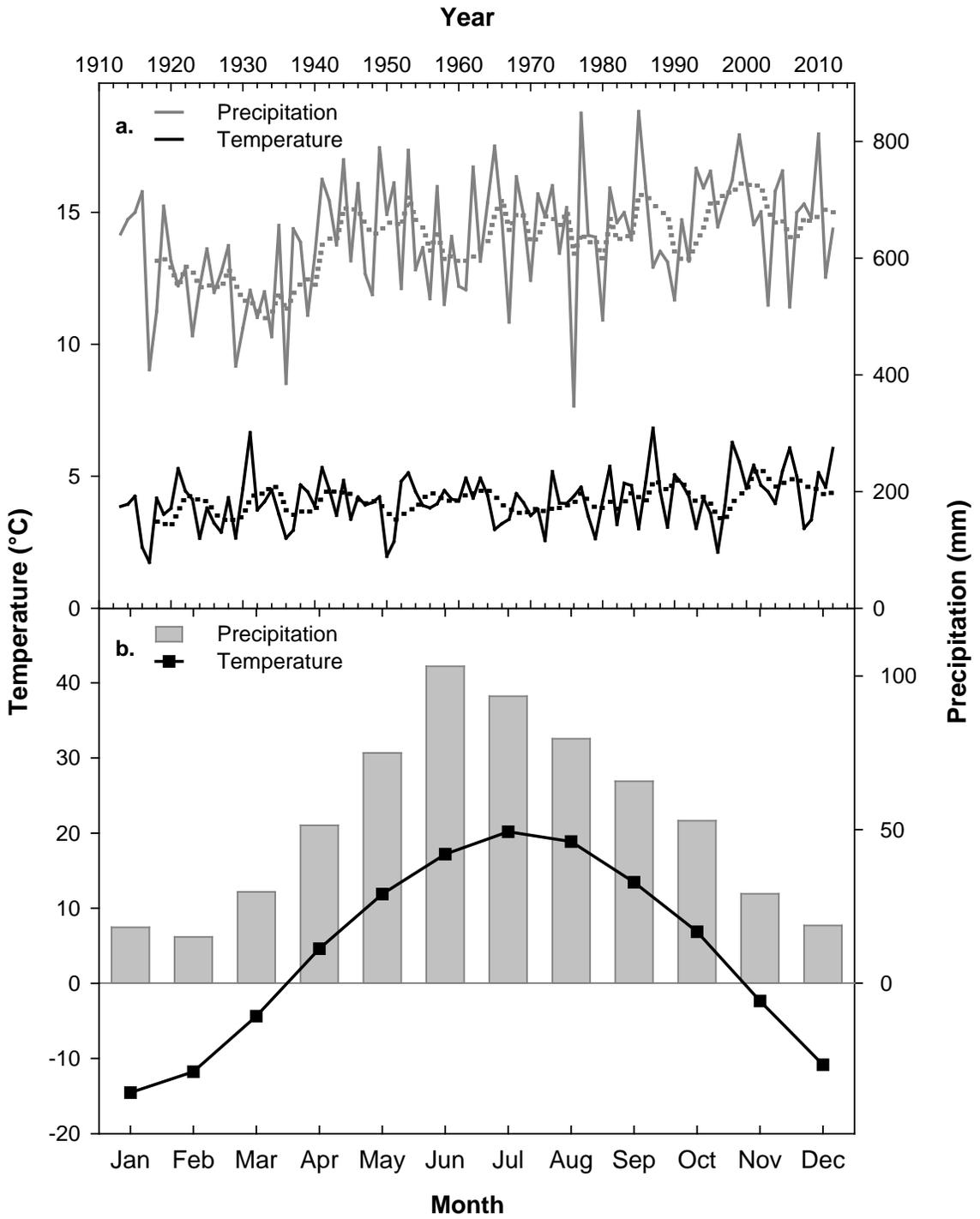


Figure 3.3.

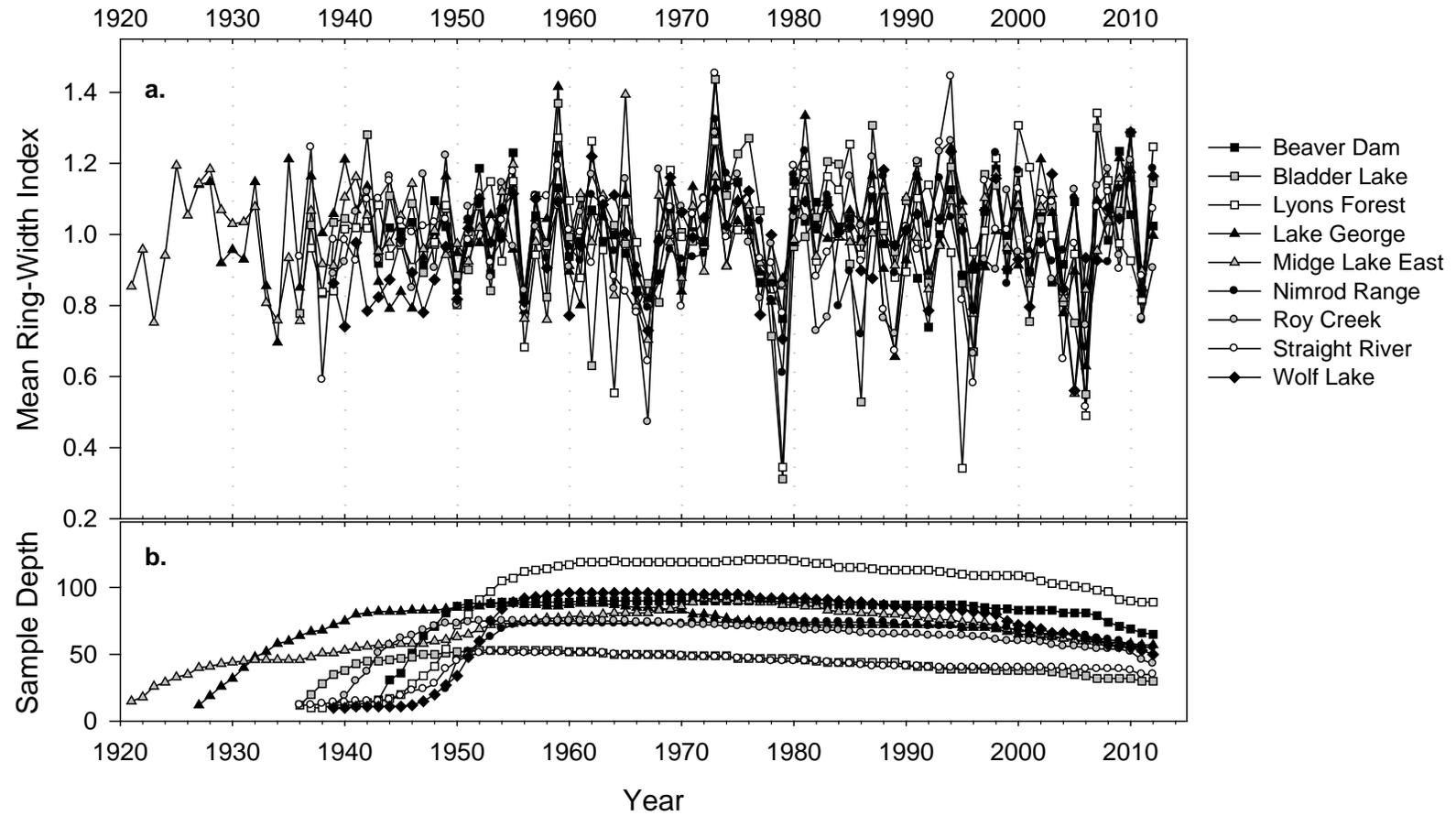


Figure 3.4.

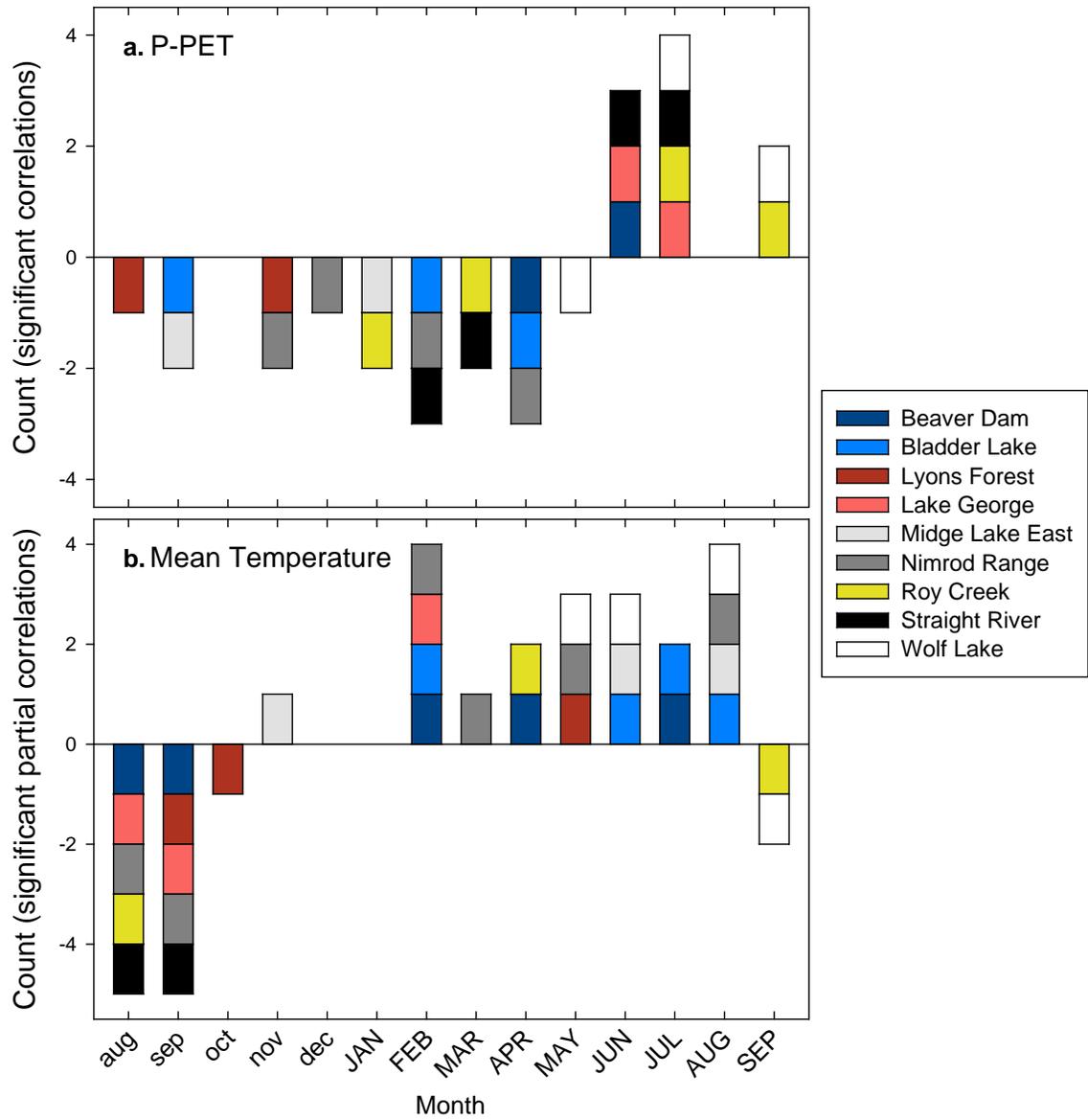


Figure 3.5.

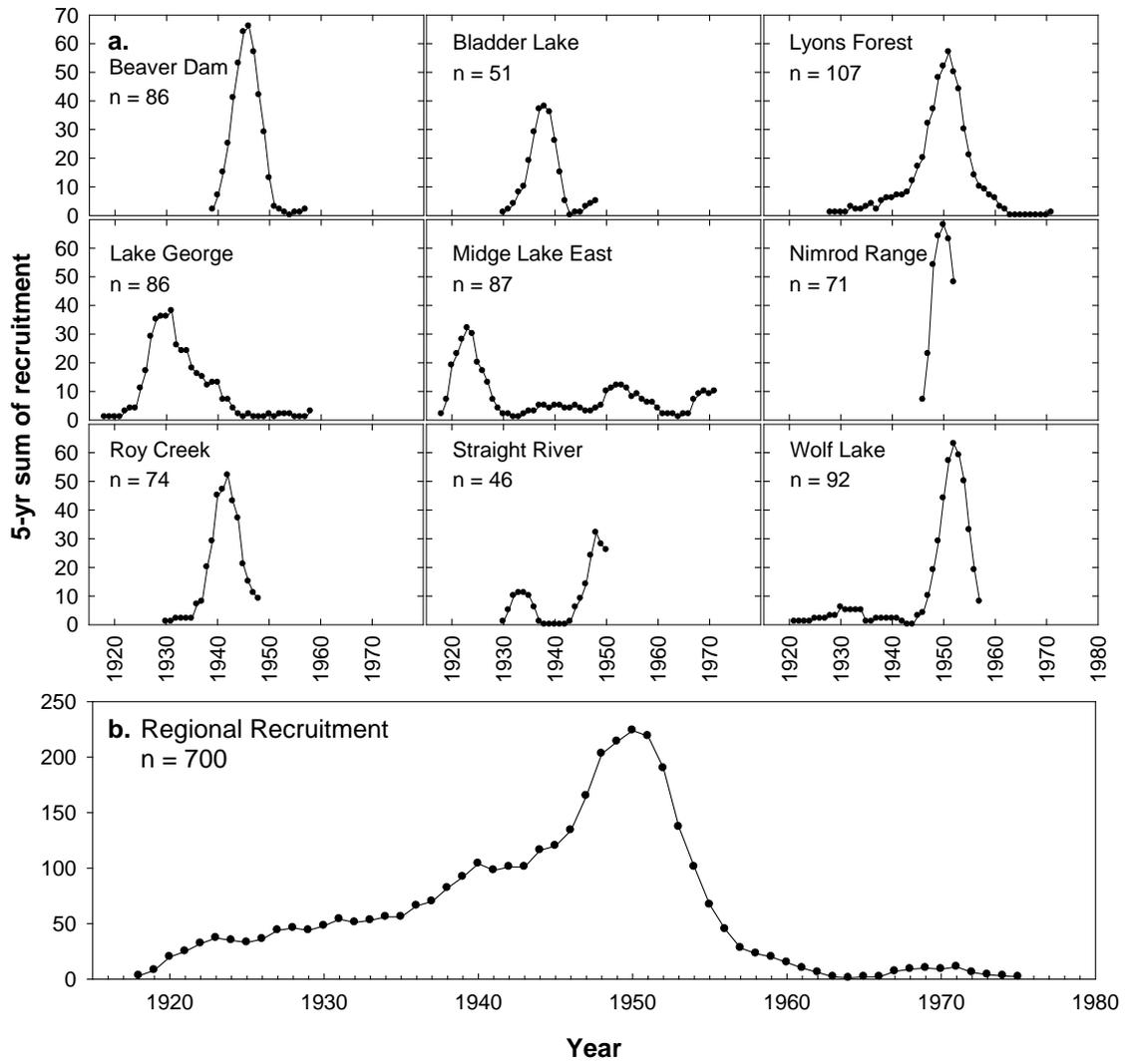
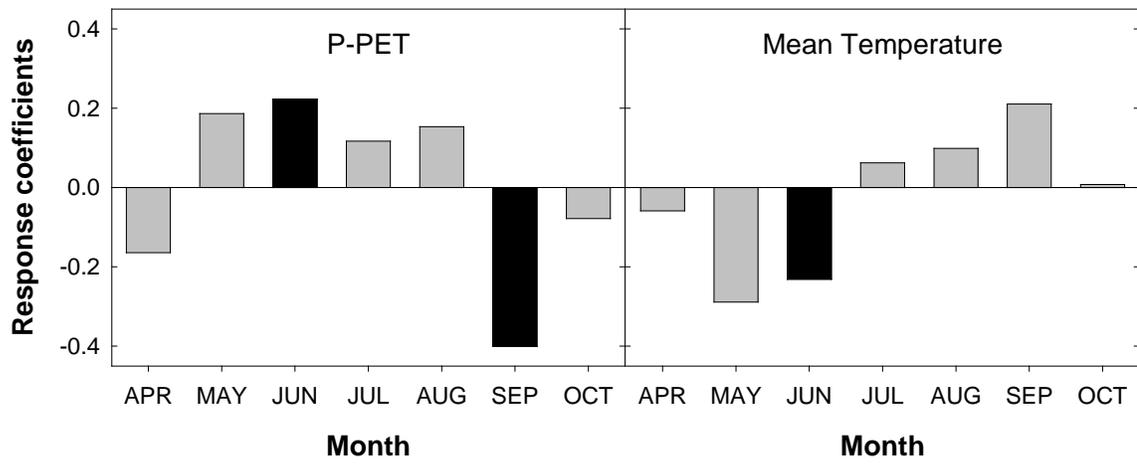


Figure 3.6.



Chapter 4: Conclusions

Collectively, the findings of this work demonstrate the natural range of variability and complexity in the range-margin jack pine (*Pinus banksiana*) forests of north-central Minnesota and the roles of climate and disturbance in shaping their development. Comparisons with other studies examining jack pine forests, particularly those in the central portion of this species' range, highlight the range-wide variability in stand development, structure, and growth and recruitment response to climate for this species. The range of structural characteristics, such as stand densities, snag abundance, deadwood volume, and spatial arrangements, in the relatively young forests examined often approximated those found in later successional forests. This range highlights the potential for high levels of early stand complexity in these systems and are reflective of a range of development patterns. Climate-growth analyses showed indirect and direct relationships with late-winter moisture and temperature, respectively, suggesting a direct relationship with the timing of dormancy release and growing season length. Additionally, growth was directly associated with moisture and temperature during the peak of the growing season. Recruitment was primarily sensitive to moisture budget but the directions of significant relationships were inconsistent among sites. Within-season examinations of this relationship showed that early growing-season cool, wet and late-season warm, dry conditions were beneficial for recruitment success. This range of relationships suggests that jack pine's future response to predicted increases in moisture deficit will be non-uniform across seasons, life stages, and the region. In both chapters, we stress that such intra-species and intra-region variability needs to be accounted for in predictive models of species distributions and forest dynamics.

Management implications

Over the past two decades, managers working with jack pine systems in this north-central Minnesota have increasingly struggled to regenerate this species on sites where it historically dominated. Chapter 2 of this thesis asks whether this is might be more related

to incongruity between the historic dynamics and contemporary use of even-aged management or the early effects of climate change along its southern range-margin. Results of this work suggest that both management and climate are contributing factors. However, the former is more readily amendable than the latter.

Because of the apparent disconnect between historic dynamics and current management techniques and goals, we suggest that managers in north-central Minnesota diminish their use of even-aged clearcutting and planting techniques in favor of managing for complex jack pine systems (Puettmann 2009). Such management approaches should allow stands to develop along multiple pathways and prescriptions are likely to include retaining heterogeneous quantities and arrangements of structural components, such as age, size, and standing and downed woody debris. Above all, managing stands for complexity requires shifting from 1) choosing a narrowly focused goal, such as full jack pine stocking within five years post-harvest, and considering a stand a failure if it does not reach such goals, to 2) selecting a variety of reasonable goals and allowing the interactions between stand conditions, management interventions, and climate to generate final outcomes so as to allow for a greater range of developmental pathways. A priority shift such as this, along with utilization of management systems suggested below, may promote increases in jack pine abundance and system success on the landscape as well as adaptive potential (Millar et al. 2007).

A critical finding of this thesis was the variation in temporal and spatial establishment patterns jack pine followed to create current mature jack pine forests. These patterns were reflective of the propensity of continuously available seed from mature jack pine to infill available growing space left from heterogeneous patterns of initial recruitment. Given these, management systems that rely on retaining mature trees as a source of propagules and heterogeneous spatial structure are appropriate. These systems can include, but are not limited to, uneven-aged variable density or seed-tree-with-reserves systems. With each of these systems regeneration establishment and success will be dependent on the

amount of passive or active soil scarification (Eyre 1938, LeBarron and Eyre 1938, Zehngraff 1943), growing season moisture, and the ability to deter browse. It is assumed that if mature trees remain on sites that have exposed mineral soil, there should be adequate seed available to promote short- (5 - 15 yr), mid- (15 – 25 yr), or long-term (25+ yr) recruitment success. This assumption is based upon results reported in this work and reports elsewhere that suggest jack pine seed availability is not limited to mast years (Burns and Honkala 1990) and new recruits, which can start to produce seed within 5-10 years of germination, can help to supplant gaps in initial regeneration (Sutton 1979) as the mature trees are removed or become decadent. Although, if short-term regeneration is desired, supplemental soil scarification and forms of artificial regeneration may be required. Pine mortality due to white-tailed deer (*Odocoileus virginianus*) browse has been noted as a major inhibitor of regeneration (Locke et al. 2007, Zenner and Peck 2009) and needs to be considered in management prescriptions. Native prairie associates should also be promoted with these silvicultural systems for both restoration and biological diversity purposes.

Multi-aged techniques, such as the individuals, clumps, and openings (ICO) method (Plotkin et al. 2002, Churchill et al. 2013) and variable retention harvest systems (Franklin et al. 1997, Franklin et al. 2007), should be further explored and utilized in the region. Our results suggest that when these methods are employed, openings as small as 100 m² could be sufficient for jack pine regeneration if appropriate seedbed conditions are present. The actual size of gaps should vary and will depend on the height and position of the surrounding mature trees, in order limit shading effects. In order to mimic the range of spatial patterns observed in our study, mature trees ranging from single, open-grown and wind-firm, individuals up to clumps of around 400 m² should be retained. Many of the sampled stands had individuals with large lower limbs that were likely site pioneers that were gradually joined in the canopy by their own progeny, suggesting that low initial density is not detrimental to long-term stand development (sensu Tappeiner et al. 1997, Donato et al. 2012). These uneven-aged techniques will

likely result in stand structures ranging from moderate density, interrupted canopy woodlands to high density stands with contiguous canopies. Prescribed burning, or other soil-scarification and understory competition reduction techniques, should be used in accordance with these systems to promote pine regeneration and curtail demographic transition to deciduous forests or shrublands.

Additionally, uneven-aged seed-tree-with-reserves and even-aged seed-tree silvicultural prescriptions should also be increasingly utilized in the region, especially given the non-serotinous nature of a majority of cones. These systems are suggested in management guides (e.g., Benzie 1977) and have been historically successful but are presently underutilized. Successful implementation of these techniques, along with site preparation by surface fires, has been documented in Saskatchewan (Chrosiewicz 1988) and elsewhere (Cayford 1967). The two-aged stand observed in our study (Straight River) suggests that these silvicultural systems would resemble natural stand development patterns. As mentioned earlier, adequate soil scarifying site preparation that exposes mineral soil is a key to the regeneration success of jack pine.

Clearcutting-based systems that rely primarily of planted jack pine have been the primary approach to managing jack pine over the past few decades. The findings of this work indicate that there are historic developmental pathways that are consistent with this regeneration method; however, results also indicate that expectations of temporal regeneration success or failure need to be updated. Results from recruitment window analysis indicate that natural regeneration of jack pine in the region is rarely fully-stocked within five years, as only one of our sites followed this temporal trend; the three other even-aged stands in our study appear to have been adequately stocked within 8 - 15 yr. This result, in conjunction with the widely observed stands originating from the fires of 1959 and 1976 near Badoura, Minnesota, indicates that relatively quick stand regeneration is a possibility in the region. However, a majority of our stands displayed protracted recruitment windows ranging from 18 – 50 yr. Most of the even- and uneven-

aged stands in our study would have likely been deemed a regeneration failure if they had been assessed at five years. This would be understandable in cases where timber product production was the only goal for the site. Although, when alternate goals, such as restoration of historical conditions, promotion of wildlife habitat and biodiversity, or creating complex, adaptive systems, are desired, time must be given for alternate stand development pathways.

Study limitations and future research

Our study included four of the five fire dependent native plant communities (NPC) of central Minnesota that can have jack pine as a major canopy component (Table 4.1); FDC34 communities were excluded because jack pine is thought to be more of a short-term canopy associate than a canopy dominant. The NPC of each study site as classified based on plant presence or absence following the dichotomous key for fire dependent communities of the Minnesota Drift and Lake Plains ecological section (Aaseng et al. 2003); even- and uneven-aged stands did not follow a noticeable pattern with community classifications, although all of the FDC23 stands were uneven-aged. Trends between structural attributes and community types were not assessed but should be in the future, potentially using ordination techniques such as nonmetric multidimensional scaling (cf. D'Amato and Orwig 2008).

Locating study sites that met the criteria for our study was a major challenge and could have resulted in us studying stands that do not adequately represent current regional jack pine forests. As recorded in our methods sections for both research chapters, we narrowed our sites down from a list created by a query of the Minnesota DNR's Forest Inventory and Modeling database. This high initial number (128) was likely inflated by the database search criteria, which included that a stand needed to have canopy and understory pine representation and be on file as at least 70 years old. Many of the stands included in this initial list had red pine as the major species and in many cases were confirmed to have no jack pine present after field visits. These areas likely had already

transitioned from jack pine communities preventing us from including them in our study. Similarly, the extensive history of logging and forest management in the area precluded many stands, even those that were younger, from being included and potentially capturing a greater range in development dynamics for these forests. Our sample represent some of the oldest jack pine stands region at the time of sampling and, given the increasing rarity of this condition on the landscape, provided a unique opportunity to document the recruitment patterns and climate relationships of this forest type before even fewer areas remain. Future studies that relax site-selection criteria, or include stand management history as a variable, may include a better representation of stands that are on the landscape in higher abundances; however, the ability to quantify the relationships between climate and growth and recruitment would be limited due to lack of temporal sample depth.

We did not quantify cone serotiny in our stands but assumed a certain level of non-serotiny played a role in observed age structures. The degree of serotiny in stands, as well as a plethora of other traits, were well documented across jack pine's range by Schoenike (1976). Although north-central Minnesota had one of the lowest abundances of serotinous cones, it should not be assumed that all cones in this region are non-serotinous.

Generalized assumptions such as this lead to a loss of appreciation of variability and are why jack pine forests are only expected to follow the "even-aged, post-catastrophic fire" dynamic. Just like any inheritable trait, serotiny is highly dependent on genetics. As such, the natural pattern of dynamics, which can affect parent mortality, growing conditions, and recruitment opportunities, plays a large role in determining the serotiny levels of progeny and the population (Gauthier et al. 1996, Radeloff et al. 2004). High-density, post crown fire recruitment has been observed within the study area, most notably after major fires near Badoura, Minnesota in 1959 and 1976. This suggests that serotiny is not totally absent in the region. Further documentation of the range of variability in this trait within the region, and others, would aid managers in determining proper expected regeneration outcomes following harvests and site preparation.

Ideal stands for dendroclimatological studies usually do not have closed-canopies (Speer 2010). A closed canopy generally results in competition between trees for resources, which can hinder the climatological sensitivity of the trees within the stand. We attempted to eliminate this competition signal through standardization prior to dendroclimatological assessments, but it is probably not possible to eliminate this entirely. Regardless, the range-margin proximity, sandy soils, and low densities of many of our stands allowed our trees to be quite sensitive to climate. The region shows promise for future dendroclimatological studies because of the xeric soils and low density stands. However, sites would need to be selected for this specific purpose and jack pine is not an ideally suited species due to its short-lived nature.

Our recruitment data was slightly limited by not being able to assess trends on an annual basis. Our age data was very reliable given most of the trees in our study were relatively young and 91% of our 1645 trees were ≤ 5 rings from pith. Even so, because cores were collected at 30 cm above the ground (cores collected > 30 cm were excluded from analysis, $n = 31$) we were still missing an uncertain number of years of growth, which is why we utilized the 5-yr running mean technique for recruitment data. The samples for developing an age-to-coring-height regression (cf. Gutsell and Johnson 2002, Fraver et al. 2011) have been collected but not fully processed or analyzed. Developing this relationship will allow us to refine our recruitment window analysis as well as climate-recruitment relationships.

Another future line of research would be to further explore input variables of the climate-recruitment response-function analysis technique. Although I feel these results are reliable, one area of improvement would be to utilize the aforementioned refinement of germination date. This improvement would allow us to pinpoint specific germination years and examine the climate data in those years to see if there are any key factors that make it a particularly good year for germination. Refinements such as these may be very

beneficial for predictive modeling purposes. Another improvement that could be made would be to include climate of the years following recruitment in analysis. Just as the climate of prior years is very important to tree growth, it could be that the climate of the two to four years following germination is as important as the year of germination. For this study, climate and recruitment data were treated with a 5-year running mean given we were working with recruitment data and seed germination likely occurred years prior to the actual recruitment date. Once germination dates were determined, as outlined above, analyses that included the climate of the years following germination could be explored to determine the role of climate during years of from being a germinant to an established recruit.

Table 4.1. Native plant communities (NPC, Aaseng et al. 2003) of north-central Minnesota that include jack pine as a canopy component, their NPC code, and the study sites designated as each of these communities. The NPC of sites was designated in the field based upon plant presence and abundance.

Native Plant Community	NPC Code	Study sites
Northern Dry-Sand Pine Woodland	FDn12	Beaver Dam
Central Poor Dry Pine Woodland	FDc12	Lake George
Central Dry Pine Woodland	FDc23	Lyons Forest, Midge Lake East, Midge Lake West
Central Rich Dry Pine Woodland	FDc24	Bladder Lake, Nimrod Range, Roy Creek, Straight River, Wolf Lake
Central Dry-Mesic Pine-Hardwood Forest	FDc34	(excluded)

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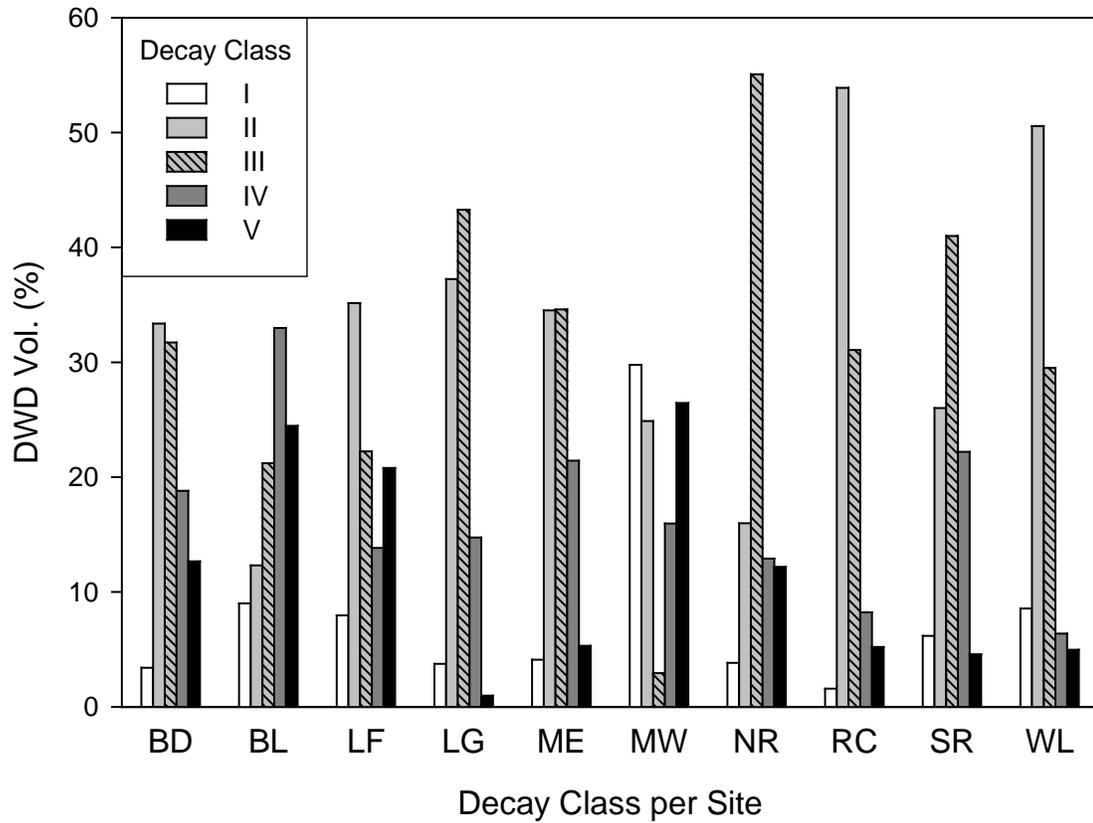
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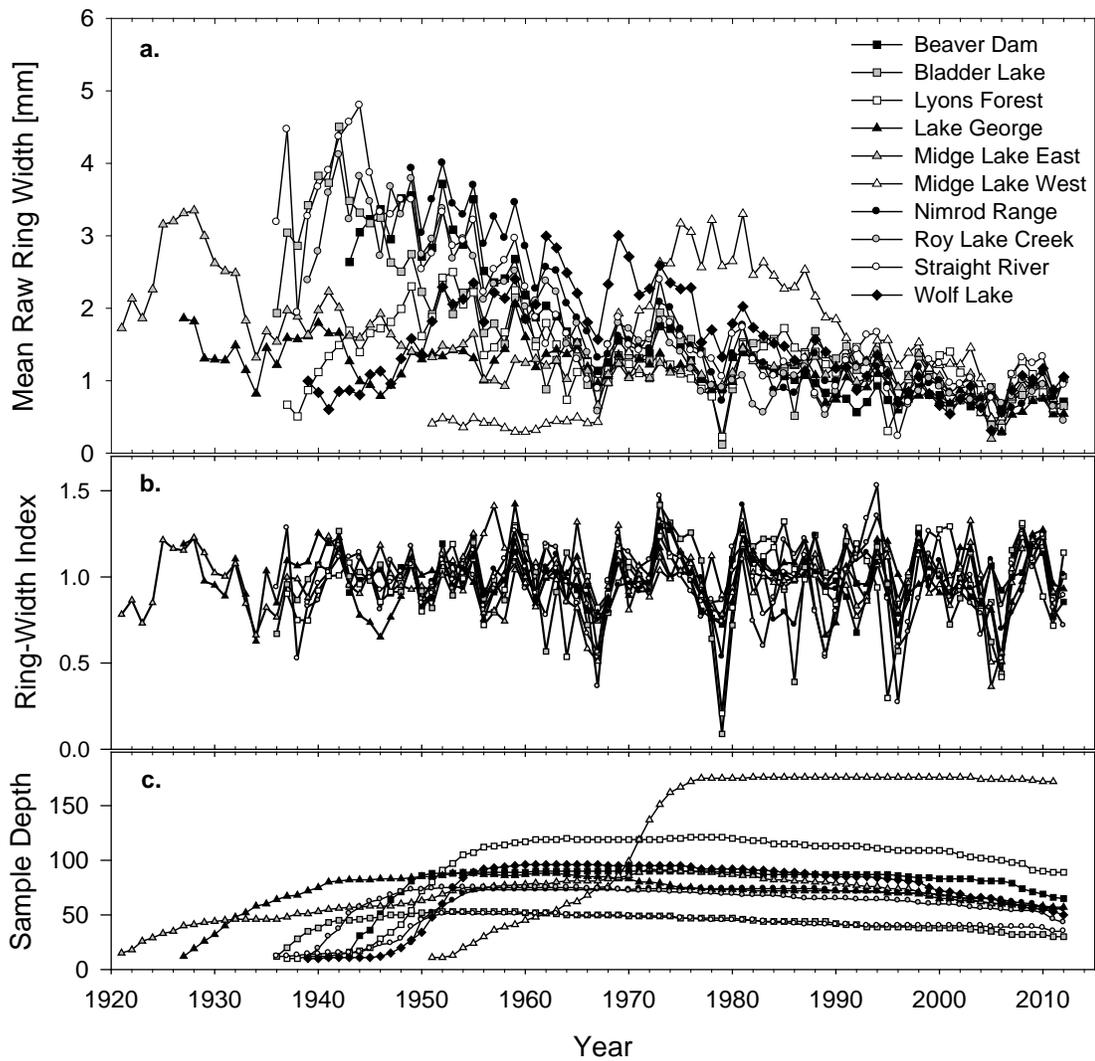
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Appendix 1.



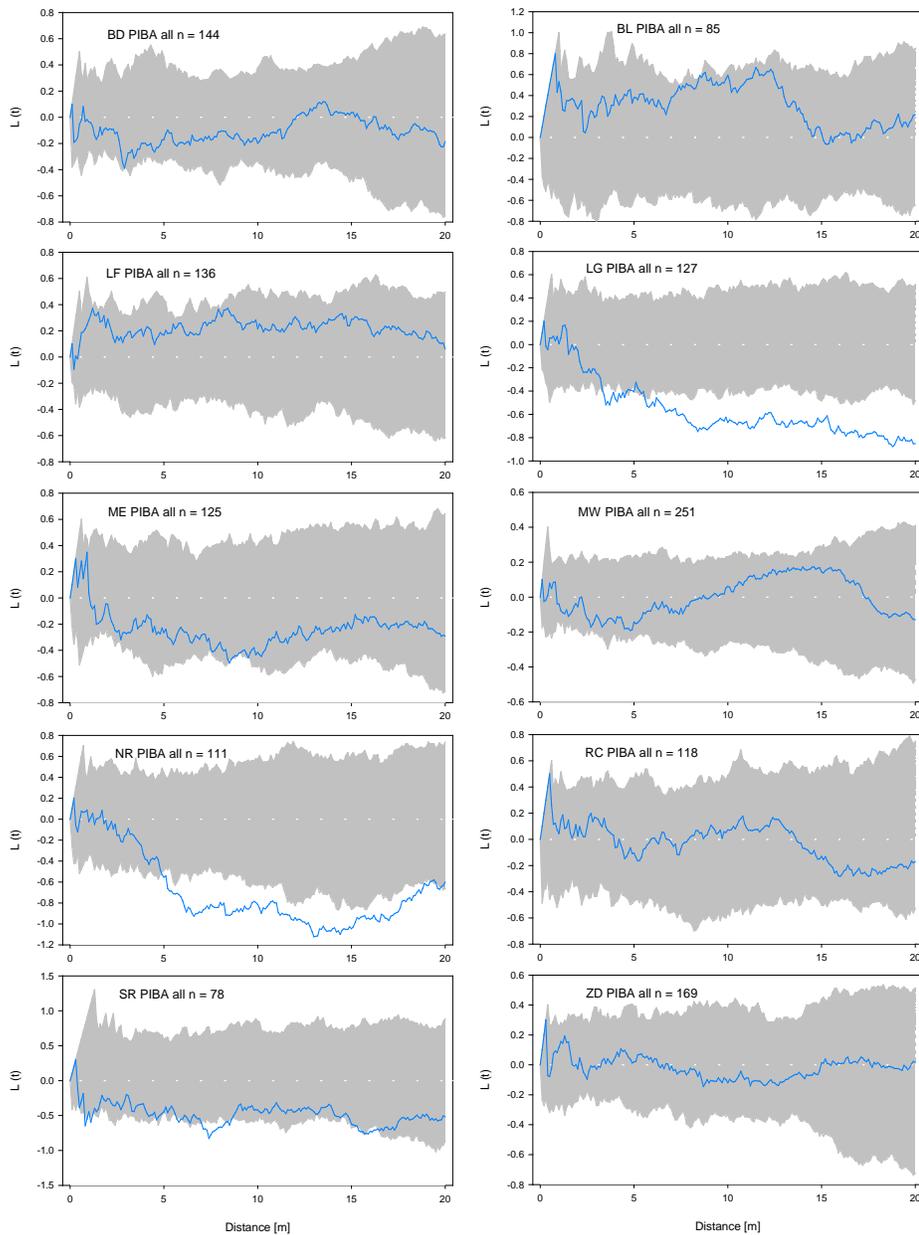
Percent volume distribution of downed woody debris (DWD, $n = 456$ intersections) per decay class at each range-margin jack pine site. See Table 2.1 for site codes and Table 2.2 for total volume at each site.

Appendix 2.



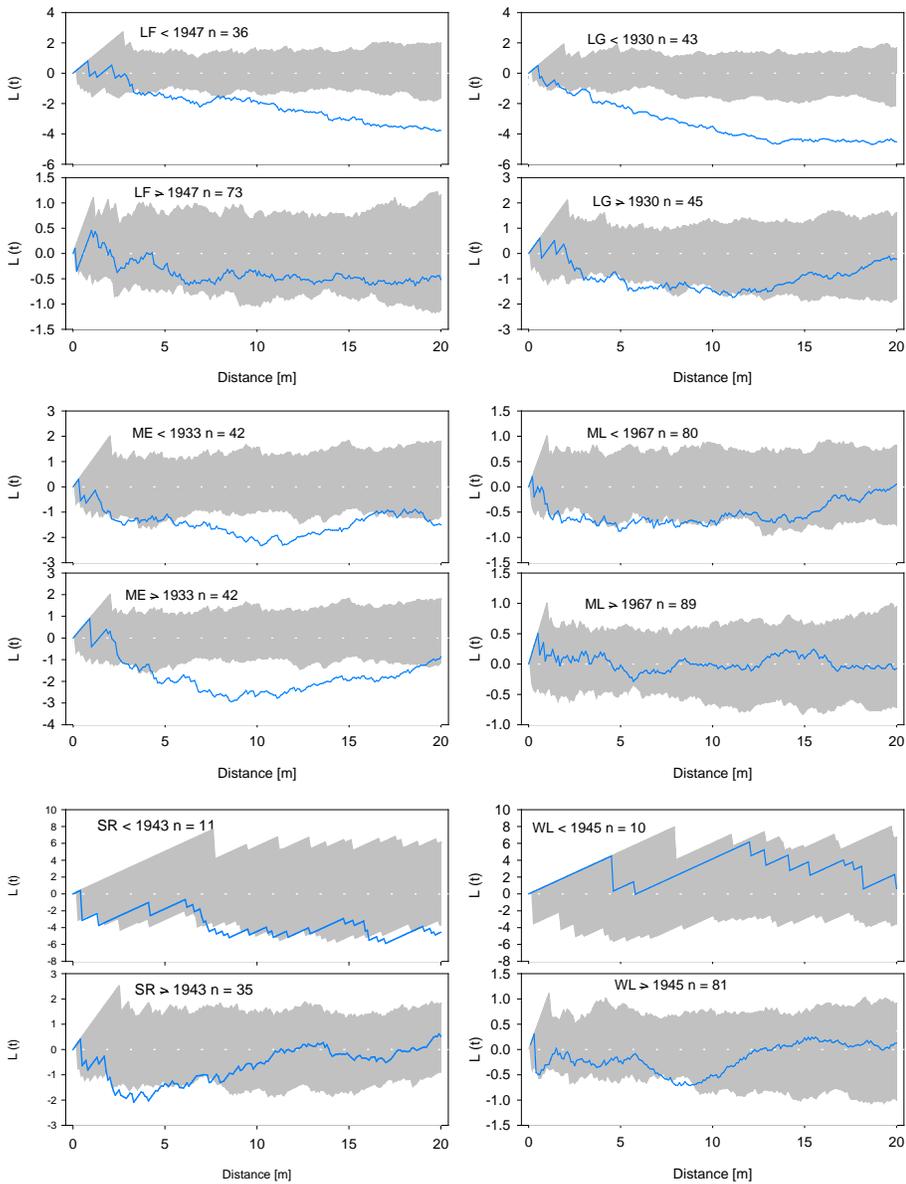
Annual mean raw ring-width chronologies (a), standardized chronologies (b), and sample depth (c) for jack pine tree-ring series at each site ($N = 926$). The raw ring-width series at each site were standardized and combined using a bi-weight robust mean to create standard chronologies.

Appendix 3.



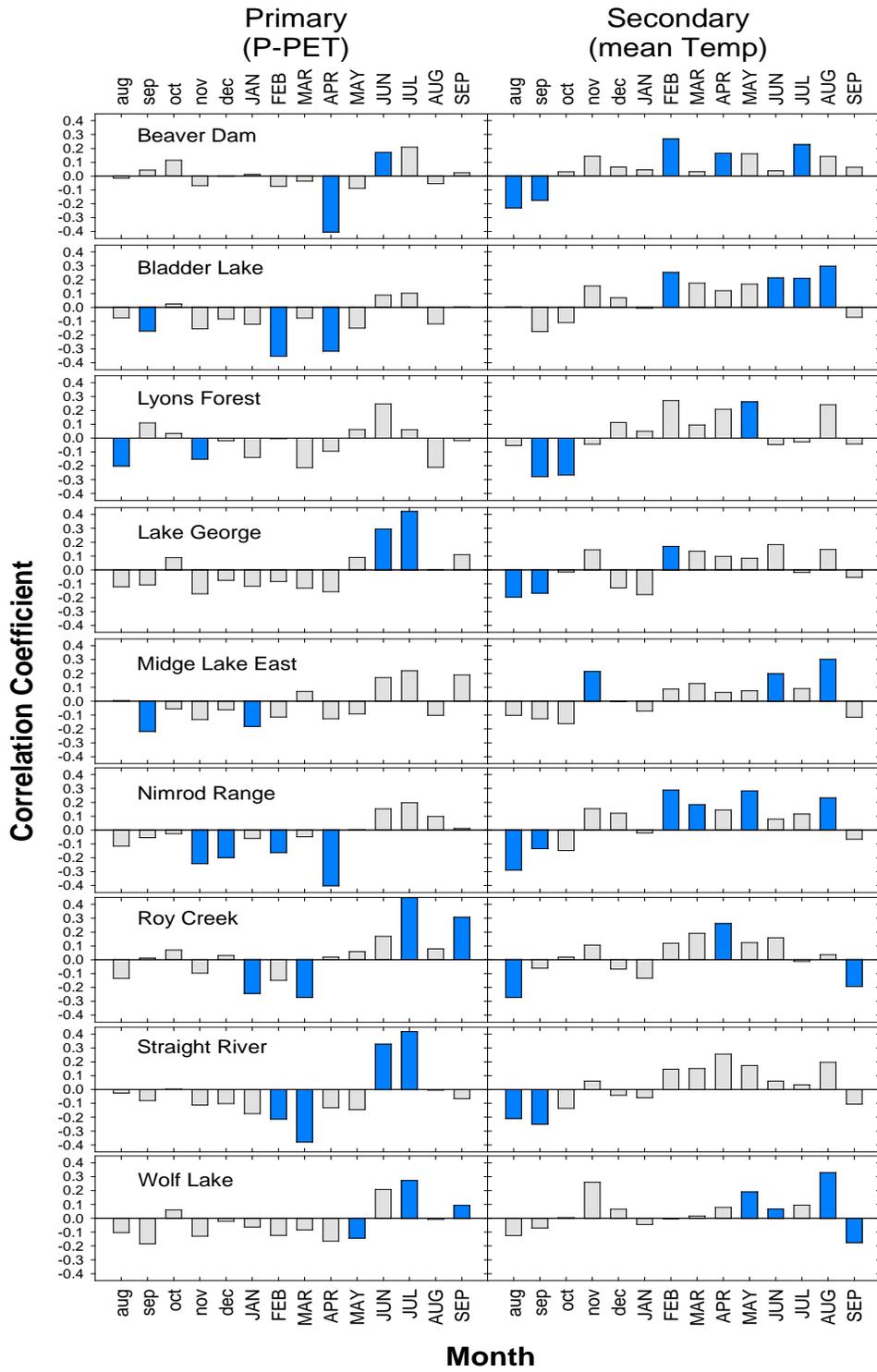
Output for Ripley's $L(t)$ (transformed $K(t)$) assessments of all living and snag jack pine (PIBA all) trees at each site. Grey bands are 95% confidence intervals of the null hypothesis of random arrangement. Positive and negative values outside of this band are indicative of uniformity and clumping, respectively (same for below).

Appendix 4



Output for Ripley's $L(t)$ (transformed $K(t)$) assessments of jack pine stem locations at sites with extended recruitment windows or multiple cohorts. Stems were separated into first and second recruitment groups based upon cohort separation, median recruitment date or an obvious break in recruitment near the median recruitment date (listed after site name).

Appendix 5



Appendix 5. Correlation and partial correlation coefficients between jack pine growth chronologies and the primary (moisture budge [P-PET]) and the secondary (mean temperature) climate variables, respectively, for each site. Residual radial growth chronologies were assessed against a 14-month climatic window from August of the prior year (lower case) through September of the concurrent year (upper case). The directionality of bars indicates either positive or negative associations with a given climatic variable; blue (dark) bars indicate significance of a relationship ($\alpha = 0.05$) as calculated by 1000 bootstrap iterations.