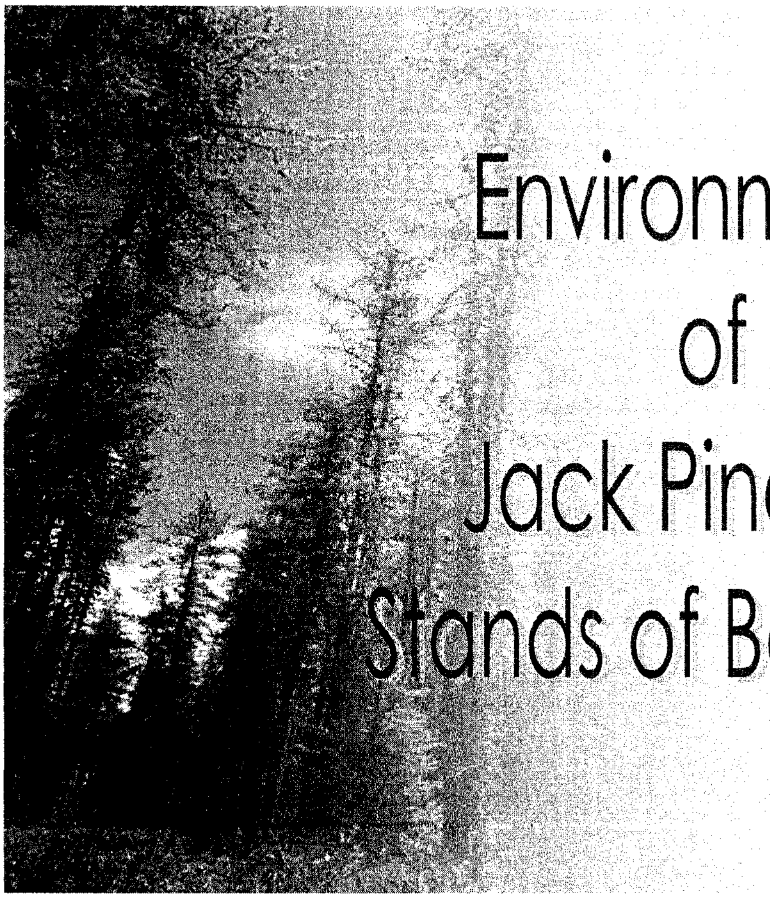

Environmental Drivers of Succession in Jack Pine-Dominated Stands of Boreal Ontario

by

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ABSTRACT

Longpre, Trevor W.F. 2007. Environmental drivers of succession in jack pine-dominated stands of boreal Ontario. 94 pp.

Key words: photo chronosequencing; stand; change through time; jack pine; non-parametric; regression trees; survival analysis; synecology; succession; sand; slope; precipitation.

Spanning boreal Ontario, photo chronosequencing was used to observe change through time in 178 stands comprised at least in part by jack pine (*Pinus bansiana* Lamb.). Linked to growth and yield monitoring plot networks and a national climate model, observed succession was associated to 17 environmental attributes specific to geographic location, topography, soil conditions, and climate. Through the application of two non-parametric analytical techniques: regression trees and survival analysis, three fundamental ecological relationships to succession were identified. Deep sands were found to be the most influential ecological driver of succession in jack pine-dominated stands of boreal Ontario, followed by slope gradient and precipitation during the growing season. Derived cumulative survival probability functions for each of these variables offers tangible means by which forest forecast models in the region can be empirically refined.

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The research presented in this report could not have been achieved without the enormous latitudes granted me by my advisor, Dr. David Morris. He allowed me to identify and explore my subject of choice in an independent manner, and provided oversight when it mattered most – all to the betterment of the final product.

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This project was undertaken in partnership with the Forest Ecosystem Science Co-operative, and the Ontario Ministry of Natural Resources (OMNR). The resources and funding provided by both organizations ensured the success of the research.

Special thanks goes to Adam Rudzki and his colleagues of the OMNR's FRI Program who for six months, mentored my training in aerial photo-interpretation.

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Of course, the support of my beautiful wife Tara strengthened my resolve to continue on the road less travelled, to invest more time in exploring a subject with which I was fascinated, when in all truth any other project would have taken half as long. Her pride in me, and loving smile has been the true payoff.

FOREWARD

This thesis has been prepared for Lakehead University in conjunction with a forthcoming technical report prepared for the Forest Ecosystem Science Co-operative. This thesis is focused upon the ecological drivers of forest succession, and presents a literature review, and discussion in support of that topic. The technical report provides explicit detail on the sampling methodology, and management-oriented results of survival analysis.

Longpre, Trevor W.F. 2008. Natural succession of jack pine-dominated stands in boreal Ontario. Forest Ecosystem Science Co-operative [In Prep.]

INTRODUCTION

While it is among the most common tree species in boreal Ontario and has a long history of study, knowledge of jack pine (*Pinus banksiana* Lamb.) succession and its relationship to environment remains predominantly qualitative.

A sound understanding of forest succession is an integral component of Ontario's current forest management planning process. This process mandates determinations of ecological sustainability, the availability of wildlife habitat, and of continued industrial wood supply to be supported by forecast models that extend for 160 years and more. Despite this reliance however, forest planners and practitioners often rely on professional opinion to generate the quantitative inferences of forest succession required by the forecast models; inferences which they themselves admit to holding little confidence. Where empirical evidence does exist to support their inferences, it is often of limited use when considering the breadth of variation typical to boreal Ontario; variation in soils, landform, vegetation, climate, geography, time-since-last-disturbance, as well as forest structure. This knowledge is further diluted as forest management planners and policy writers employ increasingly tactical models in their endeavours; models which require explicit detail regarding ecological function.

While agreement exists amongst researchers that repeated measures of forest sample plots is the best method by which empirical determinations of forest succession should be derived, the logistical implications of such an approach and the urgency of demand for the knowledge lead researchers to explore alternative means of study. A methodology is presented herein that offers a logistically-effective means by which stand succession can be observed, and by which empirical summaries of successional trends can be determined. Using this methodology, associations between environment and succession in jack pine-dominant stands are studied, and three fundamental ecological relationships are identified.

CONCEPTS AND THEORY OF FOREST SUCCESSION

Henry D. Thoreau, a notable literary figure of the 19th century and an avid naturalist essayed one of the earliest works on forest succession entitled "The Succession of Forest Trees", which he read to the Middlesex Agricultural Society in 1860 (Thoreau 1887). Intrigued by the comments of local farmers who noted that pines harvested from their woodlots were often replaced by oaks, and vice versa, Thoreau presented a case for his hypothesis that succession was chiefly influenced by seed dissemination vectors (wind, water, and animals), conifer seedbanks, canopy gaps and relative differences in shade tolerance. However, lauded as among the most prominent of American Transcendentalists[1] (Reuben 2007), Thoreau's thoughts on succession were never targeted towards-, nor apparently adopted by the scientific community.

During the close of the 19th century, botanists Warming (1896) and Cowles (1899) studied sand dune development. Their observations formally spawned the ecological concept of succession; elaborated early in the 20th century by Clements (1916, 1928, 1936) in the first tabled theory on plant succession. Clementsian theory held that following disturbance, a series of predictable changes occur in the form of invasion onto the site by 'pioneer' species, which are then gradually replaced by

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[1] American transcendentalism was a counter-culture movement started in New England during the mid-19th century that protested both religion of the Unitarian Church and intellectualism at Harvard University. The American transcendentalist philosophy was based in intuition of the individual and the divinity of nature.

increasingly shade-tolerant species until a community monoclimax state is achieved. This climax state remains the dominant condition, until another disturbance event occurs, therein returning the site to its starting condition.

Gleason (1926), a contemporary of Clements, proposed an alternative successional model, wherein a plant community is nothing more than a fortuitous assemblage of species populations, where species replacements occur on a plant-by-plant basis – driven by differences in relative life-histories, and where stochastic processes predominate. Cooper (1926) dissented against both theories, disagreeing with Clements' characterization that a plant community in a climax state was itself an "organic entity, with structure and functions corresponding to those of an individual organism", but stopped short of agreeing with Gleason that phenomena of the individual is paramount. Cooper (1926) also disagreed with Clements and Gleason's shared stance that disturbance was not an integral part of succession, weighing into the debate with a solution he described as "simplicity itself: succession being the universal process of vegetational change, all vegetational changes must of necessity be successional."

Clements and Gleason's theories dominated thinking on forest succession for much of the 20th century, with subsequent studies typically only suggesting alterations so as to account for inconsistencies found during local tests. For example, Tansley (1935) challenged the existence of a monoclimax, suggesting that multiple climax states (or polyclimax) result due to differences in edaphic factors, physiography, or disturbance. Whittaker (1953) suggested a third climax theory, where climax gradates as a function of population patterns. Early deviations from Clements and Gleason's theories were the models proposed by Watt (1947), and Egler (1954). Watt (1947) urged greater consideration of dynamic principles in studies of succession, himself suggesting that succession could be best captured not by focusing on the individual, or the community, but on dynamically-related "patches (or phases)" of vegetation that occur at scales between these extremes. Egler (1954) proposed the 'initial floristic composition' model, suggesting that succession was directly influenced by propagule availability at the site following disturbance, which itself was influenced by site history, species life histories, and stochastic factors.

As the 20th century progressed, the Clementsian theory became increasingly dismissed (for example, by McCormick 1968; Connell 1972; Colinvaux 1973; Niering and Goodwin 1974; McCune and Allen 1985; McCune and Cottam 1985) with ecologists ascribing more and more to variations and combinations of the Gleason, Watt, and Egler theories. Drury and Nisbet (1973) explained the phenomena of succession as consequences of differential growth, differential survival, and differential colonizing abilities of species adapted to grow at different points along environmental gradients – where the appearance of successive replacement of one community by another is the result of the first group of plants temporarily suppressing slower-growing successors. Cattelino *et al.* (1979) explored the adaptive traits of species persisting through a disturbance, as well as species responses to variation in disturbance periodicity; this 'vital attribute' model was refined further by Noble and Slatyer (1980). Huston and Smith (1987) presented the 'life history and competition' model, arguing that integrated understandings of natural systems at the population, community, and ecosystem levels can only be derived by individual-based models that consider both life history, and physiological traits.

Notable alternative theories were proposed by Pickett (1976), Connell and Slatyer (1977) and Tilman (1985). Pickett (1976) adopted a recommendation by Drury and Nisbet (1973) and tabled a theory of succession that was based on the genetic and evolutionary characteristics of species. Connell and Slatyer (1977) presented three alternative models of succession: facilitation, tolerance, and inhibition. The 'facilitation' hypothesis was similar to that of Clements (1928), where one species alters its environment to the point where another becomes better suited to the site, but differs from classic theories in that it recognized no climax or steady state. The 'tolerance' hypothesis was based on species life history, where relative competition and resource-use efficiencies dictate species dominance. And the 'inhibition' hypothesis had its basis in the ability of an initial cohort to prevent the establishment of successors onto the site. Here compositional change only occurred when the initial cohort died. An extension of the 'tolerance' model, Tilman's (1985) 'resource-ratio' hypothesis was that succession is driven by each species' competitive efficiencies at a given ratio of soil nitrogen (and other soil nutrients) to light – which themselves were inversely proportional, and changed in response to community development.

More recently, Cook (1996) contended that the modern concept of succession is in a continuing state of definition, but that while theories formulated throughout the 20th century are no longer wholly ascribed-to, commonalities amongst them have come to form the core of current understandings of succession. These tenets of modern succession theory include: 1) disturbance (e.g. fire, windthrow, insect herbivory) is an integral component of vegetation dynamics; 2) stochastic factors play a significant role in forest succession; 3) species life history, vital attributes, and evolution are also influential; 4) mechanisms driving succession can vary in both time and space, and more than one mechanism may be operating simultaneously; and 5) multiple successional pathways are possible.

METHODOLOGICAL APPROACHES

To date, two approaches to studying forest succession have been implemented. The first approach documents forest change by replacing time with space; observations of numerous subjects in space, having similar measured or contrived attributes, are likened to the pattern of a single subject were it observed through time. Researchers using this approach do so under the assumptions that there exists only one underlying successional trajectory; that variability in site does not influence said trajectory; and that observing numerous subjects in space, is indeed synonymous to observing a single subject through time (Pickett 1988). Bias is a limitation of this approach, as the researcher subjectively identifies which candidates belong to the successional trajectory being observed, frequently excluding stands that bear little resemblance to the preconceived trajectory, when some may in fact be early- or late-successional artefacts of the studied trend.

Under the 'space-for-time' approach, two general methodologies are adopted: 1) a 'census' methodology; and 2) an 'attribute-sequencing' methodology. The 'census' methodology generates inferences of forest succession based upon detailed stem-, or attribute-mapping (e.g. stem diameter distribution) of one or few stands, and assumes succession has linear association to the attribute gradient (as used by Zoladeski and Maycock 1990; Frelich and Reich 1995). This methodology may alternatively employ ordination techniques to identify potential relationships that exist between vegetation and environment (as used by Kenkel 1986; Watson 1997; Kenkel *et al.* 1998; Caners 2001). The 'attribute-sequencing' methodology generates inferences of forest succession by comparing stand characteristics, as they vary, when large numbers of similar stands are sequenced (usually in ordinal space) according to the gradient of one or more attributes (as used by Carleton and Maycock 1978, 1980; Cogbill 1985; Bergeron and Dubuc 1989; Desponts and Payette 1992; Bergeron 2000; De Grandpré *et al.* 2000; Gauthier *et al.* 2000; Caners 2001; Gutsell 2001; Hill 2004). Examples of sequenced attributes include: age gradients[2], time-since-disturbance gradients, size-class gradients, species importance value gradients, and stem diameter gradients. A hybrid of the 'census' and 'attribute-sequencing' methodologies is also possible.

While it is the most common approach in the literature, the assumptions inherent to the 'space-for-time' methodologies are questionable, and may lead the researcher to draw inaccurate conclusions (Pickett 1988; Kenkel *et al.* 1998; Gutsell and Johnson 2000; Caners 2001; Gutsell 2001; Hamel and Kenkel 2001). Contrary to the inherent assumptions of 'space-for-time' methodologies, researchers have repeatedly concluded that stands of different ages did not form clear successional sequences (Clayden and Bouchard 1983); site has been repeatedly shown to influence successional trajectory (Shafi and Yarranton 1973; Bergeron and Dubuc 1989; Bergeron and Dansereau 1993; Fastie 1995; Kenkel *et al.* 1998); and multiple successional pathways have been documented within a community-type and on similar sites (Fastie 1995; Kenkel *et al.* 1998; pers. comm. Vasiliauskas 2005[3]). Unless an experimental design expressly addresses such assumptions, the potential exists that inferences drawn from said analyses will be limited in inference space and application (Gutsell and Johnson 2000; Caners 2001; Gutsell 2001).

The second approach to studying forest succession is to study change through time. Hamel and Kenkel (2001) stressed that "repeated observations in the same stand

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[2] Age gradient sequencing is often referenced by authors under the misnomer: chronosequencing.

[3] Unpublished manuscript (on-going research): Natural successional dynamics of boreal forests in northeastern Ontario. Ontario Ministry of Natural Resources; Stan Vasiliauskas, 2005.

over time, are required to unequivocally describe forest [dynamics]." Under the 'change-through-time' approach two general methodologies have been adopted: 1) a 'stand reconstruction' methodology; and 2) a 'chronosequencing' methodology.

The 'stand reconstruction' methodology (as used by Desponts and Payette 1992; Gutsell and Johnson 2000; Hamel and Kenkel 2001; Gutsell 2001) uses recorded measures of living and dead vegetation on a plot to estimate a stand's composition and structure at previous points in time. One strength of this approach is that it makes no assumptions regarding the replacement sequence of trees, thus enabling depictions as to when some individuals in a stand were recruited or died (Gutsell and Johnson 2000). However, since this methodology is dependent upon dead and decomposing vegetation, the state of decomposition and the varying rates of decomposition by species limits accuracy when reconstructing a stand beyond a relatively small time frame (Desponts on Payette 1992; Gutsell 2001). Irrespective of stand age, Johnson and Fryer (1989) found the reconstruction limitation in lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. ex Loud.)-Englemann spruce (*Picea engelmannii* Parry ex Engelm.) forests to be roughly half the age of the stand.

The 'chronosequencing' methodology uses repeated observations of individual subjects through time to generate inferences of forest succession, such that 'time' is a captured variable. While two versions of this methodology appear in the literature, many authors attest to the first version as being the preferred method for studying succession (Kenkel *et al.* 1998; Caners 2001; Hamel and Kenkel 2001). This preferred method involves the long-term monitoring (repeated measures) of permanent sample plots, such that the series of enumerations yield wholly empirical measures of attributes, thereby limiting the source of error in the studied system to errors in measurement, and within-stand variation (in cases where on-site replication does not exist). The obvious drawback to adopting the repeated measures methodology for use in forest ecosystems is the enormous investments required to monitor and document subject stands throughout their development (i.e. from stand initiation, through maturity, and beyond).

Vasiliauskas (pers. comm. 2005) was able to integrate long-term repeated-measurements of plots (albeit limited to two observations in time) by relocating historic operational inventory transects in northeastern Ontario, and re-sampling along those transects. Although two observations in time are insufficient to determine non-linear trends of stands, Vasiliauskas was able to supplement the repeated-measures data, with photo chronosequencing.

Photo chronosequencing, the second version of the chronosequencing methodology, typically supplements one or more empirical measures of a forest stand, with multiple observations of that stand through time, via interpretation from numerous vintages of aerial photographs. Frelich and Reich (1995) integrated photo chronosequencing into their study of forest succession in the Boundary Waters Canoe Area Wilderness of northern Minnesota. With three photo captures, these authors were able to observe stand development over a span of 57 years. They found that jack pine-dominant canopies in the area never persisted beyond 160 years of age, and that when burned, maturing jack pine-dominated canopies will return to higher percentages of jack pine than over-mature canopies.

AUTECOLOGY AND SYNECOLOGY OF JACK PINE

Jack pine, the most widely distributed pine in Canada, has its greatest abundance in Ontario. It is a shade-intolerant, pioneer species, that is commonly found growing in early successional pure- or mixed-species stands, on a range of soil textures (Rudolph and Laidly 1990, Sims *et al.* 1990). The natural range of jack pine is shown in Figure 1.

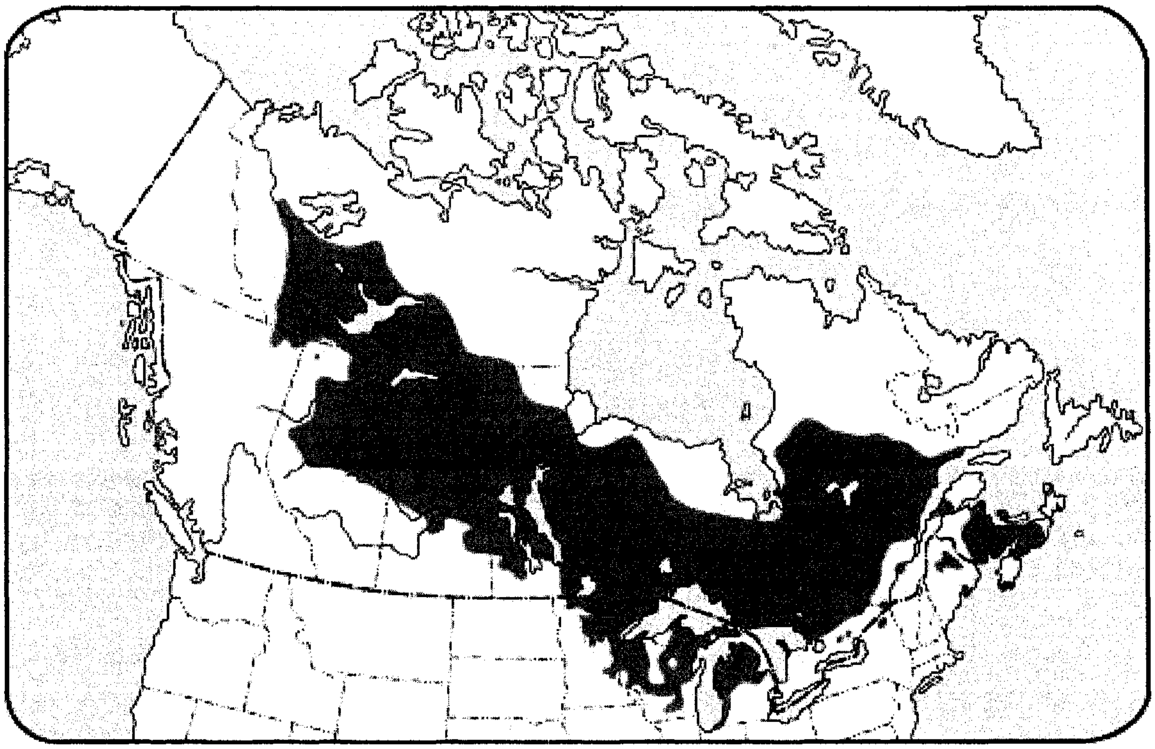

Figure 1. Natural range of jack pine (Farrar 1995).

In Ontario, the southern limit of the natural range extends westward from the Ottawa Valley, to the Haliburton Highlands, then to Georgian Bay. It conforms roughly to Rowe's (1972) delineations for the Middle Ottawa and Georgian Bay Forest Sections (sections L.4c and L.4d, respectively) of the Great Lakes-St. Lawrence Forest Region. The northern extent of jack pine in Ontario approaches the northern tree line; roughly along the 29°C mean annual maximum isotherm (Rudolph and Laidly 1990).

Climatic Associations

Tolerant of extreme air temperatures ranging from -40°C to +35°C, the natural range of jack pine in Ontario is characterized by long frigid winters, and short, warm to cool summers with low amounts of rainfall (Rudolph and Laidly 1990, Sims *et al.* 1990, Bell 1991). The frost-free period can range between 80 and 180 days, but jack pine is rarely susceptible to frost, as it does not flush early (Rudolph and Laidly 1990, Sims *et al.* 1990). Jack pine is also tolerant of a broad range of precipitation regimes, and is highly tolerant of summer droughts in excess of 30 days (Sims *et al.* 1990).

Life History

Under natural conditions, jack pine is only capable of sexual reproduction (Rudolph and Laidly 1990). The reproductive strategy, and morphological traits of the species, indicates a strong adaptation of jack pine to fire (Greene *et al.* 1999). Jack pine is a monoecious species, bearing persistent, serotinous, ovulate cones on the upper branches of the crown, whose seed viability remains high for the first 5 to 10 years after development, and total seed viability per tree, following fire, is estimated at 80% (Rudolph and Laidly 1990, Greene *et al.* 1999). Branches are persistent, but under closed canopies lower branches will die and often break off resulting in live crown height to stem height ratios of as little as 10%, (Rudolph and Laidly 1990). Greene *et al.* (1999) comment that it is probably no coincidence that jack pine, one of the most common conifer species in boreal Ontario, possesses an aerial seed bank; an effective means to colonize large burn areas.

While some of the serotinous cones produced by jack pine will open at ambient air temperatures of 27°C or more, as produced by solar radiation upon cones either in the canopy or on exposed ground, most cones will not open until exposed to temperatures of at least 50°C, as produced by fire (Rudolph and Laidly 1990, Sims *et al.* 1990). Once opened, jack pine seeds are dispersed by wind to a range of two tree heights, although dissemination is low beyond one tree height (Rudolph and Laidly 1990, Bell 1991). Wind is the primary dissemination vector for jack pine (Rudolph and Laidly 1990).

Seedling establishment requires a microsite with minimal competition, adequate moisture, adequate light, as well as a seedbed of exposed mineral soil. A mixed substrate of mineral soil and surface humus can also serve as an adequate seedbed, providing that the organic components on the surface are not thick enough to restrict moisture availability and root penetration into mineral soil (Rudolph and Laidly 1990, Sims *et al.* 1990, Bell 1991). Jack pine is also able to establish on poor quality sites (sites having low nutrient availability and rapid drainage), where most other boreal tree species cannot persist; though growth of jack pine on these sites will not be as productive as richer substrates with better soil moisture (Sims *et al.* 1990).

On regenerating sites, such as those following fire, surface temperatures may be sufficiently reduced from the shade cast by standing and fallen dead trees, that fewer seedlings experience desiccation-caused mortality, than would otherwise occur, despite jack pine's intolerance of shade (Rudolph and Laidly 1990, Sims *et al.* 1990, Bell 1991). During early development, jack pine is the fastest growing conifer, reaching breast height in as little as 4 to 8 years (Bell 1991, Vasiliauskas and Chen 2002). While considered small, and short-lived, jack pine are known to persist beyond 200 years, and can grow 20 to 30 m in height (Bell 1991).

Jack pine is very intolerant of shade, and requires full sunlight at all stages of its life cycle to achieve optimum growth (Bell 1991). As part of an understory, jack pine will not establish and/or persist under canopies having greater than 60% crown closure

(Sims *et al.* 1990, Bell 1991), or establish on a litter layer having a thickness greater than 1.3 cm (Rudolph and Laidly 1990).

Site Associations

Throughout Ontario, jack pine commonly forms mature stands on level to gently rolling sand plains, usually of glacial outwash, fluvial, or lacustrine origin (Rudolph and Laidly 1990; Bell 1991). Occurring less commonly, jack pine will also grow on eskers, sand dunes, rock outcrops, and bald rock ridges (Rudolph and Laidly 1990; Bell 1991). In northwestern Ontario, mature jack pine is most frequently found on glaciofluvial deposits and morainal tills, is less frequently associated with lacustrine soils, and is not associated with organic landforms (Sims *et al.* 1990; Bell 1991).

Jack pine-dominated stands in northwestern Ontario are frequently found on deep, dry to fresh, coarse sandy soils, and deep, fresh, fine sandy to coarse loamy soils (Sims *et al.* 1990; Bell 1991). Jack pine will also occupy sites with shallow coarse loamy soils (Sims *et al.* 1990; Bell 1991). Jack pine is less commonly found on fine-textured silt and clay soils, though theses are among the most productive substrates for jack pine. These sites tend to be productive for other species which can out-compete jack pine, reducing its frequency of occurrence (Sims *et al.* 1990; Bell 1991). Rudolph and Laidly (1990) also add that while jack pine will not naturally establish on alkaline surface soils, it will grow on soils overlying limestone; providing a normal mycorrhizal association is present.

Species Associations

While pure jack pine stands are common in Ontario, jack pine does associate with a multitude of other species. Table 1 shows associate tree species that were observed from Forest Ecosystem Classification (FEC) data to have co-occurred with jack pine populations within the study area. For northwestern Ontario, black spruce (*Picea mariana* (Mill.) BSP) occurred in 65% of those stands where jack pine had been tallied; respectively less frequently for trembling aspen (*Populus tremuloides* Michx), balsam fir (*Abies balsamea* (L.) Mill.), white birch (*Betula papyrifera* Marsh.), and several other species (pers. comm. Sawula 2003[4]). Proportional rankings varied slightly for northeastern Ontario (pers. comm. McMurray 2005[5]).

TABLE 1. Percent frequency of co-occurrence of various tree species with jack pine in stands older than 40 years, as observed from northern Ontario FEC plot networks.

	Percent Co-Occurrence with Jack Pine			
Common Name	**Northwestern Ontario**	**Northeastern Ontario**	**Latin Name & Authority**	
black spruce	65.0	87.5	*Picea mariana*	(Mill) B.S.P.
trembling aspen	25.2	35.2	*Populus tremuloides*	Michx.
balsam fir	17.5	64.5	*Abies balsamea*	(L.) Mill.
white birch	16.2	49.2	*Betula papyrifera*	Marsh.
white spruce	11.1	23.4	*Picea glauca*	(Moench) Voss
red pine	5.6	4.3	*Pinus resinosa*	Ait.
eastern white pine	2.2	5.9	*Pinus strobus*	L.
balsam poplar	1.4	2.7	*Populus balsamifera*	L.
largetooth aspen	1.1	0	*Populus gradidentata*	Michx.
eastern white cedar	1.0	2.3	*Thuja occidentalis*	L.
tamarack	0.8	3.1	*Larix laricina*	(Du Roi) K. Koch
red maple	0.5	4.7	*Acer rubrum*	L.
yellow birch	<0.1	0.4	*Betula alleghaniensis*	Britt.

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[4] FEC data for northwestern Ontario (including northcentral Ontario) were sourced from the Ontario Ministry of Natural Resources (OMNR); Kris Sawula, 2003.

[5] FEC data for northeastern Ontario were sourced from the OMNR; Sean McMurray, 2005.

Stand Dynamics

Finding that post-fire successional sequences predominantly resembled pre-fire conditions, Bergeron (2000) attributed the trend to the observation that fire cycle in most parts of the boreal forest is shorter than the life spans of dominant tree species. Cogbill (1985) argued that continual recruitment in boreal forests, leading to all-aged stands was not evident, as the majority of trees establish within the first 30 years after fire disturbance, and dominate stand conditions for up to 250 years with mortality becoming prominent only after 130 years. Further, Cogbill (1985) stated that many observations of succession are simply expressions of differential longevity and conspicuousness of contemporaneously-established tree species. Together, these inferences would suggest that succession in the boreal forest over the first century of development is largely determined at stand initiation.

The pattern which indeed emerges in the literature with respect to forest succession in ecosystems comprised at least in part by jack pine, is rapid establishment after fire of jack pine, trembling aspen, and black spruce, in somewhat varying proportions that approximately parallel pre-fire compositions (Carleton and Maycock 1978; Kenkel 1986; St-Pierre *et al.* 1992; Frelich and Reich 1995; Green and Johnson 1999; Gauthier *et al.* 2000). St-Pierre *et al.* (1992) found that more than 95% of seedlings established in the first three growing seasons after fire. Though regeneration in the sub-canopy layers is generally poor in stands with high proportions of jack pine, ingress and establishment by black spruce, balsam fir, white spruce, and eventually eastern white cedar may occur (Carleton and Maycock 1978; Kenkel 1986; St-Pierre *et al.* 1992; Chambers 1995; Frelich and Reich 1995; Kenkel *et al.* 1998; Gauthier *et al.* 2000) at rates influenced primarily by the presence of proximate seed/vegetative sources

(Carleton 1982), by the presence and depth of soil (Carleton and Maycock 1978; Carleton 1982; Kenkel 1986; OMNR 1997; Kenkel *et al.* 1998), by the moisture- and nutrient-availability characteristics of that soil (Kenkel *et al.* 1998), by the depth of the litter layer (Rudolph and Laidly 1990), and among others, by the presence and abundance of mosses (e.g. Schreber's moss), herbs (e.g. macrolichens of the subgenus *Cladina*), and low ericaceous shrubs implicated in preventing seedling establishment (Carleton 1982). White birch may establish in the canopy or in sub-canopy layers; either contemporaneously at stand initiation via seed or vegetative propagules, or it may ingress later via seed (Frelich and Reich 1995; Kenkel *et al.* 1998). In some cases, jack pine and trembling aspen regeneration has also been noted to establish in canopy gaps and under sparse canopies (Sims *et al.* 1990; Bell 1991; Desponts and Payette 1992; Kenkel *et al.* 1998, pers. comm. Vasiliauskas 2005).

As jack pine stands age beyond 100 years, directional change in canopy composition occurs, characterized by the gradual loss of jack pine and trembling aspen, with dominance shifting to black spruce and other contemporaneously-established and ingress species, with eventual dominance by black spruce (Cogbill 1985; St-Pierre *et al.* 1992; Frelich and Reich 1995; Woods and Miller 1998; De Grandpré *et al.* 2000). Relatively pure jack pine stands on productive sites may age in excess of 140 years prior to experiencing declines in gross total volume or basal area (Woods and Miller 1998). Of jack pine stands on dry sandy or rocky sites, while eventual succession is often to black spruce, near non-existence of understory regeneration may cause canopies to remain dominated by jack pine for long periods. Slowly decreasing in density, these communities sometimes become "savannah-like" (Carleton and Maycock 1978; Carleton 1982; Kenkel 1986; Kenkel *et al.* 1998).

Carleton (1982) noted that the occurrence of surface (non-stand-replacing) fire (even in savannah-like communities having no previous understory) can cause the re-establishment of both jack pine and black spruce on sites, or of just black spruce. Following catastrophic (stand-replacing) fire, Frelich and Reich (1995) noted that balsam fir and white cedar were eliminated from sites, requiring re-invasion by seed to establish themselves on the site after the initial cohort has established; with re-establishment rates heavily dependent upon distance to surviving proximal seed sources. Greene and Johnson (2000) noted the same trend for white spruce and tamarack.

Frelich and Reich (1995) also implicated nutrient feedbacks on the soil from litterfall and shading as playing dominant roles in determining succession. Kenkel (1986) concluded that succession in jack pine was influenced by substrate type, drainage class (soil moisture), soil particle size, as well as depth of the organic layer. Bergeron (2000) concluded that species life-history traits such as longevity, regeneration strategy, growth rate, and shade tolerance are the primary influential variables upon successional process, with shade tolerance topping that list. Woods and Miller (1998) concluded that both depth of soil and depth of surface organic layer (LFH layers) influenced observed rates of cull, and by association the persistence of jack pine populations. Gauthier *et al.* (2000) concluded that ecoregion, surficial deposit, and time-since-fire were important variables that influence succession. Not specific to jack pine but also pertinent, Jan (2000) noted the cumulative effect of environmental attributes over succession.

FOREST SUCCESSION IN ONTARIO: CONTEXT FOR APPLICATION

A sound understanding of forest succession is an integral component of Ontario's current forest management planning process, which mandates determinations of ecological sustainability, the availability of wildlife habitat, and of continued industrial wood supply to be supported by forecast models that extend for 160 years and more (OMNR 2004a). Yet, despite having a strong and direct influence on the outputs of these forecast models (OMNR 2004b), forest succession inputs remain almost exclusively based on professional opinion (Yemshanov and Perera 2002); this point conceded by the Ontario government (for example, Drescher *et al.* 2006; Sobze *et al.* 2006), who identified its remediation as a priority strategy in the province's 2004 wood supply forecast (OMNR 2004b):

> "The ability to accurately predict wood supply is limited by the quality of the information [upon which we rely during] forest management planning . . . . . . a more comprehensive understanding of forest succession trends [will] benefit current and future wood supply."

Drescher *et al.* (2006) studied the level of certainty held by forestry practitioners in northern Ontario, with respect to their knowledge of forest succession. It was therein concluded that despite the perceived familiarity most practitioners have of local and regional forests, "uncertainty of forest succession knowledge in Ontario is variable but often high, and can sometimes be related to ecological factors." This revelation led the authors to recommend no delay in improving the state of knowledge on forest succession in boreal Ontario.

While broad interpretations of forest succession drawn from primary literature (often only qualitative in nature) are typically supplemented by professional opinion to quantitatively calibrate strategic, non-spatial models (e.g. Ontario's Strategic Forest Management Model - SFMM), spatial models (e.g. Landis, Patchworks, and Ontario's Boreal Forest Landscape Dynamics System - BFOLDS) are exponentially more complex, and thus require more detailed inputs than current scientific literature and professional opinion-based resources can reliably provide. In a recent modeling exercise, Yemshanov and Perera (2003) found that a general lack of detail in primary literature addressing forest succession, limited their abilities to properly tailor spatial models to reflect boreal dynamics in Ontario. Despite this point, spatial modeling has become a fully integrated component of Ontario's forest management planning process (OMNR 2002), and there is an increasing reliance on spatial modeling in forest policy development (for example, OMNR 2003).

PROBLEM STATEMENT

To date, the experimental designs of most succession studies have not explicitly sought to capture the breadth of variation typical to northern Ontario; variation in soils, landform, vegetation, climate, geography, time-since-last-disturbance, as well as forest structure. Until fundamental ecological relationships related to forest succession have been identified, the heterogeneous nature of boreal Ontario's relief could confound forest succession analyses whose sole focus is resultant trajectories of stands. The objective of this study was to identify such relationships.

HYPOTHESIS

It is herein hypothesized that local environmental attributes influence the successional trends of jack pine-dominant stands in boreal Ontario.

The null statement follows:

$H_0^{(0)}$: *Succession, as it is observed in jack pine-dominated stands in boreal Ontario, is not influenced by local environmental attributes.*

METHODS

STUDY AREA

The study area is bounded to the south by latitude 47.5° N, to the north by latitude 52.5° N, to the east by longitude 79.5° W, and to the west by longitude 96° W. Extending throughout Ontario's Boreal forest region (Rowe 1972), the study area has a physiography that ranges from lowland peat bogs, to deep fertile upland soils, to bedrock covered by thin layers of soil, moss, or lichens (OMNR 2005), and is well within the distribution range of jack pine and many associate boreal tree species.

Climate within the study area was described by Chapman and Thomas (1968) as modified continental (modified due to presence of the great lakes to the south), with cold winters typified by low precipitation, and hot summers typified by high precipitation and frequent cyclonic storms resulting from the mixing of warm humid air masses from the south and cooler drier air from the north. The growing season ranges from 146 to 230 days (Mackey *et al.* 1996), depending on locale, topography, and landform – starting as early as April 25th.

Figure 2 shows the location of the study sites and the corresponding ecoregions of northern Ontario. Ecoregional delineations in the figure demark known geological and macroclimatic variation across northern Ontario. The dominant features of each of the four illustrated ecoregions are described briefly by Crins (pers. comm. 2007[6]), with supplemental information drawn from the work of Mackey *et al.* (1996):

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[6] Unpublished manuscript (in preparation by several authors): The Ecosystems of Ontario – Part 1: Ecozones and Ecoregions. Ontario Ministry of Natural Resources; William Crins, 2007.

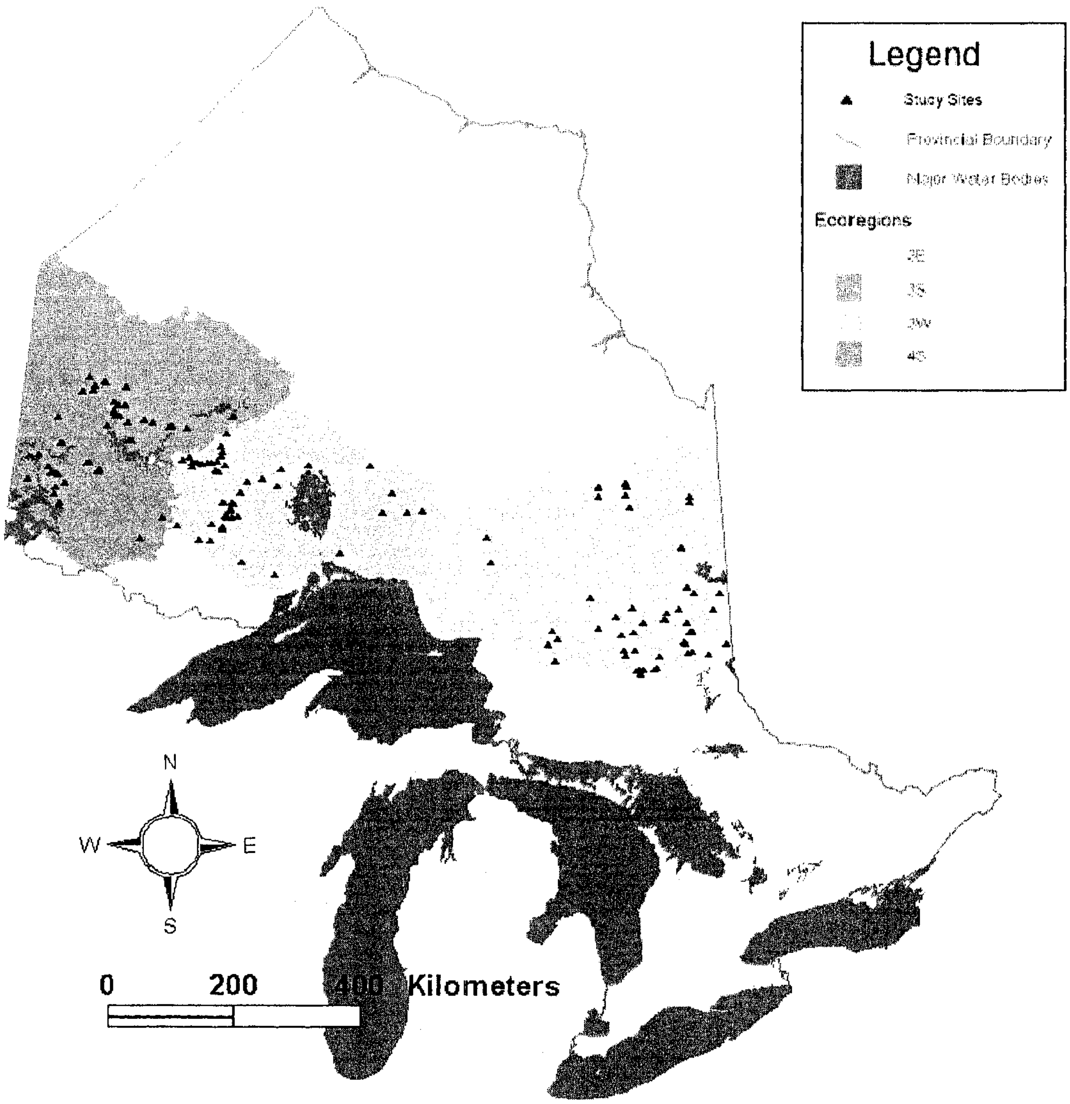

Figure 2. Distribution of study sites throughout Ontario (n = 178).

Lake Abitibi Ecoregion (3E)

The surficial geology in the Lake Abitibi ecoregion is diverse, prominently featuring the Clay Belt in the northeastern-most portion, and ground moraine in most other areas. In addition, end moraines, spillways, glacio-fluvial deposits and substantial aeolian deposits are scattered throughout the ecoregion. The terrain is highly variable, ranging from rugged and strongly broken terrain in the western portion where the bedrock is overlain by shallow drift, to weakly broken in the east (pers. comm. Crins 2007).

Soils in the western and southeastern portions are poorly developed, mainly due to steep terrain exposing rock outcrops leaving little soil. Much of the southern ranges are blanketed with podzols, developed on deep sands and rocky areas, with scattered pockets of brunisols. The northwest range is typified by luvisols, on well drained calcareous clay and silt plains, whereas gleysols and peats are predominant in the Clay Belt where drainage is impeded (pers. comm. Crins 2007).

Forest cover in the ecoregion is mainly mixed and coniferous, with small amounts of deciduous cover. The vegetation in this ecoregion is boreal, with canopies comprised mainly by black spruce, white spruce, balsam fir, jack pine, tamarack, white birch, trembling aspen, and balsam poplar. Sparse spruce forests overlying organic soils are common. Ecoregion 3E falls within Rowe's (1972) Boreal Region, spanning four forest sections: Northern Clay, Missinaibi – Cabonga, Central Plateau, and Superior (pers. comm. Crins 2007).

Annual precipitation in the ecoregion ranges from 726 to 1149 mm per year, with summer rainfall accounting for 25 to 30% of that measure. Growing seasons vary between 170 and 200 days (Mackey *et al.* 1996).

Lake Nipigon Ecoregion (3W)

Landscapes in the Lake Nipigon ecoregion vary from strongly broken in the south, to gentle and weakly broken relief in the north and west. Ground moraine is the primary landform, but considerable glaciolacustrine and glaciofluvial deposits encircle the morainal deposits that fringe Lake Nipigon (pers. comm. Crins 2007).

Dominating the region, well-drained and coarse-textured soils show brunisolic and podzolic development patterns, and in areas of fine-textured materials, luvisols are present. Rock outcrops comprise a fifth of the region, and peats and gleysols occupy the frequently associated poorly drained sites and bedrock depressions (pers. comm. Crins 2007).

Forest cover in the region is typically boreal, largely comprised of mixed and coniferous stands, and occasionally deciduous cover. Growing season moisture deficits, compounded by the prevalence of shallow soils lends to an intense fire regime, characterized by frequent large fires. The ecoregion is contained mainly within Rowe's (1972) Nipigon and Superior forest sections, with some representation in the Central Plateau (pers. comm. Crins 2007).

Climate in the Lake Nipigon ecoregion rapidly reflects boreal conditions along a northerly gradient, as the modifying influences to of Lake Superior and Lake Nipigon decrease with distance. Annual precipitation ranges from 760 to 1087 mm, of which approximately 26% falls during the summer season, and the growing season here lasts between 205 and 230 days (Mackey *et al.* 1996).

Lake St. Joseph Ecoregion (3S)

The landscape of the Lake St. Joseph ecoregion is characterized as gently sloping plains of shallow sands and loams overlying bedrock, broken at broad intervals by esker and moraine ridges, with pockets of lacustrine clays. Exposed bedrock extends over a quarter of the landscape, mainly in the south where the elevation increases. Soils are comprised primarily of low-base sands and loams, as well as coarse and medium granitic sands. Two thirds of the region's soils are dystric brunisols, with the remainder comprised by humo-ferric podzols, and bedrock exposures. In low-lying areas, silty clay soils, brunisolic luvisols, gray luvisols, and mesisols are typical, with humic gleysols occurring in areas of saturated mineral soils. The shallow bedrock sites are often covered by folisolic (upland organic) materials (pers. comm. Crins 2007).

Dense and sparse coniferous forests dominate the landscape, with scattered occurrences of mixed forests and treed bogs. Dominated by shallow soils, and experiencing a periodically dry climate, this ecoregion experiences intense and frequent fire disturbance. Ecoregion 3S is largely situated within Rowe's (1972) Northern Coniferous forest section. Upland forests are dominated by jack pine and black spruce, with older sites sometimes including white spruce and balsam fir. Trembling aspen and white birch can occur together or in mixtures with jack pine and black spruce (pers. comm. Crins 2007).

Annual precipitation in the Lake St. Joseph ecoregion ranges from 770 to 1134 mm per year. While 26% of this amount is summer rainfall, significant moisture deficits during the growing season commonly occur. The growing season in this region can range between 182 to 219 days (Mackey *et al.* 1996).

Lake Wabigoon Ecoregion (4S)

Substantial portions of the landscape in the Lake Wabigoon ecoregion are characterized by exposed bedrock and very shallow soils – especially in the west. In the east, varying depths of ground moraine as well as lacustrine deposits occur, with a large clay plain noted near Dryden, Ontario. These lacustrine deposits, as well as scattered pockets of low-lying silt and clay form weakly broken terrain, while the rest of the ecoregion is moderately broken. Luvisols dominate the silt and clay sites, while eluviated dystric brunisols and weakly-developed podzols dominate the remaining landscape that is not exposed bedrock (pers. comm. Crins 2007).

Forest cover is largely comprised of boreal mixed and coniferous stands with sizable areas of bare or sparse canopies over bedrock in the west, where dry climate, shallow soils and an intense fire regime trending towards large fires limit forest productivity. The southern region of 4S is located within Rowe's (1972) Quetico forest section, and the northern portions within the Upper English River and Lower English River sections (pers. comm. Crins 2007).

With the shortest growing season of those ecoregions profiled (ranging between 146 and 170 days), and comparatively little precipitation (ranging from 550 to 785 mm annually, of which 40% is summer rainfall, Mackey *et al.* 1996), ecoregion 4S is relatively cool and dry, suggesting that it is significantly influenced by the adjacent prairie climate, and therefore endures frequent summer drought (pers. comm. Crins 2007).

SAMPLING METHODS

Photo chronosequencing was adopted as the methodology by which forest succession would be sampled. This methodology was practical as it capitalized upon past investments made by project partners; investments in aerial photographs, equipment, and empirically-determined information for site.

221 study sites were identified from growth and yield monitoring plot networks of the Ontario Ministry of Natural Resources (pers. comm. Sawula 2004[7]) and the Forest Ecosystem Science Co-operative (pers. comm. Wood 2004[8]) on the basis that the stand initiated from wildfire, and jack pine was known to have occupied the site.

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[7] Permanent Sample Plot Network, Ontario Ministry of Natural Resources; Kris Sawula, 2004.

[8] Permanent Growth Plot Network, Forest Ecosystem Science Co-operative; Dave Wood, 2004.

For each study site, aerial photographs were obtained from the province's archive, which when sequenced, captured the site at four points in time. The photographic record of development typically spanned 45 years, ranging from 1946 to 1997, and averaged 15 years between photo captures. Growth and yield plot locations were marked onto the aerial photographs, and corresponding stands were delineated to a maximum radius of 100 m from the plot. Ecoelements embedded within the stand that were distinctly different from the targeted conditions were themselves delineated and excluded from consideration. Canopy composition was then interpreted[9] from the sequenced photographs for each site (±1%, by species). To minimize bias and improve accuracy in photo interpretation, canopy data from the growth and yield plots were used as ground-truth benchmarks.

Figure 3 illustrates the application of photo chronosequencing to derive dependent variable data for one of the study sites. In the presented example, dependent variable data on relative composition by species was interpreted for four points in the stand's development (from photos dated 1950, 1965, 1982, and 1995). In 1950, 22 year old post-fire regeneration was observed to be primarily comprised by jack pine and trembling aspen. By 1965, a strong black spruce understory was just starting to ingress into the 37 year old canopy – assuming a 25% relative composition over the next 17 years. Ingress of black spruce into the established jack pine and aspen canopy was observed to continue through 1995.

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[9] Interpretations of photo images were made by this author, and may be subject to unknown bias related to species identification and estimations of relative composition.

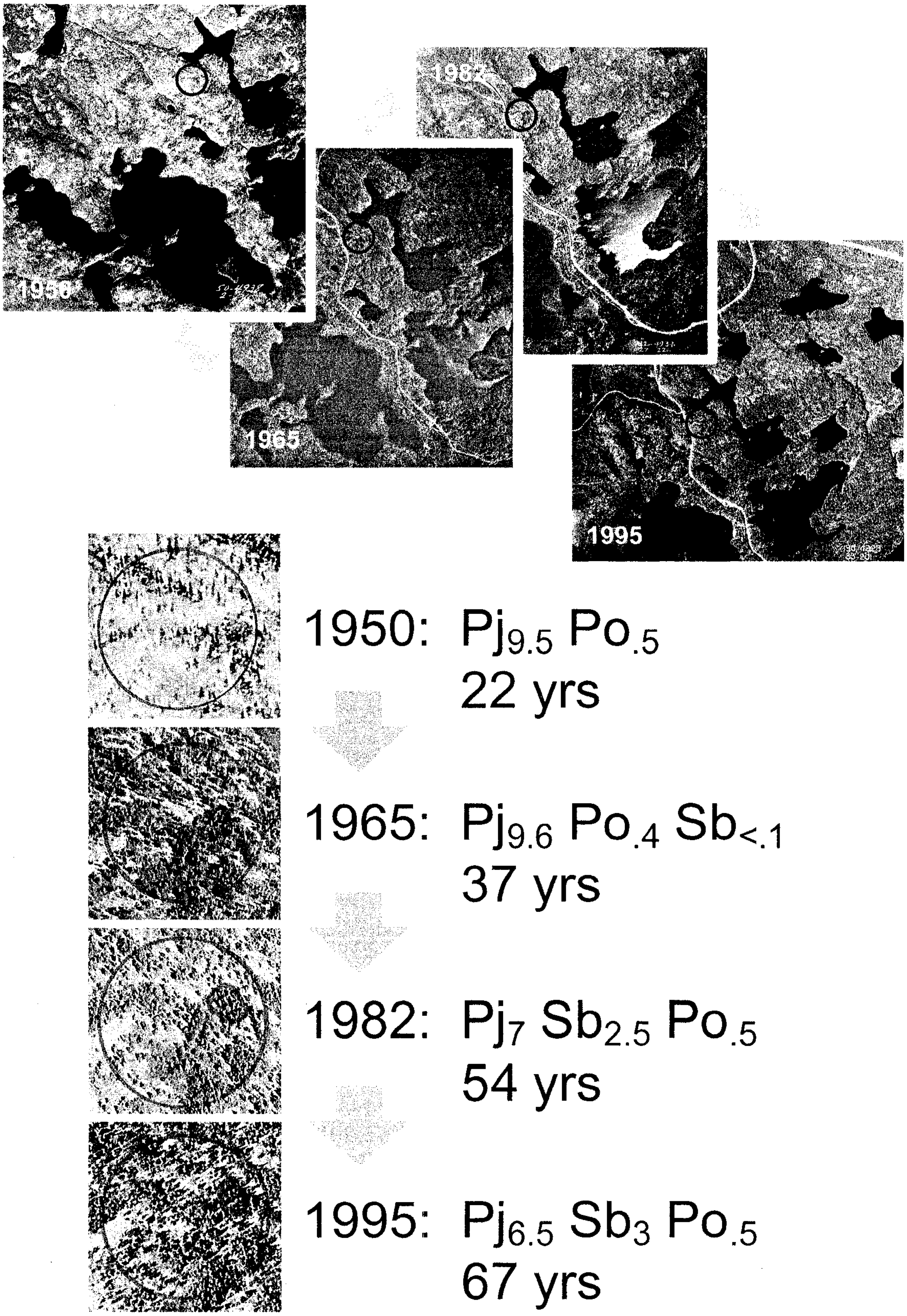

Figure 3. Example application of photo chronosequencing for a stand, observing ingress of black spruce into a jack pine-trembling aspen canopy over a period of 45 years.

Of 221 examined sites, only 178 were retained for analysis. To minimize complexity in the dataset, those sites with an observed presence of species other than jack pine, black spruce, trembling aspen, and white birch were dropped from consideration; as were sites where recent fire bisected the period of observation into two of shorter duration. Table 2 lists 17 environmental attributes specific to geographic location, topography, soil characteristics and climate that were considered as potential drivers of succession in jack pine-dominant stands.

TABLE 2. List of environmental variables considered as potential drivers of forest succession.

- Geographic Location
  - Longitude
  - Latitude
- Topogaphy
  - Elevation
  - Slope Gradient
  - Slope Aspect*
  - Slope Position*
  - Landform*
- Soil Conditions
  - Mode of Deposition*
  - Depth to Bedrock*
  - Moisture Regime*
  - Dominant Soil Texture*
  - Sand in the Soil Profile
  - Coarse Loams in the Soil Profile
- Climate
  - Annual Precipitation
  - Length of the Growing Season
  - Growing Degree Days
  - Precipitation During Growing Season

Note: * Nominal (categorical) variable

Elevation and climate data specific to each study site was sourced from models developed by the Canadian Forest Service (pers. comm. McKenny 2007[10]). All other independent variable data were drawn from the records and field notes of the growth and yield monitoring plots. Though representation across the study area was found to be good, sparse occurrences were observed for nominal variables having multiple categories. In most cases, under-represented categories were either dropped from testing, or were grouped with closely-associated categories. Sampled distributions of the environmental attributes are presented by ecoregion in Appendix 1.

ANALYTICAL METHODS

The sampling design presented in this report expressly sought to capture the range of environmental variation typical to northern Ontario, and was therefore purposely non-random in nature. As a consequence, parametric testing was not appropriate. Instead, summaries of successional patterns are presented, and two non-parametric analytical techniques were used to investigate environmental relationships to succession: regression trees, and survival analysis. Unlike parametric methods, these techniques can accommodate small, non-random sample populations.

Regression Trees

There are two notable applications of regression trees in studies of forest productivity and succession. McKenny and Pedlar (2003) developed a regression tree from Ontario's Forest Ecosystem Classification data to derive a predictive model of jack pine site index based on local climate and soil attributes. Their model suggested total

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[10] The Canadian Forest Service's selected climate data were drawn from daily weather station measures collected from 1961 through 1990, modeled to tri-variate point locations (latitude, longitude, and elevation) using thin-plate spline smoothing algorithms (BIOCLIM / ANUCLIM); Dr. Dan McKenny, 2007.

soil depth, depth of the B soil horizon, annual precipitation, precipitation during the growing season, and precipitation seasonality were useful predictors of jack pine site index. Fan *et al.* (2006) developed regression trees from tree mortality data for oak-dominated forests of Missouri's Ozark highlands, with an aim to derive a predictive model of species longevity based on stem characteristics and stand structure. The resultant model suggested that tree species, crown class, diameter at breast height, and basal area of larger trees were useful predictors of tree mortality.

Regression trees are applied to identify potential predictors of a continuous dependent variable (for example: relative abundance in a canopy by jack pine) by exploring bi-modal distributions of independent variables (Breiman *et al.* 1984). For the current study, four regression trees were developed; each associating environmental attributes to jack pine abundance at successive points of stand maturation (20, 40, 60, and 80 years since fire). Subsets of varying sizes were used to develop the regression trees (52, 119, 117, and 63 stands, respectively) as none of the 178 studied stands were observed across all four of the selected points of post-fire development. There were too few stands observed beyond 80, and below 20 years since fire to sanction the development of additional regression trees. In both cases, models would have been based on fewer than 25% of the studied stands – a threshold subjectively chosen to minimize risk that the subset would inadequately reflect the full dataset.

In developing each regression tree, the subset was split into two groups, based on either an explanatory variable's grouped categories (in the case of a nominal variable) or a scalar threshold (in the case of a continuous variable). Each sub-sample was again split; the process repeated until no meaningful split could be found, or until a minimum sub-sample size was reached. For this study, subdivisions beyond 10% of the original subset were not permitted.

The conditions by which stands are split into two groups are based on an iterative search across all categorical groupings and scalar thresholds of all variables. That grouping or threshold which yields the lowest least squares residual value within the two sub-samples is selected as the optimal splitting rule. When graphically displayed, as in Figure 4, the regression-based decision tree (or "regression tree") features the sequenced binomial splitting rules (termed: decision nodes, depicted as orange rectangles) and the summary statistics of each final sub-sample population (termed: terminal node, depicted as green ovals).

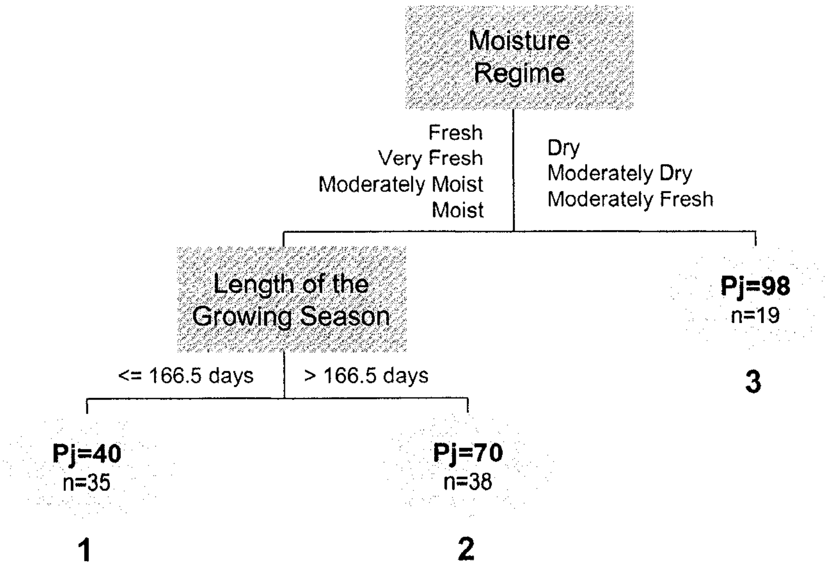


Figure 4. Example regression tree predicting jack pine abundance in the canopy.

In Figure 4 the dataset was optimally split into three sub-samples; first on the basis of moisture regime, and then by length of the growing season. In the first split, dry, moderately dry, and moderately fresh sites were separated from those with moister soils. Channelled to the right, into terminal node 3, median jack pine abundance on these 19 drier sites was found to be 98%. Stands overlying fresh, very fresh, moderately moist, and moist soils were further split based on the length of the growing season. In this case, stands experiencing growing seasons of 166.5 days or less in duration, were partitioned into terminal node 1, corresponding to a median jack pine abundance of 40%. The remaining 38 stands occupied terminal node 2 and had a median abundance of 70%.

In developing each regression tree, a validation procedure tailored to small datasets was applied. When working with large datasets, a portion of the data can be held in reserve for use in calculating error estimates (actual vs. predicted error). Terminal nodes surpassing user-defined limits for error estimates can be pruned (discarding the associated decision node) until an optimal tree is derived. However, working with small datasets (as in this study), one does not wish to lose what could be important data for the development of a regression tree by reserving it for testing. Alternatively, a 10-fold cross-validation procedure was applied. This procedure entailed the development of 10 additional models, using random subsets of the data (90% of the stands used to develop the original regression tree). These additional regression trees were then compared to the original model, and only those decision nodes that were common to all regression trees were retained; the others were pruned. In addition, the validity of each sub-division was tested using a post-hoc analysis of variance (ANOVA) procedure. Those decision nodes not testing at probabilities of significance above 95% ($p \leq 0.05$) were also pruned.

The regression trees were developed using the software: CART Extended Edition version 6.0 (Salford Systems 2006). The ANOVA procedure was applied using the software: SSPS version 15.0 (SPSS 2006). Detailed descriptions of the application and mechanics of regression trees are provided by Breiman *et al.* (1984).

Survival Analysis

Fan *et al.* (2006) presented an early application of survival analysis to study forest succession; applying it to tree mortality data in the oak-dominated forests of Missouri's Ozark highlands. Arguing that tree survival is a stochastic process, highly variable over time and space, with many contributing factors, the authors stressed that traditional parametric approaches to modeling survival are unable to capture this variation; especially in natural, mixed-species forests. Fan *et al.* (2006) developed a regression tree to predict tree mortality, based upon stem characteristics and stand structure. Using the Kaplan-Meier method of survival analysis, cumulative survival probability functions were derived from the samples in each of the regression tree's terminal nodes, and comparatively tested. The authors concluded that in mature oak forests, the persistence probability of red oak was three to six times lower than those of white oak, hickory, or short-leaf pine, and surmised that such results provided the practical information necessary to guide development of silvicultural prescriptions that reduce mortality.

Survival analysis is a technique to study 'time-to-event'. For the current study, stand succession from a jack pine-dominant canopy (jack pine ≥ 70%) to conditions with less or no jack pine (< 70%) was the 'event' of interest. While there was no ecological imperative for the selection of 70% as the succession-event threshold, it is frequently the standard by which stands are defined as jack pine-dominant for forest management planning in northern Ontario (for example, Ride *et al.* 2004). Survival analysis was applied to that subset of 126 stands which were observed to be jack pine dominant, testing the influences of local environmental attributes upon jack pine persistence, first individually, and then attributes in combination.

A strong argument for the use of survival analysis to study forest succession is that no assumptions are made as to when similar stands will experience the event. Instead, the approach embraces the concept that stands having similar canopies, on similar sites will still experience the succession-event across a broad range of ages. Rather than generating a single trajectory to summarize the dynamics of all canopies, survival analysis focuses upon the probability through time that stands will cross a predetermined event-threshold.

The following example is provided to help describe the basic nature and application of survival analysis: After a forest fire, a researcher observes six jack pine-dominant stands as they establish and develop through time; recording the year in which the canopy was observed to shift away from dominance by jack pine (Table 3).

TABLE 3. Elapsed time until canopy is observed to shift away from dominance by jack pine.

Study Plot	Time-To-Event (Years)
a	65
b	100
c	40
d	65
e	45
f	80

In generating a life table (Table 4), the dataset is partitioned into age classes, and the proportion of stands that survives from one class to the next is calculated, as is cumulative survival. Alternatively, the dataset could be parsed into the smallest measures of time (1 year increments), and a step-function can be traced across years to produce a precise cumulative survival trend (red, Figure 5). From the figure, the predictive inference might be made that there exists a 33.3% probability that a jack pine-dominant canopy will persist beyond 77 years of age.

TABLE 4. Example life table

Age Class	No. Entering Age-Class	No. of Events Observed	Proportion Terminated	Proportion that Survived	Cumulative Survival
1-20	6	0	0%	100%	1.0
21-40	6	1	17%	83%	0.83
41-60	5	1	20%	80%	0.67
61-80	4	3	75%	25%	0.17
81-100	1	1	100%	0%	0.0

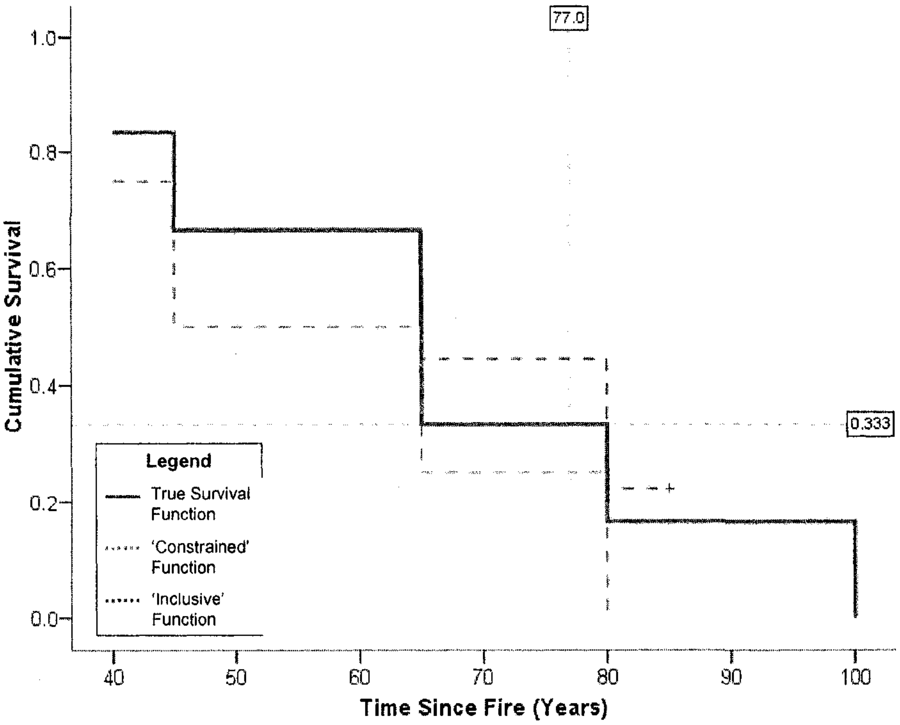


Figure 5. Example cumulative survival for true vs. 'inclusive' vs. 'constrained' functions.

But what if the researcher was not able to observe all study plots indefinitely? If for whatever reason, the researcher was only able to monitor forests for 85 years, that person would not have observed the event for study plot b. And what if plot d was harvested at age 50? The true persistence times of 100 and 65 years for plots b and d respectively, would be unknown to the researcher.

One option is to discard those samples where the event was not observed, and generate a 'constrained' cumulative survival trend (dashed green, Figure 5). When compared to the true function, discarding plots b and d yielded a 'constrained' function that underestimates true probabilities of survival at any age. Further, the function suggested that no jack pine-dominant canopies should be expected to persist beyond 80 years of age, despite the fact that we know one subject (plot b) had not yet been seen to succeed when the period of observation ended in the subject's 85th year of development.

Survival analysis however, permits the consideration of censored cases when deriving survival functions. Cases are considered censored when they were not observed through the full range of their development. In this example, plot d was censored at age 50 because the stand was harvested and could no longer be monitored. Plot b was censored at age 85 because the researcher terminated the period of observation. Because plot d was observed for 50 years without noting an event, that information has value. While it cannot provide insight to the proportions of stands that survived beyond 50 years of age, it can help to derive the proportions of stands that persist up to 50 years of age. Similarly, plot b can help to derive an 'inclusive' survival function (dashed blue, Figure 5) for the first 85 years of development; causing the function to more closely approximate the true function. As depicted, the function derived via survival analysis, where censored observations were considered when calculating annual survival, was a far better approximation of the true function; in this case, matching it perfectly over the first 65 years of development, with some overestimation over the next 20, and indication that the true function extends beyond the limit of what could be plotted – indicating a 20% probability that stands aged beyond 85 years would remain dominated by jack pine.

Two methods of survival analysis are commonly applied when testing the influence of explanatory variables; both were used in this study. The Kaplan-Meier method is non-parametric, and has the capability of plotting multiple survival functions. When used in combination with the Log Rank test statistic, the statistical significance of compared functions can be determined. This procedure was used to individually test the bi-modal or categorical influences of independent environmental variables upon jack pine persistence. For each variable, iterative preliminary exploration identified the optimal bi-modal or categorical splits.

Variables independently suggested to influence succession at a 75% significance level ($\alpha = 0.25$) were then tested together using Cox Regression. The Cox Regression method of survival analysis is semi-parametric – relying on the Chi-Square test statistic, and is capable of multivariate modeling. Using a backwards-stepwise procedure, the multivariate model identified variables that influenced succession at a 95% significance level ($\alpha = 0.05$), despite their respective confounding effects upon each other.

Survival analysis was performed using the software: SPSS version 15.0 (SPSS 2006). Detailed descriptions of the application and mechanics of the Kaplan-Meier and Cox Regression methods are provided by Collett (2003).

RESULTS

SUCCESSIONAL PATTERNS

While shifts in relative species compositions occurred in the majority of stands, much of the observed succession was a reflection of differential growth rates and responses to suppression between contemporaneously established populations. In only 16 of 178 cases (9% of stands) was a second cohort observed to enter the canopy, and then only included black spruce or white birch. Of that count, only 4 stands saw the ingress of a species in the second cohort that wasn't already present in the first (ingress from a neighbouring seed-source). Even when considering stands that had been excluded for having some measure of balsam fir or white spruce (two species that commonly ingress as later cohorts), the proportion of such ingress only rose to 14% (31 of 221 stands).

Figure 6 illustrates the species mixtures observed at the study sites, as well as species ingress patterns; including stand counts for each. Stand counts associated to a species mixture (numbers within blue bubbles, e.g. 47 observed occurrences of 'Pj+Sb') denote those sites where no changes to species complements were observed during the period of observation (regardless of compositional shifts between component species). Counts associated to arrows in Figure 6 denote the number of stands where ingress of new species was observed. For example, at 18 sites, a jack pine canopy was observed to experience ingress by black spruce (arrow pointing from 'Pj' to 'Pj+Sb' bubbles). These counts are independent from those reported within the blue bubbles.

Eighteen stands (not featured in Figure 6) were observed to have lost a species from the canopy during the period of observation. In most of these cases, the loss was a reflection of the suppression of white birch or black spruce populations during the first few decades of development. To a lesser extent, the loss of sparse populations were observed in mature canopies, and in one case, an overmature but still dominant jack pine population dropped completely from the canopy when the site was last observed some 48 years later, 152 years after fire.

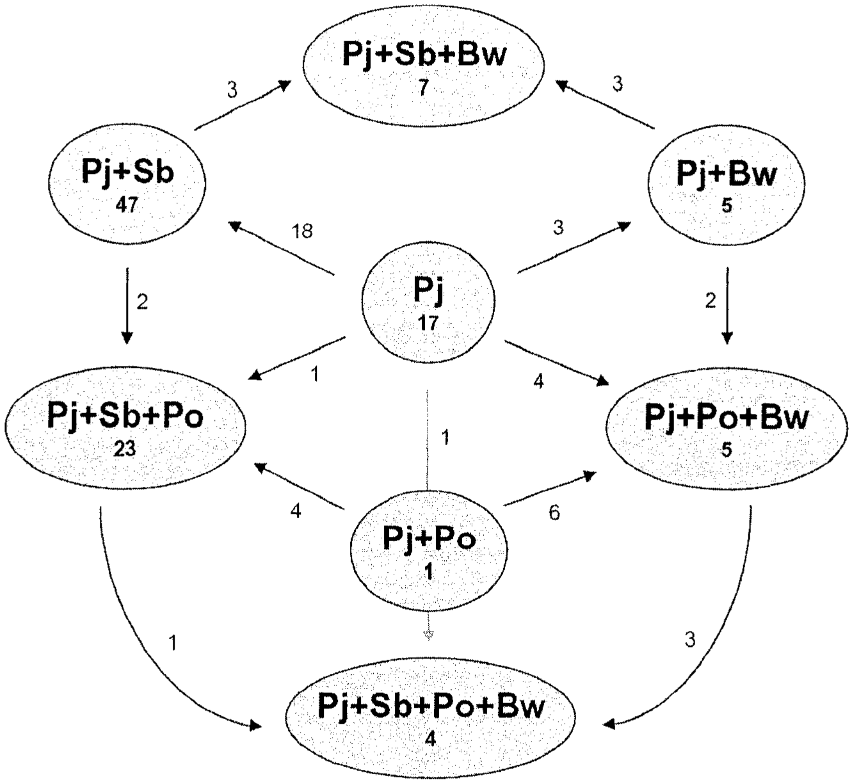


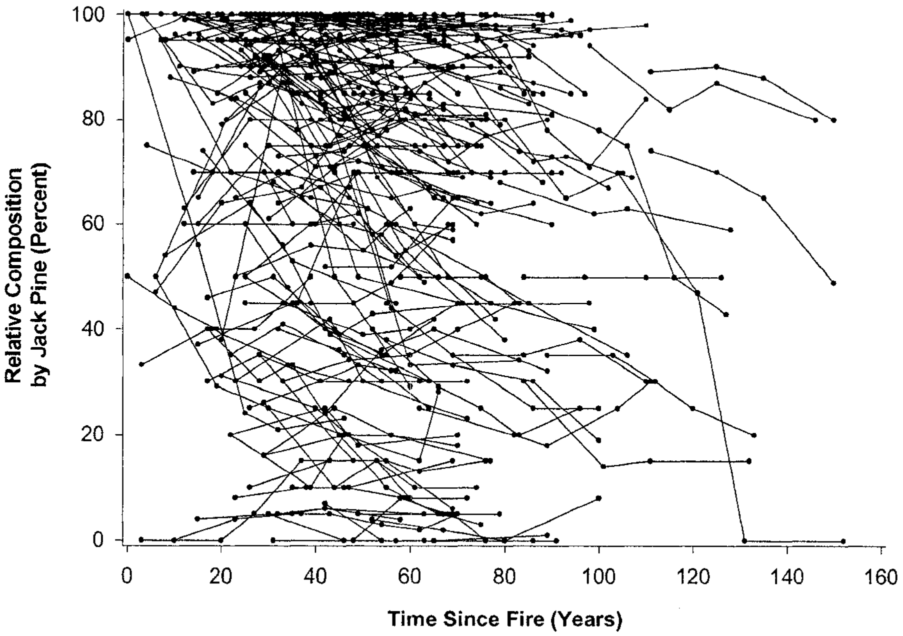
Figure 6. Observed species mixtures and ingress dynamics (n=160).

As the figure shows, black spruce was a frequent associate of jack pine; observed in 79% of stands. Trembling aspen and white birch were observed at about half of that frequency (41 and 35%, respectively). When considering only the ingress patterns, black spruce is again the most common associate species to jack pine (59% of 51 cases), followed by white birch, and to a far lesser extent, trembling aspen (35 and 20%, respectively).

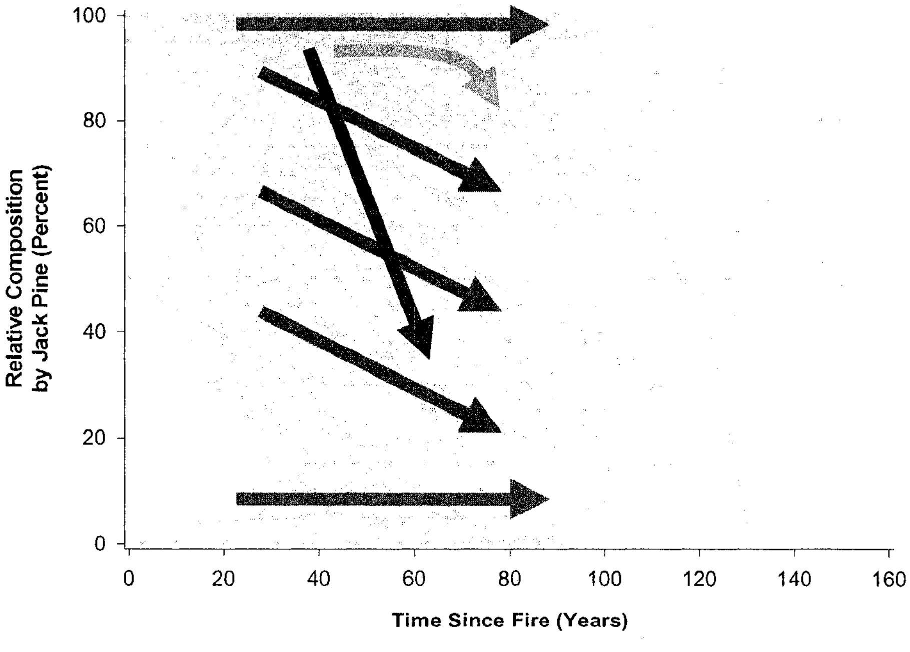
Centred in the diagram, 17 jack pine stands were never observed to experience ingress, while nearly twice that number recruited combinations of black spruce, white birch, and trembling aspen. Trembling aspen occurred frequently in combination with jack pine and black spruce ('Pj+Sb+Po'), and less frequently in other mixtures. Rarely was trembling aspen noted to ingress into a canopy, and even more rarely was it observed alone with jack pine. In contrast, white birch was noted to ingress and co-occur with any combination of species.

Figure 7a summarizes the observed changes in jack pine abundance through time, for all stands, relative to all other species. In addition to the previous figure, Figure 7a illustrates well the structural features of the sampling design; where, in addition to variability in jack pine abundance relative to associate species, stands were sampled for varying lengths of time, and at varying points in their post-fire development. Figure 7a further illustrates the considerable variation and complexity in sampled canopy dynamics – ranging from stable conditions as stands aged, to precipitous shifts in canopy composition.

The study sites generally had high abundances of jack pine, with most stands observed at ages between 10 and 90 years. This was likely a reflection of the non-randomized structure of the growth and yield sampling designs upon which this study relied. While the study considered any candidate having any measure of jack pine, growth and yield sampling designs in Ontario historically targeted conifer-rich stands of near-commercial ages. While current growth and yield sampling is no longer so limited in scope, these networks may still show some imbalance.



a)



b)

Figure 7. Jack pine abundance dynamics observed of 178 stands. Depicted: a) relative composition by jack pine (relative to all other species) plotted against time since fire; and, b) four common trajectories (distinguished by colour).

Four common trajectories for jack pine abundance through time were observed over the range of stands and ages (Figure 7b). Included among them, level trajectories (no slope, depicted in green) denoted no change in jack pine abundances while observed. Other stands were observed to have experienced moderately-negative trajectories (depicted in blue) and steeply-negative trajectories (depicted in red), respectively showing moderate to precipitous reductions in relative abundance of jack pine in the canopies. Alternatively, the trajectories of some stands were initially observed to be level, only later to transition to moderately- or steeply-negative trajectories, showing the onset of change (depicted in orange).

Forest canopies showing no change (level trajectories) were commonly found throughout all ranges of jack pine abundance and age, though they were mostly clustered at the highest abundances, and to a lesser extent at the lowest abundances. While stands initially observed to be stable, later showing losses (onset trajectories) were observed at numerous points throughout Figure 7a, the bulk of these stands were also clustered at high abundances; often dropping from pure jack pine. Stands showing moderate drops in relative abundance by jack pine (moderately-negative trajectories) were the most conspicuous trends. They were observed in high numbers at all ranges of jack pine abundance. In contrast, relatively few stands were observed to experience precipitous drops in jack pine abundance (steeply-negative trajectories). While several of the older stands were counted among this group, most occurrences were observed in young stands. A small number of stands were observed to initially experience moderate-to-large increases in jack pine abundance (positive trajectories, not presented in Figure 7b). In these cases, jack pine was not initially visible on the photographs but was soon-after viewed to overtop other species on the site. The frequency of such observations declined rapidly with age. It is worth noting that for stands across the full range of jack pine abundance, once canopies experienced moderate to rapid declines, the rate of decrease rarely abated.

ENVIRONMENT AS A PREDICTOR OF JACK PINE ABUNDANCE

Four regression trees were developed to predict jack pine abundance in canopies at successive points of development (20, 40, 60, and 80 years since fire), using environmental attributes as predictors.

Regression Tree: Year 20

For these 52 young stands, jack pine abundance could not be linked to variation in environmental conditions – a valid regression tree could not be developed.

Regression Tree: Year 40

For these closed-canopy, mid-rotation stands, a regression tree was developed that split the 119 study sites into 2 terminal nodes defined by soil texture (Figure 8a). After four decades of development, shifts in jack pine abundance were largely driven by soil texture. At year 40, those sites dominated by coarse soils (sands) were predicted to have a median jack pine abundance of 92% (terminal node 2), and a distribution of samples predominantly clustered at high values of abundance (Figure 8b). In contrast, jack pine abundance on sites dominated by medium-, and fine-textured soils (terminal node 1) was predicted at 66%, with a more variable population distribution; ranging from 0 to 100%.

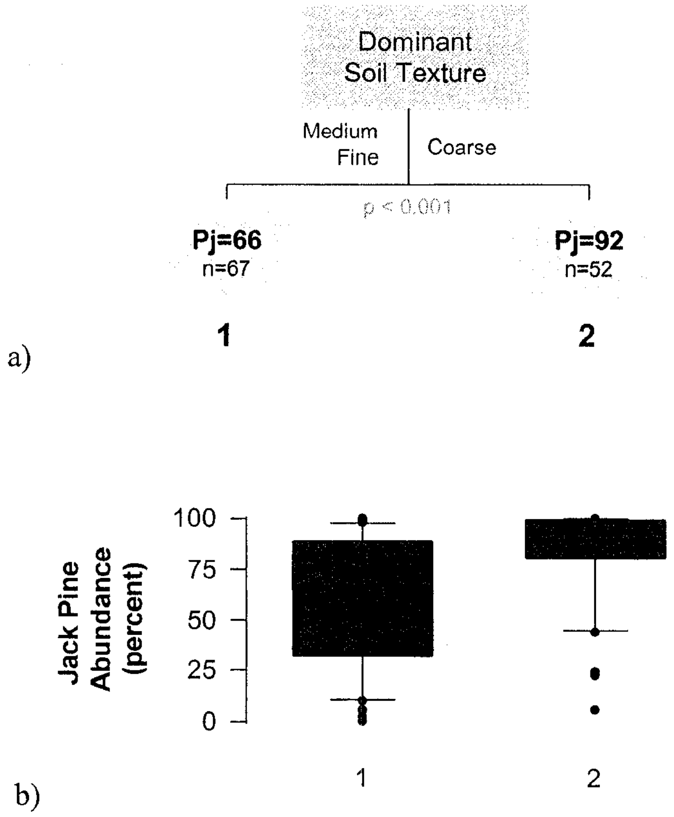


Figure 8. Regression tree: Year 40. Depicted: a) Regression tree predicting jack pine abundance; and, b) associated sample population distributions by terminal node.

Regression Tree: Year 60

After six decades of competition for resources, a more complex regression tree linked three environmental attributes to jack pine abundance in 117 stands: sand in the soil profile, moisture regime, and slope position (Figure 9a). Here, sandy soils were again the most conspicuous splitting rule; similar to the first decision node in the previous regression tree. In this case, the presence of more than 86 cm of sand in the soil profile yielded a jack pine abundance prediction of 96% (terminal node 4), with sites in this group clustered at very high abundances of jack pine (Figure 9b). Those sites having less than 86 cm of sand in the soil profile were then split on the basis of soil moisture regime. Those sites with very fresh to moist soils were found to have a median jack pine abundance of 36% (terminal node 1), whereas those on dry to fresh soils were again split, this time on the basis of slope position. Stands positioned on crests, toe slopes, and depressions were together predicted to have a jack pine abundance of 40% (terminal node 2), as compared to 80% on all other slope positions (terminal node 3).

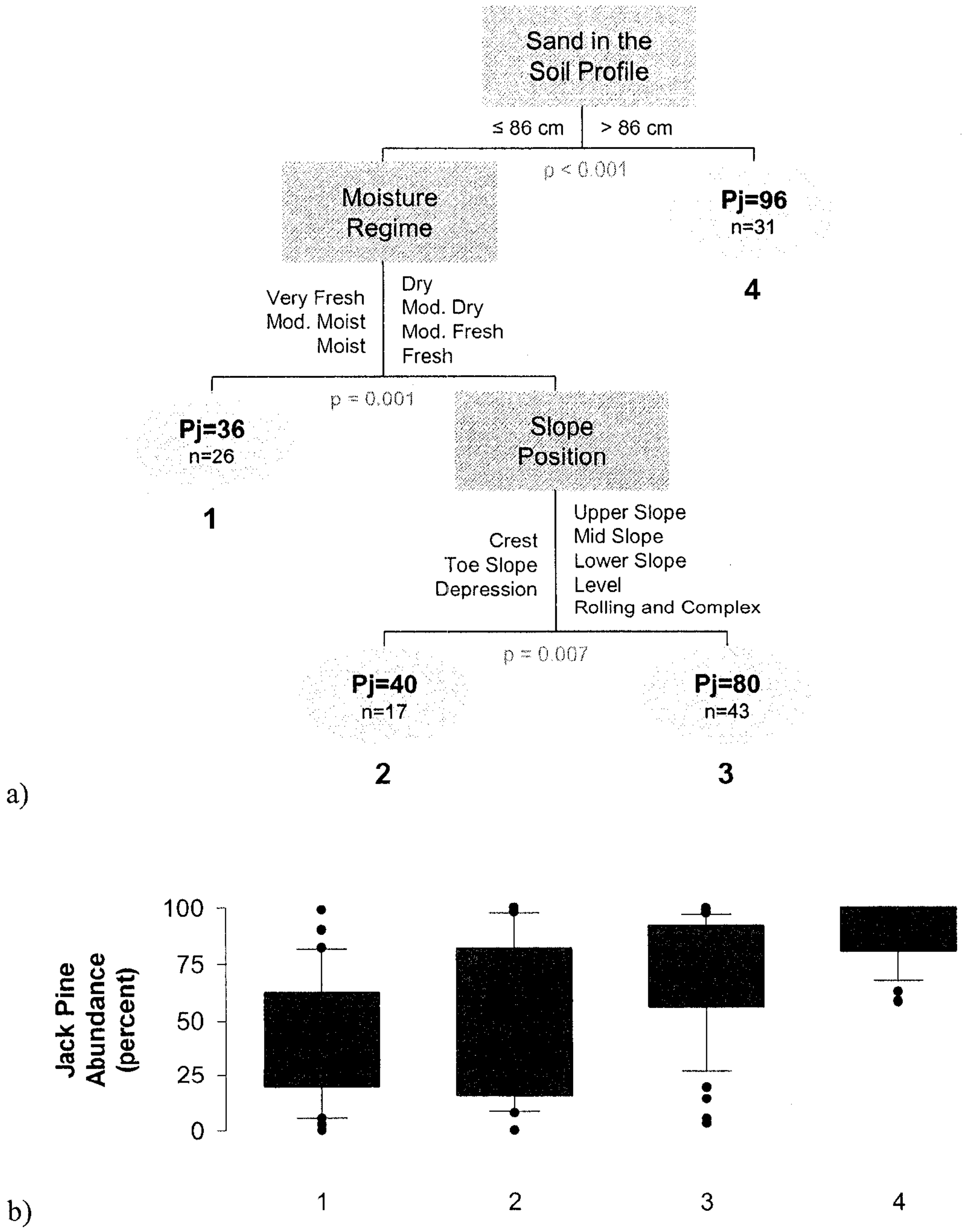


Figure 9. Regression tree: Year 60. Depicted: a) Regression tree predicting jack pine abundance; and, b) associated sample population distributions by terminal node.

The dataset was investigated further to rationalize the groupings in terminal nodes 2 and 3, based on slope position. While all species occurred at similar frequencies in both groups, 82% of the stands grouped into terminal node 2 were positioned on crests, with an average soil depth of 38 cm. In contrast, 93% of stands grouped into terminal node 3 were proportionally split on level terrain, middle-, and upper slope positions with soil depth becoming progressively more shallow with slope gradient (averaging 96, 64, and 43 cm, respectively). These supplementary figures suggest that jack pine abundance has a slightly positive correlation to soil depth; showing that jack pine was less likely to maintain dominance in 60 year-old stands on shallow soils.

Due to the high variability associated with jack pine abundance for stands grouped into terminal nodes 1 through 3, splitting stands on the basis of moisture regime and slope position yielded limited information for predicting jack pine-dominance. At best, grouping sites with very fresh to moist soils, on less than 86 cm of sand in the soil profile only helps to identify candidates that aren't likely to have jack pine-dominant canopies.

When interpreted together, it would seem that deeper drier soils retain higher abundances of jack pine as stands age. The deep sandy sites (terminal node 4), and soils having less than 86 cm sand in the soil profile, but a dry to fresh soil moisture regime, and a slope position associated to moderate or deep soils (terminal node 3) both predicted high abundances of jack pine. Conversely, stands on moister or shallower soils (terminal nodes 1 and 2) are more likely to see ingress by competitor species, or increased losses of jack pine.

Regression Tree: Year 80

A final regression tree was developed using 63 mature stands (Figure 10a). The model suggested five environmental attributes could predict jack pine abundance in stands, 80 years after fire: sand in the soil profile, length of the growing season, slope gradient, moisture regime, and elevation.

Again, sandy sites were the first to be split-out in the regression tree, although slightly deeper sands (90 cm) became the determinate threshold (Figure 10a). Unlike the previous models, these sandy sites were further split, based on the length of the growing season. Those sites experiencing longer growing season (in excess of 166.5 days) were predicted to retain jack pine in high abundances (97%, terminal node 6). In these older stands, sandy sites that have shorter growing seasons were predicted to have lower (70%, terminal node 5), and more varied jack pine abundances (Figure 10b).

Supplementary analysis of the dataset revealed that on average, sandy sites experiencing shorter growing seasons, experienced 165.5 fewer growing degree days, and 0.6°C lower average temperatures during the growing season. It may however, be useful to note that this decision node (based on length of the growing season) was the weakest trend in the regression tree (last decision node to be identified), and might reflect one or more artefacts of the dataset. The supplementary analysis supports this assertion, showing that on average, those stands experiencing longer growing seasons were situated on slopes 12% steeper than their counterparts, and half of the stands experiencing shorter growing seasons also counted for half of all stands to have a known presence of carbonates in the soil.

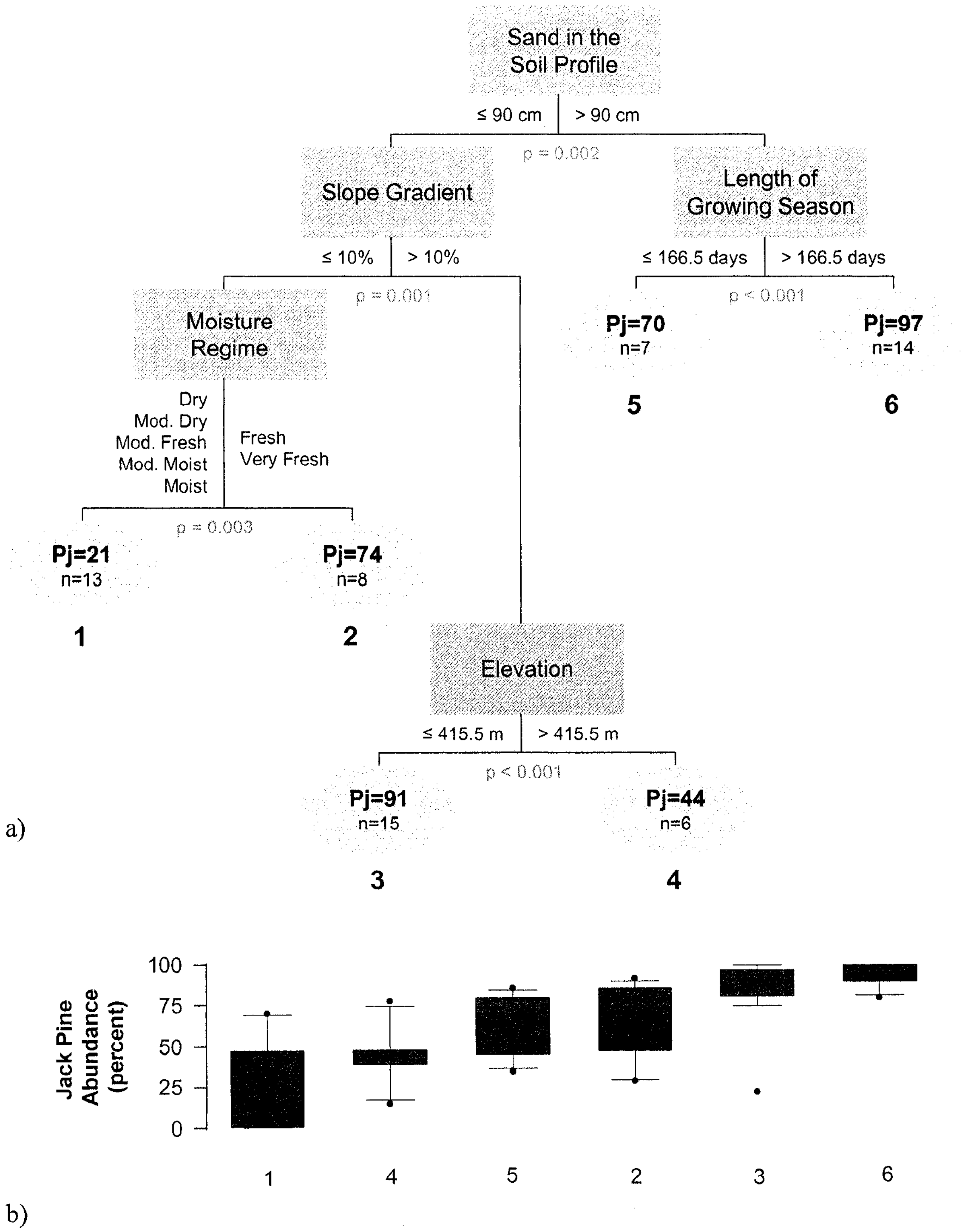


Figure 10. Regression tree: Year 80. Depicted: a) Regression tree predicting jack pine abundance; and b) associated sample population distributions by terminal node.

Perhaps not coincidentally, the remaining sites (those with less than 90 cm sand in the soil profile) were first sub-divided based on a 10% slope threshold; the stands on the moderate slopes (> 10% slope) retained a median abundance of jack pine 53 percentage points higher (at 88%) than those on more level terrain. Stands situated on moderate slopes at lower elevations (≤ 415.5m) retained high abundances of jack pine in the canopy (94%, terminal node 3), as compared to those at higher elevations (44%, terminal node 4). While this trend may be valid, the possibility also exists that the split based on elevation was an ecoregional artefact. Supplementary analysis of the stands grouped into terminal node 4 showed that 67% were from ecoregion 3W. The analysis also showed that 67% of the stands grouped into terminal node 3 were from ecoregion 3S. When contrasted, stands in terminal node 4 were on average, situated at elevations 95 m higher (at 462 m), had shorter growing seasons (by 9 days), 174 fewer growing degree days, and a 0.6°C lower average temperature during the growing season than those in terminal node 3. However, the decision node based on elevation should not be summarily dismissed. Stands from both of these ecoregions may be predisposed to grouping in terminal nodes 3 or 4. As shown in Figure 21 (Appendix 1), stands situated at elevations above 415.5 m were predominantly located in ecoregion 3W, and ecoregion 3S is characterized by gently sloping plains (this dataset showing average slopes of 14%) comprised of shallow sands and loams (this dataset showing average sand contents of 42 cm in the soil profile).

For those sites on relatively level terrain (slope < 10%), the further sub-division of fresh and very fresh moisture regimes from all other sites helped to split stands with moderately high abundances of jack pine (terminal node 2), from those moderately low abundances (terminal node 1). The greatest utility of this split for predicting jack pine-dominance, may be limited to the exclusion of stands grouped into terminal node 1. Here, supplementary analysis showed stands overlying shallow, rapidly-draining soil, and others overlying deep soils of mixed sands, coarse loams and silts were less able to retain high abundances of jack pine in their canopies.

When interpreted together, stands associated to moderate slopes (terminal nodes 3 and 4 together, as well as terminal node 6) were associated to higher abundances of jack pine, and those experiencing shorter growing seasons (terminal nodes 5 and 4) were less able to retain high abundances of jack pine. Again, shallow soils were linked to higher relative compositions of black spruce, trembling aspen and white birch.

ENVIRONMENT AS A PREDICTOR OF JACK PINE PERSISTENCE

Survival analysis was applied to determine whether any of the studied environmental conditions could be linked to the persistence of jack pine at high abundances (relative to other species) in forest canopies. Specifically, 126 jack pine-dominant stands (jack pine $\geq$ 70%) were observed to identify the age at which succession to abundances below 70% occurred. Those succession-events were then linked to local environmental conditions, and determinations made as to whether significant differences in cumulative survival existed between bi-modal or categorical distributions within each of the 17 environmental attributes.

Prior to testing, the dataset was analyzed to ascertain whether the 70% threshold determinate of jack pine-dominance appropriately captured jack pine succession. At issue, stands shifting from 70 to 69% jack pine for example, could not be differentiated in the analysis from those dropping from 100 to 20%; both would register as succession-events. An overabundance of stands at or near the 70% threshold might confound efforts to associate environment and jack pine persistence. This however, was not the case; stand distributions are plotted in Figure 11 as a complete population, and then segmented by censored and non-censored (event) status.

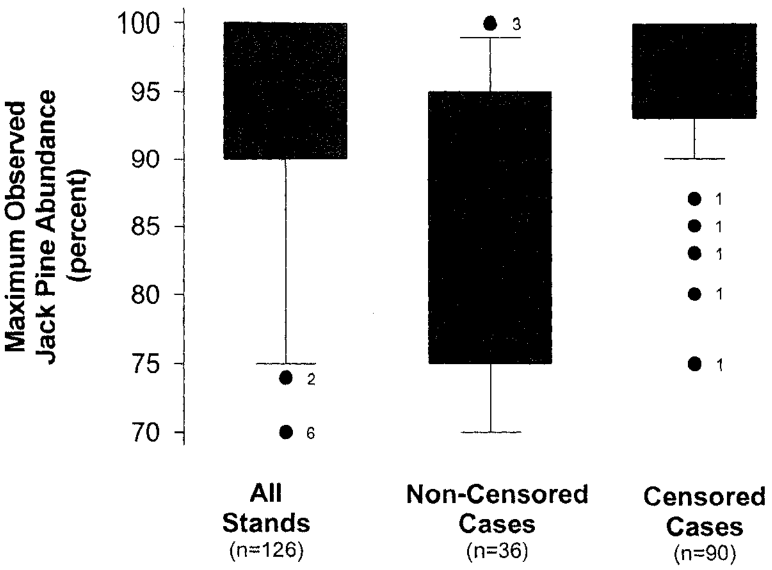


Figure 11. Distribution of censored vs. non-censored (event) cases in dataset.

In the figure, few stands are shown to have highest observed abundances at or near the 70% jack pine threshold. While only a 1% drop in jack pine was sufficient for 6 stands to register as experiencing the succession-event, on average, these stands were observed to drop in abundance by 20%. When considering the distribution of non-censored cases (stands that experienced the succession-event), their highest observed abundances were very broadly-, and evenly-distributed throughout the 70 to 100% range. Not surprisingly, it was mostly stands initially observed at the highest of abundances that were never observed to drop below 70% (censored cases).

The high number of censored cases (n = 90) relative to non-censored cases (n = 36) indicates a mismatch between the lifespan of jack pine populations, and the length of time that the sampled stands were observed; though not prohibitively so. Each of the survival analyses presented in this study showed good distributions of censored and non-censored cases, though ideally, researchers strive for the smallest possible number of censored cases so as to ensure the greatest accuracy in their predictions.

Also prior to testing, a single cumulative survival probability function was derived from all stands (Figure 12). This common survival function showed there was a 25 percentage point drop in survival probability (0.75 probability of continued persistence for jack pine-dominant canopy conditions) in the first 75 years after fire, then a 49 percentage point drop over the subsequent 35 years (0.26 probability at age 110). Although the survival function later appears to level-off, there were few older stands to contribute to the analysis. As a result, subsequent survival analyses were limited to the first 90 years of canopy development.

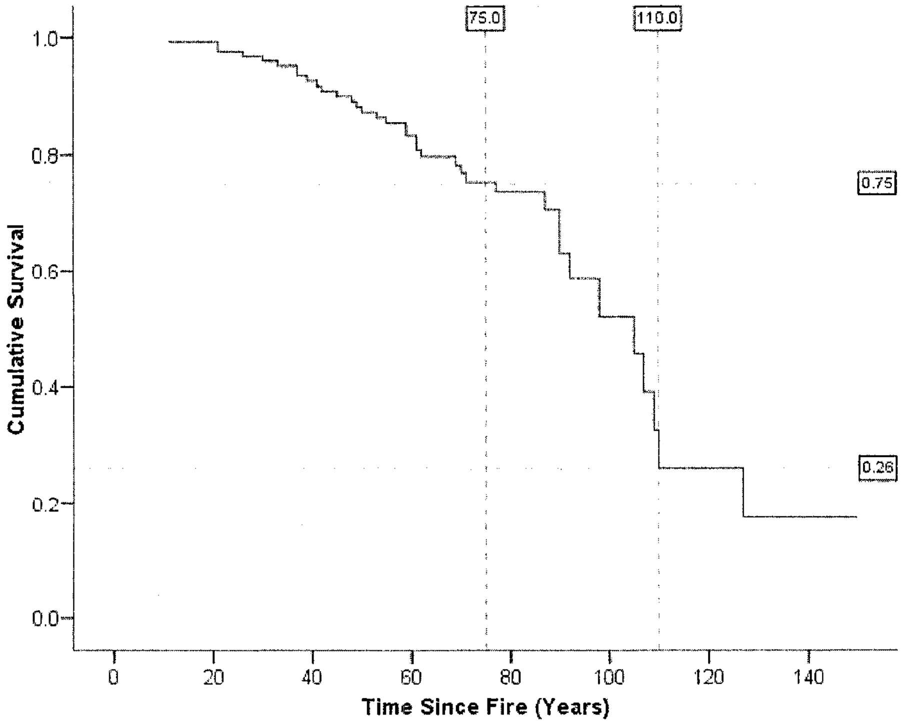


Figure 12. Cumulative survival function for all stands (n = 126).

For each of 17 environmental variables specific to geographic location, topography, soil characteristics, and climate, two or more cumulative survival probability functions were comparatively tested for significance (Table 5). When individually testing each continuous variable, iterative preliminary testing identified the bi-modal distribution (cutting the dataset into two groups) which yielded the highest probability of significance. For categorical variables, preliminary exploration involved lumping, or dropping categories from consideration until an optimal model was found.

TABLE 5. Survival analysis results.

	df	Independent Testing		Multivariate Model	
		Statistic	Significance[i]	Statistic	Significance[ii]
Geographic Location					
Longitude	1	0.01	.932		
Latitude	1	0.38	.538		
Topogaphy					
Elevation	1	4.08	.043 *	-	-
Slope Gradient	1	10.55	.001 *	6.88	.009 *
Slope Aspect	3	1.64	.651		
Slope Position	1	5.65	.017 *	-	-
Landform	3	1.13	.770		
Soil Conditions					
Mode of Deposition	2	0.07	.964		
Depth to Bedrock	2	1.83	.402		
Moisture Regime	2	0.53	.466		
Dominant Soil Texture	2	2.72	.099 *	-	-
Sand in the Soil Profile	1	3.74	.053 *	4.52	.033 *
Coarse Loams in the Soil Profile	1	6.39	.011 *	-	-
Climate					
Annual Precipitation	1	0.36	.550		
Length of the Growing Season	1	0.44	.506		
Growing Degree Days	1	0.03	.867		
Precipitation During Growing Season	1	8.08	.004 *	4.00	.045 *

Note:
[i] $\alpha = 0.25$
[ii] $\alpha = 0.05$
* $p \leq \alpha$
\- excluded via backwards stepwise regression

Seven variables were found to individually influence the persistence of jack pine-dominant canopy conditions ($\alpha = 0.25$): elevation, slope gradient, slope position, dominant soil texture, sand in the soil profile, coarse loams in the soil profile, and precipitation during the growing season. These variables were in turn included in a multivariate model to identify those variables having significant influence ($\alpha = 0.05$) over succession while accounting for the confounding effects of the other influential variables. Summarized in Table 5, the multivariate model itself tested significant at a probability above 99.9% ($p < 0.001$), and identified site, soil, and climate as having an important influence over succession. Using a backwards stepwise procedure, only 3 of the 7 variables were retained in the final model: slope gradient, sand in the soil profile, and precipitation during the growing season.

Slope Gradient

Survival functions associated with two slope sub-groups (0% and > 0% slope) are presented in Figure 13. The survival functions associated to level and sloped terrain diverged after 25 years of development; the difference increasing with age. In the subsequent 70 years, stands on level terrain were shown to have much lower probabilities of persisting as jack pine-dominant canopies than those on sloped terrain. For example, the difference in survival probability between the two functions was only 12.2 percentage points (0.965 - 0.843 = 0.122) at year 40, but more than doubled (0.825 - 0.543 = 0.282) by year 80.

Sand in the Soil Profile

Preliminary testing identified 50 cm as the optimal bi-modal split for sand in the soil profile; the associated survival functions are plotted in Figure 14.

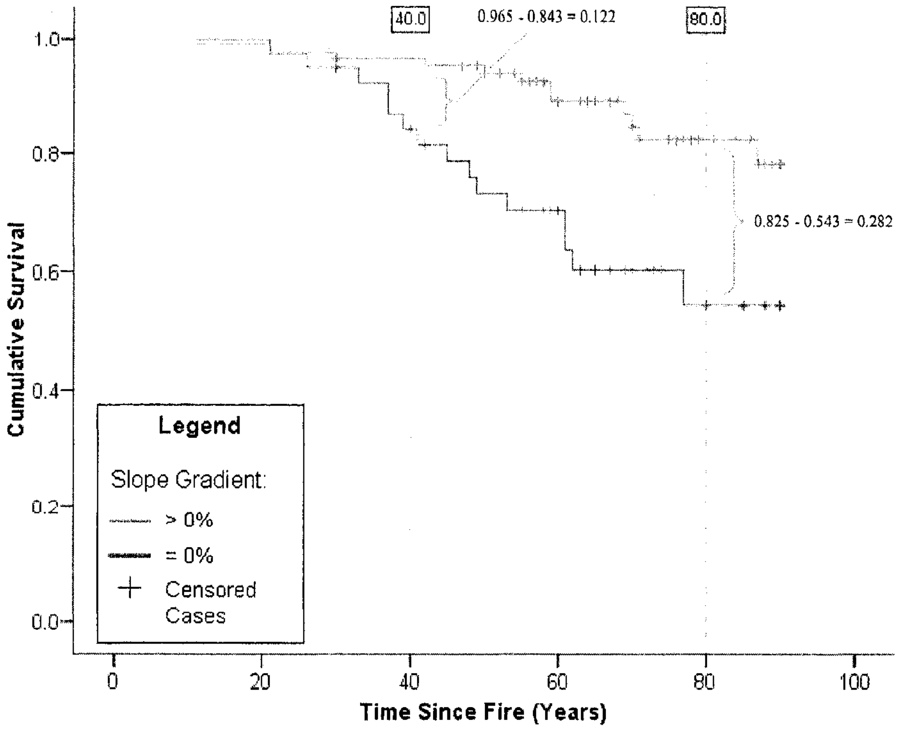


Figure 13. Survival functions for stands on level (n = 39) vs. sloped (n = 87) terrain.

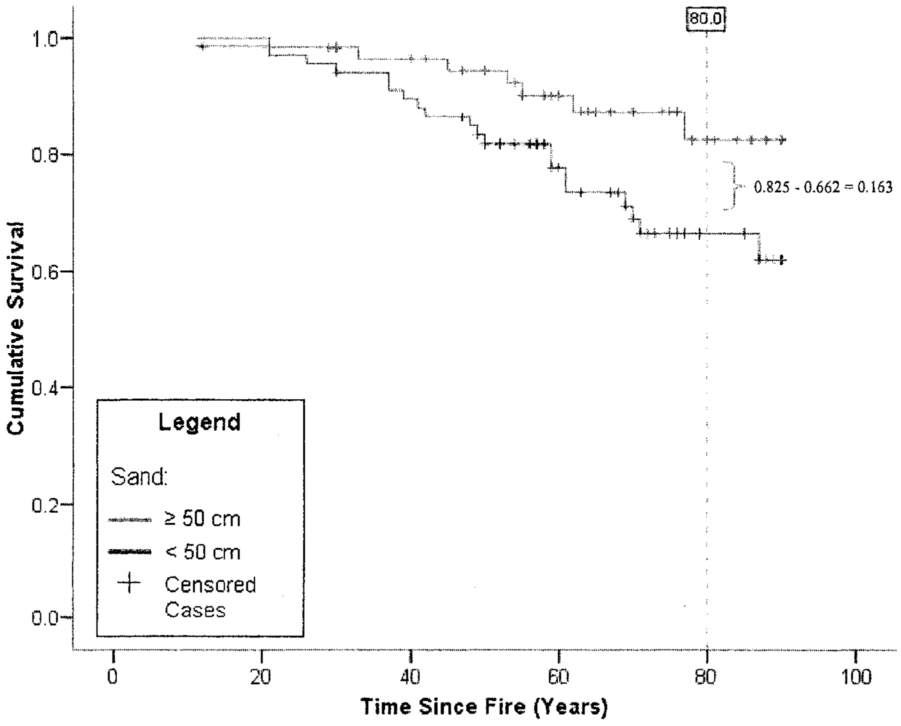


Figure 14. Survival functions for stands overlying soils with high (n = 58), vs. low (n = 68) sand content.

Showing little difference in the first two decades of development, the survival functions then diverge. Those stands overlying deep sandy soils (≥ 50 cm sand) were observed to persist with jack pine-dominant canopy conditions in higher proportions at any age, than those overlying lesser depths of sand. Interestingly, the degree of separation between the functions was not as pronounced as it was for the slope functions; differing in probabilities by only 16.3 percentage points (0.825 - 0.662 = 0.163) at age 80.

Precipitation During the Growing Season

In addition to slope gradient and sand in the soil profile, precipitation during the growing season was also found to bear influence over the persistence of jack pine-dominant canopy conditions. Survival functions associated to two sub-groups, split at a precipitation threshold of 428 mm are plotted in Figure 15.

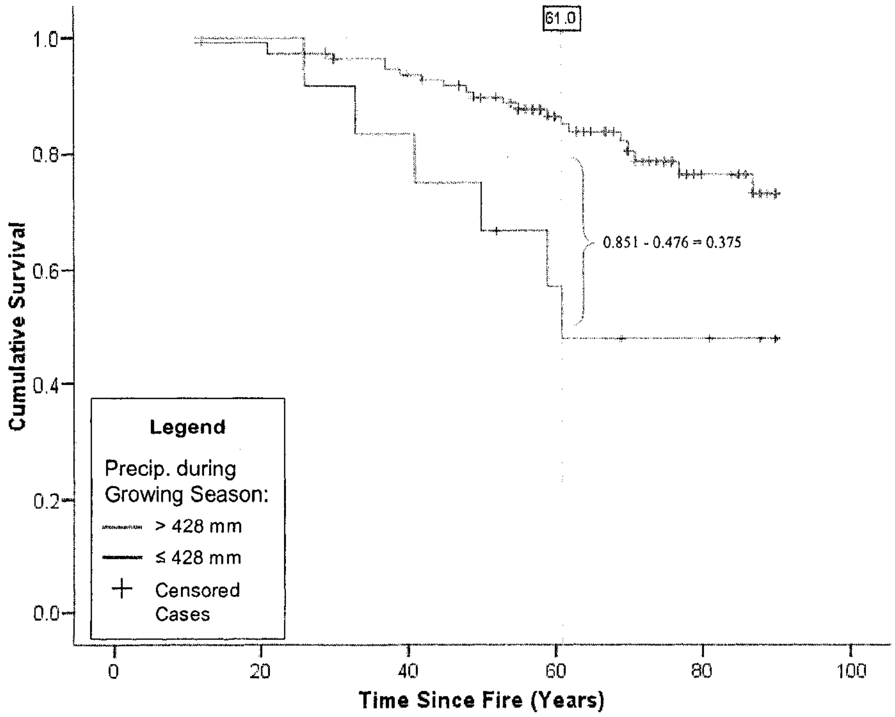


Figure 15. Survival functions for stands experiencing more (n = 112), vs. less (n = 14) than 428 mm precipitation during the growing season.

The 428 mm threshold split the dataset at the lower 35th percentile of the sampled range of precipitation during the growing season (379.4 to 517.9 mm), though only captured 8% of stands in one of the groupings. Despite this potential deficiency in sample size for the low-precipitation sites ($\leq$ 428 mm), the survival functions did show definite divergence after 25 years of development. Jack pine-dominant stands receiving less rain were less likely to retain high abundances of jack pine. At 61 years of age, there was a 37.5 percentage point difference in survival probability (0.851 - 0.476 = 0.375).

Supplemental reviews of the dataset revealed that on average, the low-precipitation sites received 123 mm less precipitation annually (623 vs. 746 mm), 59 mm less during the growing season (404 vs. 463 mm), and were situated at elevations 127 m lower than the other stands (258 vs. 385 m). On these sites, black spruce occurred in all stands (vs. a frequency of 79% in the entire dataset), white birch occurred half as often than in the entire dataset (14 vs. 35%), and trembling aspen occurred at approximately the same frequency (43 vs. 41%).

When mapped (Figure 16a), low-precipitation sites appeared to be clustered in three areas of the province (far west, far east, and just west of Lake Nipigon) with another single site in the western portion of ecoregion 3E. While spread across the landscape, with the appearance that they are intermixed with the remaining study sites, the locations of the low-precipitation sites are immediately rationalized when contrasted against the surface model of precipitation during the growing season for Ontario (Figure 16b). Between each of the clusters, the map shows ranges of higher precipitation during the growing season.

While one might suspect that lower persistence of jack pine-dominance on low-precipitation sites might be associated to growing season and temperature constraints, it should be noted that on average, these sites had comparatively longer growing seasons (175 vs. 171 days), had 117 more growing degree days (1368 vs. 1251 gdd), and had higher average annual (1.2 vs. 0.9°C) and growing season temperatures (13.2 vs. 12.7°C) than the rest of the sites.

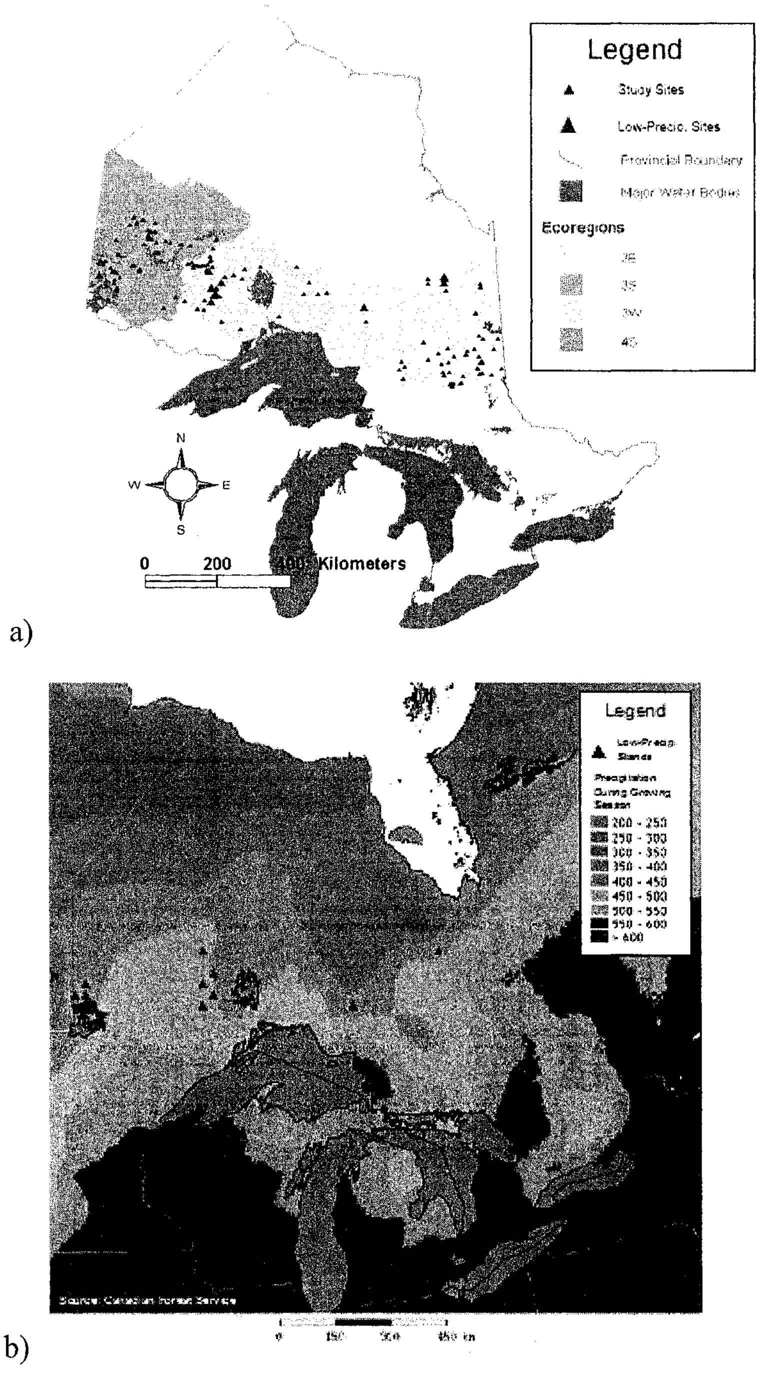


Figure 16. Mapped locations of low-precipitation sites (n = 14): a) relative to the rest of the dataset (n = 112); and b) relative to the surface model of precipitation during the growing season for Ontario (CFS 2007).

DISCUSSION

SUCCESSIONAL PATTERNS

Observations of species' compositional change through time for the 178 stands supported Cogbill's (1985) argument that continual recruitment in the boreal forest is not the norm, in that species predominantly establish at stand initiation, then dominate the canopy for a century or more. Rarely during data collection were species populations observed to collapse from the canopy, and ingress populations were normally contemporaries to the canopy cohort. Much of the observed succession was attributed to the relative growth rates, and influence of suppression upon species that pioneered the site following disturbance. This would suggest that succession in jack pine-dominant canopies over the first century of development is largely determined at stand initiation.

Black spruce was by far the most commonly observed co-occurring species (Figure 6). Given its role as a pioneer species, moderate-to-high shade tolerance, propensity for natural recruitment in the understory, and long lifespan (Sims *et al.* 1990), it is reasonable to assume that black spruce will figure prominently in most late-successional derivations of jack pine-dominant stands; thereby supporting the conclusions of Desponts and Payette (1992), and De Grandpré *et al.* (2000) that in prolonged absence of fire, these stand compositions shift towards dominance by black spruce.

Jack pine-trembling aspen mixtures were comparatively rare, and most of these canopies were quickly observed to experience ingress by a third or more species (Figure 6). Observed interactions between jack pine and trembling aspen were consistent with those described by Longpré *et al.* (1994), and Béland *et al.* (2003) who found that while trembling aspen proved a stronger competitor than jack pine, both species are influenced more by intra-specific competition and really have no competitive influence over each other. Once distinguishable on a photograph, proportional shifts were rarely observed in jack pine-trembling aspen canopies; at least until white birch or black spruce ingressed. Béland *et al.* (2003) explained that this trend was often due to each species' tendency to grow separately, in clumps, than to intricately mix – leaving inter-specific competition to occur only on the border of neighbouring clumps, and intra-specific competition to occur to a greater degree within. Clumps of clonal aspen were frequently observed in the photographs whenever the species was noted.

White birch was commonly observed to initiate or ingress into canopies of most any species mixture (Figure 6). Also consistent with the findings of Longpré *et al.* (1994) and Béland *et al.* (2003), white birch rarely affected other populations in a canopy as suppressed individuals generally grew up from underneath, often in a canopy gap that it itself had created early in the stand's development. Longpré *et al.* (1994) noted white birch to be an inferior competitor to jack pine as it was invariably overtopped by the pines, but also found that when in combination with white birch, jack pine populations had comparably different structural features that might influence its persistence on a site (comparable to pure jack pine canopies and jack pine-trembling aspen mixes). Attributing the effect to jack pine seedling mortality due to shading by white birch regeneration early in canopy development, Longpré *et al.* (1994) contended that the remainder of these jack pine populations undergo lesser amounts of intra-specific competition, thereby freeing them to commit their limited resources to radial growth, rather than to height growth. Such populations of jack pine would conceivably have greater stability, and larger canopies and root systems than those that grew under high-density conditions, thereby making them less susceptible to competition. While an intriguing concept, insufficient replication within older stands precluded a confirmation of this theory.

Frelich and Reich (1995) found that directional change in canopy composition for jack pine-dominant stands was characterized by the gradual loss of jack pine and trembling aspen, replaced by contemporaneously initiated, and regenerated black spruce and white birch. Early gap-phase dynamics has been cited as the mechanism by which such loss and regeneration occurs (McCarthy 2001). Under this process, canopy density drops with age, as individual or group mortality due to inter- and intra-specific competition causes micro-gaps, allowing greater amounts of light to penetrate to the forest floor. This in turn provides tree species in the understory with the resources and space required to slowly grow into the canopy. This gap-phase process, however, was not evident when viewing the stands from chronosequenced photographs. Instead, ingress of understory black spruce and sometimes white birch into the canopy appeared more consistent to what Hunter and Barbour (2001) called "through-growth". Under this theory, the growth of understory populations were slowed when outpaced by jack pine, but never halted (as they might have been, under gap-phase dynamics – when waiting for a canopy gap to open). In time, these species infiltrated into the canopy; not in the spatially- and temporally-scattered manner one might expect from gap-phase dynamics, but as a cohesive group. This trend was likely driven by the comparatively high amounts of light penetration through jack pine canopies to the forest floor (compared to deciduous or shade-tolerant conifer species) that was noted by Messier *et al.* (1998). While Cumming *et al.* (2000) described classic gap-phase dynamics in trembling aspen canopies, where full sun and space was required for aspen to grow beyond the sapling stage to fill the gaps, an identical trend in jack pine is doubtful.

Reputed to grow in pure, even-aged stands (Rudolph and Laidly 1990), the frequency by which jack pine remained the exclusive species within canopies was surprisingly low (Figure 6). Just over a quarter of the stands under investigation (47 of 178 stands) were observed at some point in time to have a pure jack pine canopy. Of that count, only 17 (less than 10% of the stands) persisted as such beyond their respective periods of observation; and many of those stands were observed early in their development. While authors such as Carleton and Maycock (1978), Carleton (1982), Kenkel (1986), and Kenkel *et al.* (1998) made a point of noting that on dry sandy and rocky sites, a near non-existence of understory regeneration causes canopies to remain dominated by jack pine in open canopies for long periods – becoming "savannah-like", when considering the time required to get to this state, and considering local fire cycles, achieving a savannah-like condition may be an ecological rarity. No such conditions were observed in the dataset.

The common incidence of stands showing no change or the late onset of loss in Figure 7 suggests that jack pine is quite capable of maintaining stable populations for long periods in mixed canopies (beyond 125 years in one case). While the presence of competing species on a site may not presuppose declines in jack pine abundance, when declines did occur, they were generally of a moderate rate. This again may be an influence of what was a fully-stocked jack pine canopy, experiencing through-growth (Hunter and Barbour 2001), such that the steady ingress of black spruce is leading to gradual shifts in relative abundances without causing rapid declines in jack pine populations. Black spruce is entering the canopy, but not yet shading out the jack pine;

jack pine mortality at this point in time is still probably due to intra-specific competition in the upper canopy.

On some occasions, either rapid increases or decreases in jack pine abundances were observed; primarily in young stands. Observance of these shifts was most likely an artefact of photo interpretation difficulties. The transparent (fuzzy) appearance of jack pine on aerial photographs (Zsilinsky 1966) is compounded by their small size, and large stem counts typical to early post-fire regeneration (St-Pierre *et al.* 1992).

ENVIRONMENTAL DRIVERS OF JACK PINE SUCCESSION

Regression trees were used in an exploratory capacity to gauge the underlying premise of the research: that local environmental attributes indeed influence forest succession, and to gain insight as to their relations. Survival analysis was also used to explore, and then to test synecological associations to environment. For the purposes of this discussion, the causality of those environmental attributes associated in the analyses to measures of jack pine abundance and persistence is presumed.

The regression tree model using stands sampled after two decades of development was reported to have no optimal solution; no local environmental attributes were proven useful to predict jack pine abundance in the canopy at Year 20. This null result would suggest that beyond any influence local environmental attributes might play in the establishment of jack pine populations post-fire, the dynamics between species in the first few decades of development is not influenced by site-quality factors. More likely, stand dynamics of young canopies are driven by pre-disturbance factors, seed source availability, and species' comparative life histories and growth rates, as they compete for soil nutrients and water (regardless of quality and amount) prior to canopy closure in what Kenkel (1988) termed “the early scramble phase.” When testing the influence of environmental attributes using survival analysis, this trend was again noted. For each plotted variable (Figures 13 through 15), contrasted survival functions never diverged until after 20 to 25 years of development.

After four decades of development (Figure 8), dominance by coarse soils (sands) in the soil layer predicted high abundances of jack pine in canopies. This overriding effect of sand to retain high abundances of jack pine continued into stand maturity (Figures 9 and 10), though at some point after the sixth decade, the effect began to diminish. For some stands, the cumulative effects of sand over succession were eventually diluted by climate – specifically, by the length of the growing season. Lower abundances of jack pine were recorded on sandy sites experiencing shorter growing seasons (fewer than 166.5 days). Even though the sands were deep on these sites, stands growing in areas that experienced shorter growing seasons faced comparably greater amounts of competition as the climate during the growing season was not as extreme as those areas with long growing seasons, thereby negating jack pine’s drought tolerance and other life history advantages.

As an aside; in their description of jack pine silvics, Rudolph and Laidly (1990) noted from the works of Plonski (1960) that mean annual increments of volume within jack pine canopies of average productivity begin to culminate after six decades of development. This trend may contribute to an ecological rationale for the observation in this study where jack pine on deep sands experienced losses of abundance at the same point in development. Sixty years may represent an ecological limit for jack pine on some sites, both in productivity and competitive capacities.

The importance of sands as a predictive indicator of succession away from jack pine-dominant canopies was also confirmed via survival analysis. Dominant soil texture (to which sand is associated), and sand in the soil profile, were both found to independently influence persistence (Table 5). When added to the multivariate model, sand in the soil profile proved highly significant, despite the confounding influences of two other important environmental drivers retained in the final model.

The association of deep sands to the persistence of jack pine-dominant canopies is well-established in the literature. Amongst many examples, Kenkel (1986) identified ten variants of jack pine-dominant community types, most of which had a described association to deep sands. More recently, Kenkel *et al.* (1998) made an extensive summary of forest dynamics in northwestern Ontario wherein two stand types were dominated by jack pine, both of which again were described as predominantly overlying sandy soils. The survival analysis confirmed that those stands overlying deep sands had higher probabilities of survival; persisting longer than those with less or no sand. For example, 82% of jack pine-dominant stands overlying deep sands survived as such for more than 90 years, whereas only 62% of stands on other site types survived as long.

Differential life histories (Bergeron 2000) coupled with the low moisture- and nutrient- availability characteristics of the soil (Kenkel *et al.* 1998) may give jack pine the conclusive advantage on these sites that saw such high abundances reported in the three regression trees. While jack pine may not be highly productive on these sites, it can maintain canopy stature far beyond what competing species can manage.

Slope gradient was also suggested to be a driver of succession in jack pine-dominant stands. The variable was featured in the last regression tree (Figure 10) as a second-order decision node, splitting the sites at a threshold of 10%. Stands situated on slopes of lesser grades than 10% did not maintain high abundances of jack pine. Even for those sites on deep sands, abundances were generally higher when stands were on moderately sloped terrain (> 10% slope).

Although the determinate threshold (0% slope) did differ from that in the regression tree (10%), slope was found to be highly significant in the survival analysis (Table 5). At year 90, only 20% of stands on sloped terrain (compared to 45% for level terrain) were observed to have succeeded to canopy compositions where jack pine no longer dominated (Figure 13). The stands on level terrain likely experienced greater competition than those on sloped terrain, due to the greater likelihood for access to the water table, or to finer-textured soils that have greater nutrient loads and water retention capacity. These associated conditions offer other species a chance to outcompete jack pine. In contrast, stands on sloped terrain are more likely to experience increased drainage, and by association, shallower, drier and coarser (more poorly formed) soils, as well as increased exposure to the elements. Here, competitor species may be less capable of establishing themselves and competing with jack pine.

In the literature, slope was frequently found to mediate differences in forest productivity and succession. Schmidt and Carmean (1988) showed that on sands, jack pine site index was inversely associated to slope, and Brisson (1992) found that on tills, slope may be a better determinant of productivity than texture. Host *et al.* (1987) found the patterns of compositional change in oak-dominated ecosystems of lower Michigan were strongly related to topographic and edaphic differences among glacial landforms; slope figuring prominently among those factors. Clayden and Bouchard (1983) identified slope as an obvious controlling factor of soil coverage and depth - thereby influencing succession; an argument supported by Bridge and Johnson (2000) who investigated vegetational gradients along slope profiles.

In addition to sand and slope, precipitation during the growing season was also suggested to be an important driver of succession in jack pine-dominated stands. While it was not featured in any of the regression trees, the variable was found significant in the survival analysis (Table 5). In the literature, total precipitation during the growing season was directly linked to jack pine productivity by McKenny and Pedlar (2003). In developing a regression tree to predict site index for jack pine using site and climatic variables, precipitation during the growing season was twice identified as a third-order splitting rule (variable: "total precip. during period 3", Figure 17). In both cases, higher amounts of rainfall on sites with moderate-to-deep soils yielded higher predictions of site productivity.

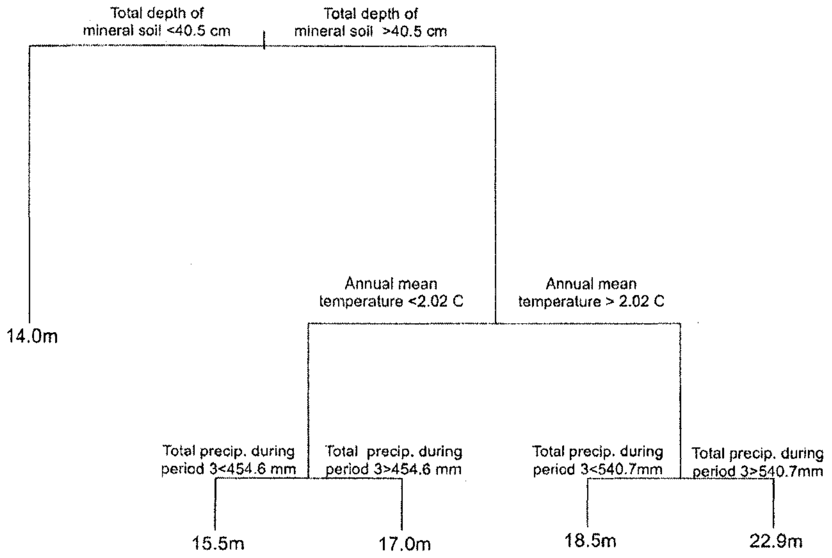


Figure 17. Regression tree predicting jack pine site index (McKenny and Pedlar 2003).

By 61 years of age, only 47.6% of stands in the current study receiving less than 428 mm precipitation during the growing season retained high abundances of jack pine in their canopies (Figure 12). That compared to 85.1% survival for stands receiving more precipitation. This trend seems counterintuitive. Jack pine is generally considered to have the competitive advantage on dry sites, yet was observed here to have lower probabilities of persistence at any age than sites receiving more precipitation. Supplementary analyses showed there to be no association to the trend by any growing season or temperature constraints. At best, 428 mm precipitation during the growing season may represent an ecological limit to jack pine-dominance of canopies. At any location in boreal Ontario, black spruce and trembling aspen may have a competitive advantage over jack pine that is only revealed when precipitation is consistently low. Dang and Cheng (2004) found that black spruce and trembling aspen seedlings were better able to grow in colder soils than jack pine, but not as effectively in warmer soils. This ability to begin growth when the soils are still too cold for jack pine would permit both species to make use of precipitation that fell earlier and later in the year than could jack pine. In areas of the province where sufficient rainfall (> 428 mm) occurs during the growing season, this advantage may be masked by jack pine's optimal growth in warm soils (Dang and Cheng 2004), and other life history advantages such as tolerance to drought (Sims *et al.* 1990). Jack pine still occurs in areas receiving low-precipitation, but does not persist as long as the dominant canopy component. In these regions, jack pine may rely on comparatively shorter fire cycles to maintain a strong presence on the landscape. Brooks *et al.* (1998) noted a similar trend in mature jack pine forests; concluding that moisture limited the southern extent of the range for jack pine and cold soil temperatures limited its northern extent. Perhaps in the mid-range low-precipitation sites identified in the current study, both factors that limit the northern and southern extents of jack pine are having a synergistic effect on the persistence of jack pine-dominant canopy conditions.

A number of other variables were also suggested to influence jack pine succession. In both the regression tree exercise (Figures 8 through 10), and independent variable survival analysis (Table 5), dominant soil texture, slope position, and elevation were identified as important, though none of these variables were retained in the multivariate survival analysis. Independent variable survival analysis also suggested coarse loams in the soil profile to be important, and moisture regime was featured in two of the regression trees. Many of these factors were echoed in the findings of Bridge and Johnson (2000), who concluded that slope position was an important determinant of forest composition as down-slope profiles were often analogous to increases in nutrient (soil texture) and moisture (moisture regime) gradients. Béland and Bergeron (1996) also listed surface deposit (soil texture, soil depth, and bulk density) and moisture regime as predictors of potential jack pine productivity. Gauthier *et al.* (2000) concurred.

While a number of other variables were not shown to be significant by either of the analytical techniques, some of these findings may be artefacts of the sampling design and the small size of the sample population. Landform for example, is commonly thought to influence succession (Hills 1952, Host *et al.* 1987). However, sparse representation across the twelve landform categories limited the test to just four: ground moraines, outwash plains, lake plains and bedrock sites (Table 9, Appendix 1). In the instance of slope aspect (Table 7, Appendix 1), the growth and yield monitoring plot networks upon which this study relied tended not to target anything more than slight-to-moderate slopes, resulting in low representation in all slope aspect categories and an overabundance of null values (null aspect – as a function of no slope).

MANAGEMENT IMPLICATIONS

Survival analysis may prove to be a viable solution to the development of empirically-based forest succession input parameters for forest management planning and other forecast models. Using photo chronosequencing, estimations of "time-to-event" can be made across all site conditions for any of Ontario's parks and forest management units. While the application of survival analysis in this study was of the most basic nature, more sophisticated designs (Collett 2003) can easily accommodate complex forest unit[11] definitions and situations where time-to-event is measured not from stand initiation, but from the succession-event of another forest unit. For example, stands in a mixed conifer forest unit may have initiated as a mixed conifer, or may have initiated as a jack pine dominant forest unit, only later to shift to mixed conifer. For any forest unit, quantitative estimates could be derived for what proportions of stands undergo succession to another forest unit, and what proportion never leaves.

Survival functions can provide even the most sophisticated models with annual increments of probability-based succession rules, or can be tailored to report in longer increments. In the case of Ontario's non-spatial planning tool: the Strategic Forest Management Model (SFMM), the life table associated to the survival function featured in Figure 12 can be segmented into 20-year age-classes, and derived proportions of

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[11] Forest units are defined for reporting purposes in forest management planning as aggregates of forest stands that have similar species compositions, that develop in a similar manner, and will be managed under the same silvicultural system (OMNR 2004a).

terminated stands for each age class (dashed box, Table 6) can serve as respective succession probabilities in the forecast model (Figure 18).

TABLE 6. Life table for all stands (n = 126).

Age Class	No. Entering Age-Class	No. of Subjects Censored	No. of Terminal Events	Proportion Terminated	Proportion that Survived	Cumulative Survival
0-19	126	1	1	1%	99%	0.99
20-39	124	7	8	7%	93%	0.93
40-59	109	25	10	10%	90%	0.83
60-79	74	34	7	12%	88%	0.73
80-99	33	20	5	22%	78%	0.57
100-119	8	1	4	53%	47%	0.27
120-139	3	0	1	33%	67%	0.18
140-159	2	2	0	0%	100%	0.18

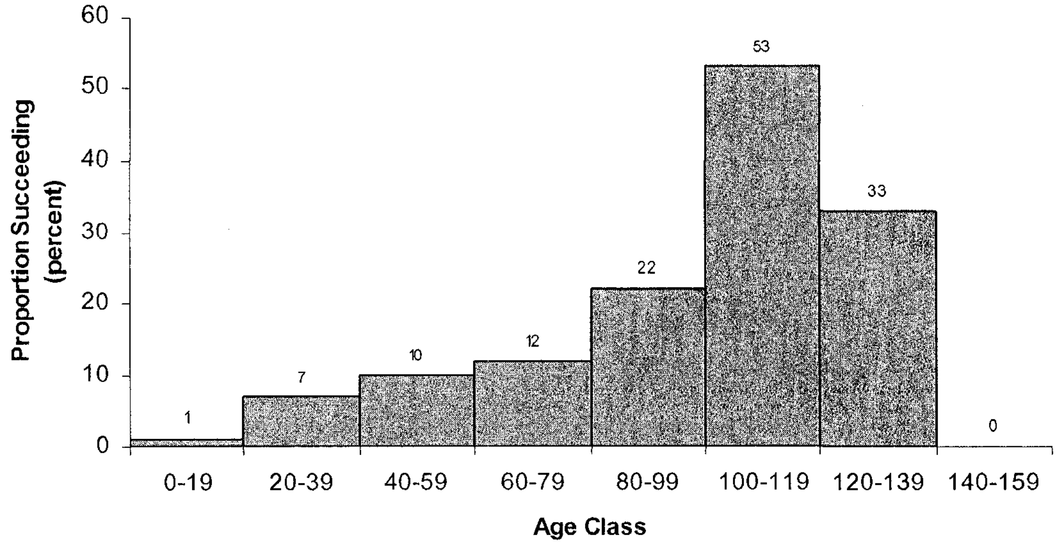

Figure 18. An example of SFMM succession rules for a jack pine-dominant forest unit using the survival analysis approach.

While cautioned against inferences drawn for stands much beyond 90 years of age, the application of the succession inputs depicted in Figure 18, would result in 18% of jack pine-dominant stands persisting as such beyond 140 years of development.

Survival analysis on its own, however, provides only half the picture. It addresses the question: ‘When does it leave?’, but not ‘Where does it go?’. For its suitability to address the second question, logistic regression appears to be a likely complement to survival analysis. In the current study however, the sample population was too small to permit the application of logistic regression; only anecdotal evidence on successional destination could be offered.

Should forest practitioners wish to improve the accuracy of their forecast models, they could refine them by incorporating one or more of the environmental attributes identified in this study as having a significant influence upon the persistence of jack pine-dominant conditions in forest canopies. With the advent of forest resources inventories that feature ecosite information, or in combination with landform and site estimates available from Northern Ontario Engineering Geology Terrain Study maps (Gartner *et al.* 1981), or with the use of the national climate model (pers. comm. McKenney 2007), jack pine-dominant forest units could be divided into one or more subordinate forest units. For example, two jack pine-dominant forest units, one for sites on deep sands, and one for those on other soil conditions could be created, with each featuring tailored succession inputs.

Survival analysis also has a potential application to study climate change. A second version of the Cox Regression method of survival analysis is capable of considering time-dependent covariates (Collett 2003). When applied with historic monthly or annual climate measures, inferences can be drawn to summarize the influence of change in each climate variable upon forest succession.

CONCLUSION

The hypothesis argued that local environmental attributes influence the successional trends of jack pine-dominant stands of boreal Ontario. In testing the associated null statement, cumulative survival probability functions for the persistence of jack pine-dominant canopies were independently derived for-, and tested across 17 environmental variables specific to geographic location, topography, soil characteristics, and climate. Were the null statement true, testing would have revealed low probabilities of significance ($p > 0.05$) for all variables, suggesting that none of them bear influence over succession. This was not the case; a select few variables were found to independently influence the persistence of jack pine-dominant canopies. Further, some of the influential variables were found to remain significant when added to a multivariate model. On these findings, the null statement to the hypothesis was rejected, suggesting plausibility of the notion that local environmental attributes have influence over succession of jack pine-dominant stands in boreal Ontario.

Above all, deep sands were found to be influential ecological drivers of succession in jack pine-dominated stands of boreal Ontario, followed by the topographic and climatic variables: slope gradient, and precipitation during the growing season. Using the discussed inferences for each driver in combination with existing forest and climate information resources for northern Ontario, efforts to model jack pine succession can be empirically refined.

It is recommended that in any similar study of jack pine succession, special focus be made to sites receiving less than 428 mm precipitation during the growing season, so as to corroborate the findings of this study. It is recommended that similar studies to this be undertaken for other tree species in boreal Ontario, so as to determine the primary ecological drivers for dominant canopy-types, and for mixedwood conditions. It is further recommended that photo chronosequencing could be used 'en-masse' across entire forest management units and parks, in the absence of corresponding samples of site, to derive empirically precise inputs to both spatial and non-spatial landscape forecast models – or at the very least to test the accuracy of inputs derived by other means. The resources, and photo history already exist within much of boreal Ontario to carry out each of these recommendations.

The application of photo chronosequencing was a logistically-effective method of sampling through time to observe succession within forest canopies. While otherwise an effective approach, very narrow selection criteria when selecting candidates for this study did prove burdensome. The investment per sample stand during data collection ranged from 0.5 to 1 person days (averaged across activities). However, the time required to exclude a sample, based on the selection criteria took almost as long. If a similar study were to be undertaken, it is advisable to apply less rigorous criteria for selection (i.e. a target species or disturbance type). Invest the extra time to derive a much larger, much broader dataset – and thereby achieve economies of scale.

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APPENDIX

APPENDIX 1
DISTRIBUTIONS OF ENVIRONMENTAL ATTRIBUTES

The influences of 17 environmental attributes were explored and tested in this study (listed in Table 2). To convey the breadth of representation of Ontario's boreal landscapes that were captured in the sample, the distributions of study sites are presented for each variable, referenced by ecoregion.

VARIABLES SPECIFIC TO GEOGRAPHIC LOCATION

Two variables specific to geographic location were considered: latitude and longitude. In addition to Figure 2, the latitudinal and longitudinal distributions of stands are presented in Figure 19 and 20, respectively.

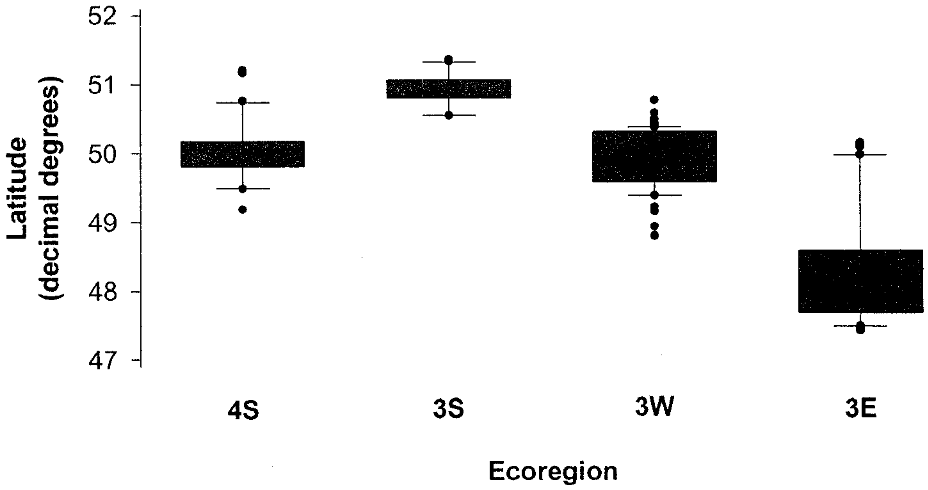

Figure 19. Distribution of stands by latitude.

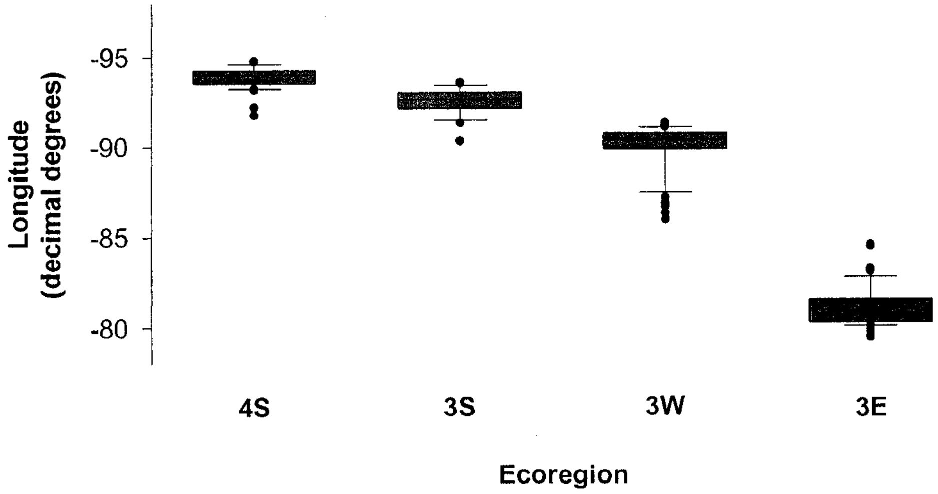

Figure 20. Distribution of stands by longitude.

The distributions across both variables showed the relative geographic breaks that characterize each ecoregion.

VARIABLES SPECIFIC TO TOPOGRAPHY

Five variables specific to topography were considered for their influence over succession: elevation; slope gradient; slope aspect; slope position; and, landform. The distribution of stands across ecoregions by elevation is presented in Figure 21. The relative distributions by elevation, show how the western-most populations (those in ecoregions 4S and 3S) are all located on the height of land, whereas some stands in 3W, and several in 3E were located on the lower reliefs of either the Ottawa River, Lake Nipigon, or Lake Superior basins. The highest-elevation sites were also found in ecoregion 3W.

The distribution of stands by slope gradient is presented in Figure 22. Here it is seen that the majority of samples were on level terrain or moderate slopes.

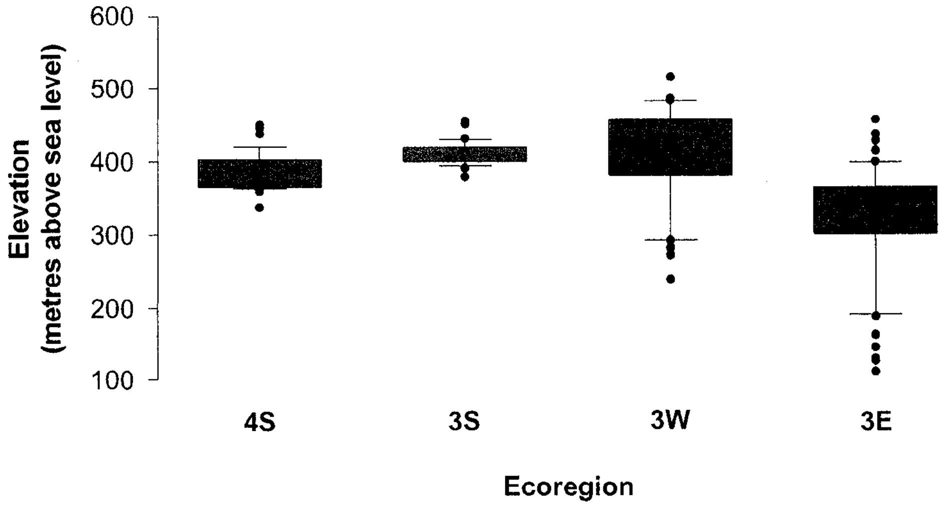

Figure 21. Distribution of stands by elevation.

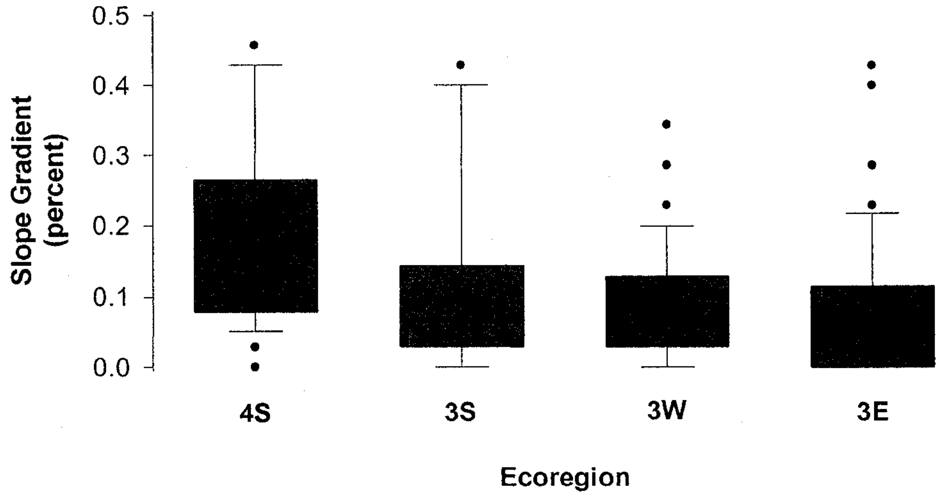

Figure 22. Distribution of stands by slope gradient.

The imbalance toward level terrain or moderate slopes may be an artefact of the sampling design. Growth and yield monitoring plots upon which this study relied, are typically only installed on terrain that is accessible to industrial harvesters. While a growing number of plots are being established on steep slopes and rough or broken terrain, both of the utilized plot networks undoubtedly show continued imbalance.

The distribution of stands by slope aspect is presented in Table 7. While the distribution appears to be quite good across categories and ecoregions, these numbers are inflated due to the high representation of slight slopes observed in Figure 22.

TABLE 7. Distribution of stands by slope aspect.

Slope Aspect	**Ecoregion** **4S**	**3S**	**3W**	**3E**
Northeasterly	2	4	5	5
Northwesterly	10	2	18	4
Southeasterly	12	9	7	5
Southwesterly	7	7	6	14
Null Entry	2	8	20	31

The distribution of stands by slope position is presented in Table 8. Representation was low in four of the variable's categories: lower slopes, toe slopes, depressions, and rolling and complex terrain.

TABLE 8. Distribution of stands by slope position.

Slope Position	**Ecoregion** **4S**	**3S**	**3W**	**3E**
Crest	5	2	9	4
Upper Slope	17	9	9	15
Middle Slope	9	5	16	7
Lower Slope	-	1	1	3
Toe Slope	-	2	1	1
Depression	-	-	-	7
Level	2	10	17	19
Rolling and Complex	-	1	3	3

Note: - no representation

The distribution of stands by landform is presented in Table 9. Here, the high number of categories dramatically diluted the representation across both categories and ecoregions. Only five categories were represented in all ecoregions, and of those, only three might be considered to have tolerable representation for testing.

TABLE 9. Distribution of stands by landform.

Landform	Ecoregion			
	4S	3S	3W	3E
Lake Plain	1	4	5	2
Beach	1	4	3	2
Delta	1	-	-	-
Outwash Plain	3	13	18	37
Dune	-	-	-	1
Spillway	1	-	-	-
Esker		-	-	2
Drumlin	1	-	-	-
End Morraine	-	-	3	-
Ground Morraine	13	5	16	12
Rock Ridge	9	-	2	-
Bedrock	3	4	9	3

Note: - no representation

VARIABLES SPECIFIC TO SOIL CONDITIONS

Six variables specific to soil conditions were considered for their influence over succession: mode of deposition; depth to bedrock; moisture regime; dominant soil texture; sand in the soil profile; and, coarse loams in the soil profile. The distribution of stands by mode of deposition is presented in Table 10.

TABLE 10. Distribution of stands by mode of deposition.

Mode of Deposition	Ecoregion 4S	3S	3W	3E
Lacustrine	3	7	8	5
Eolian	-	-	-	1
Fluvial	1	1	-	1
Glacio-Fluvial	13	13	21	36
Basal Till	-	-	1	-
Morainal	15	6	19	12
Bedrock	1	3	7	3

Note: - no representation

While many categories share commonalities in soil attributes, only the lacustrine, glacio-fluvial, morainal, and bedrock modes of deposition had representation in all ecoregions.

The distribution of stands by depth to bedrock is presented in Table 11. Moderate soil depths are those where bedrock lies at less than a metre below the mineral surface. Shallow soils are those where bedrock lies less than thirty centimetres from the mineral surface.

TABLE 11. Distribution of stands by depth to bedrock.

Depth to Bedrock	Ecoregion 4S	3S	3W	3E
Shallow	6	3	7	3
Moderate	19	6	13	5
Deep	8	21	36	51

While ecoregion 4S showed a greater abundance of communities overlying less than one metre of soil (corresponding to both the moderate and shallow depth categories) than it did on deep soils, the distribution of soil depth in ecoregions 3S, 3W, and 3E were approximately proportional, having greatest abundances on deep soils, and smallest abundances on shallow soils.

The distribution of stands by moisture regime is presented in Table 12.

TABLE 12. Distribution of stands by moisture regime.

Moisture Regime	Ecoregion 4S	3S	3W	3E
Dry	3	2	1	3
Moderately Dry	14	10	18	17
Moderatly Fresh	7	6	13	12
Fresh	6	8	13	12
Very Fresh	2	2	6	5
Moderatly Moist	-	1	3	3
Moist	1	1	1	7

Note: - no representation

Moisture regime classes were represented in all ecoregions, though as expected, the distribution of jack pine on moist soils was greater in the eastern-most regions. Further, across all ecoregions a unimodal distribution was noted, with jack pine frequencies peaking on moderately dry and moderately fresh soils, tailing to fewer occurrences on the moist sites.

The distribution of stands by dominant soil texture is presented in Table 13. Soils of the sandy texture class were categorized as coarse soils. Similarly, soils of the coarse loamy texture class were categorized as medium soils, and those of all other texture classes were grouped as fine soils.

TABLE 13. Distribution of stands by dominant soil texture.

Soil Texture	Ecoregion 4S	3S	3W	3E
Fine	2	2	3	5
Medium	13	13	16	29
Coarse	14	8	13	8

Coarse and medium textured soils both had good representation in each ecoregion. Fine textured soils were also represented in every ecoregion, but at lower frequencies.

Figures 23 and 24 respectively depict the distribution of stands by representation of sands, and coarse loams in the soil profile. Each value represents the proportion of the first meter below the mineral surface represented by each texture (representation by bedrock inclusive). While only sands and coarse loams are presented, all soil texture classes were investigated; the majority found to have no influence.

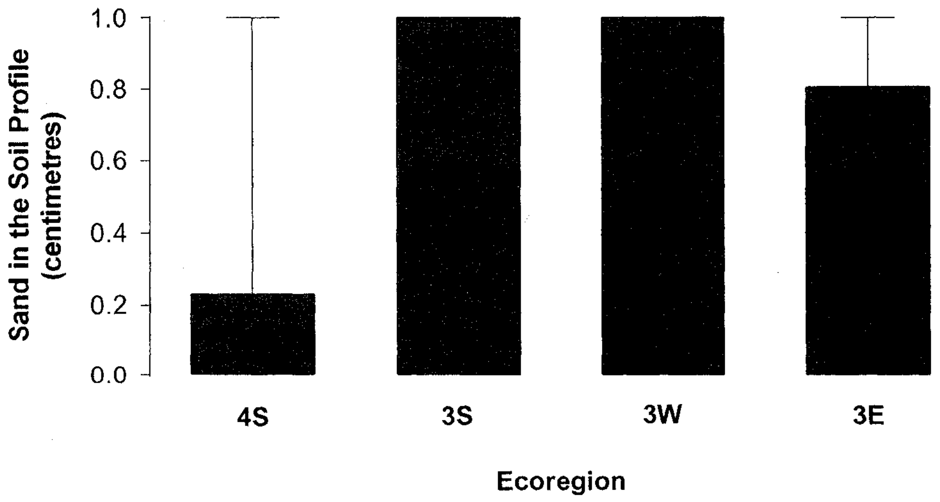

Figure 23. Distribution of stands by sand in the soil profile.

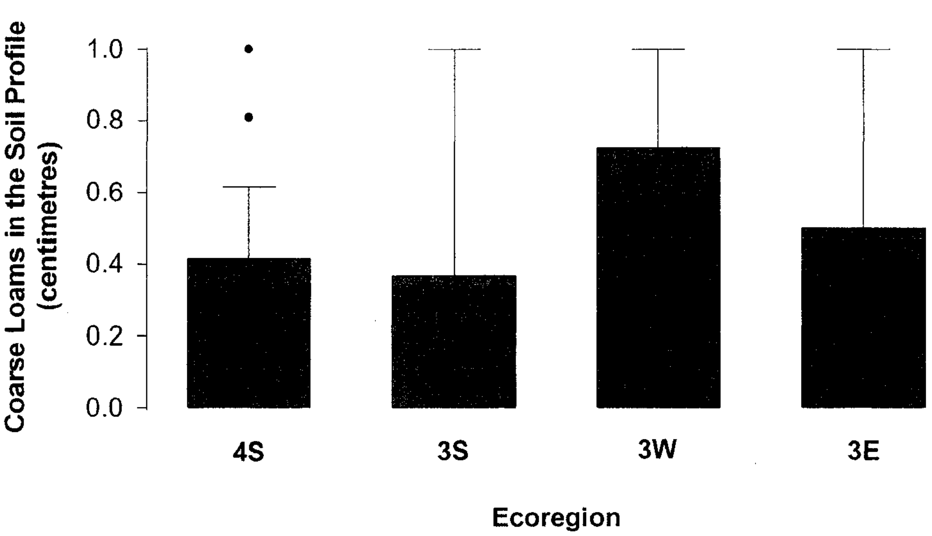

Figure 24. Distribution of stands by coarse loams in the soil profile.

In the case of sands in the soil profile, variability was consistent across ecoregions 3S, 3W, and 3E. Deep sands were comparatively rare in ecoregion 4S. Coarse loams in the soil profile were somewhat consistent across all ecoregions.

VARIABLES SPECIFIC TO CLIMATE

Four variables specific to climate were considered for their influence over succession: annual precipitation; length of the growing season; growing degree days; and precipitation during the growing season. The distribution of stands for each of the variables are presented in Figures 25 through 28, respectively.

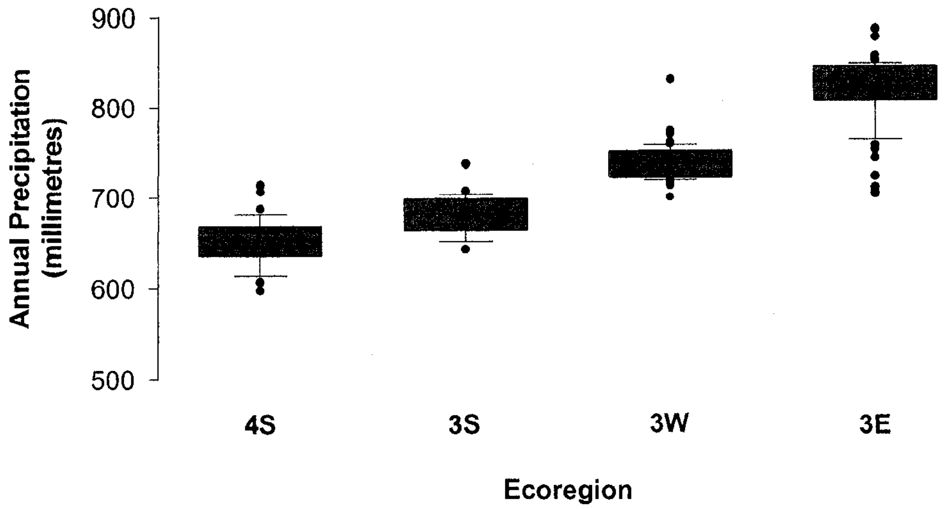

Figure 25. Distribution of stands by annual precipitation.

In Figure 25, the easterly progression of ecoregions shows an expected increase in annual precipitation.

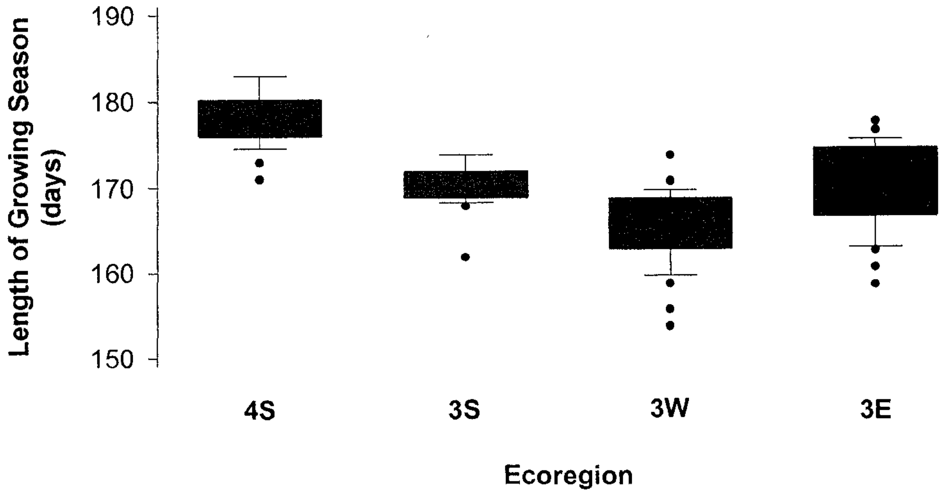

Figure 26. Distribution of the stands by length of the growing season.

Here it is noted that on average, sites in ecoregion 3W experience the shortest growing seasons. It is also noted that similar trends exist between the distributions featured in Figure 26, and those in Figure 27.

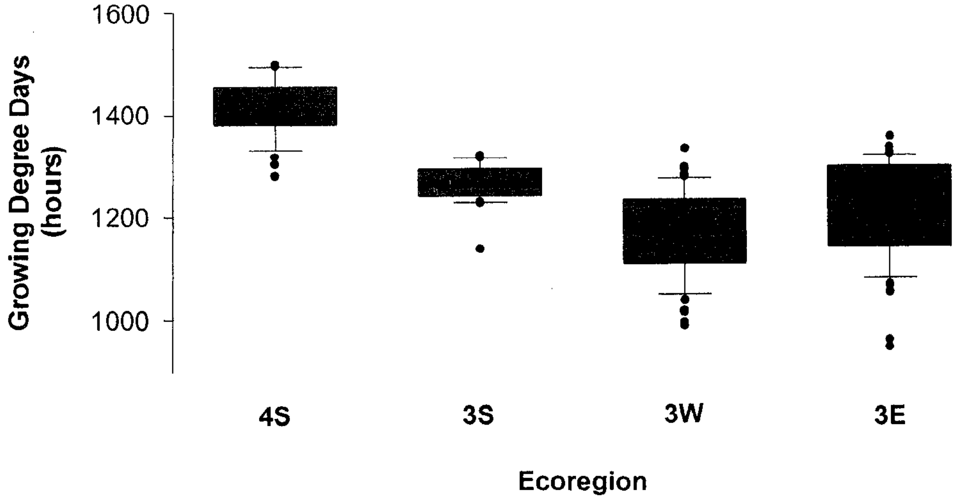

Figure 27. Distribution of stands by growing degree days.

In Figure 27, ecoregions 4S is shown to have many more growing degree days than the others – by 500 hours in some cases. In contrast, little variation existed for precipitation during the growing season, when stratified by ecoregion (Figure 28).

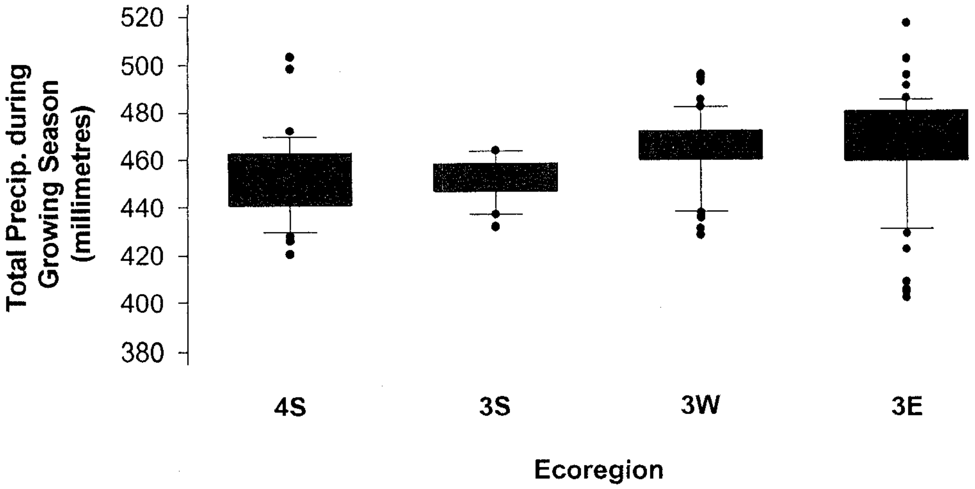

Figure 28. Distribution of stands by precipitation during the growing season.