

MORPHOLOGICAL VARIATIONS IN JACK PINE (PINUS BANKSIANA)

ALONG ITS'

CENTRAL TO NORTHERN POPULATION RANGES

BY

LISA MARIE KELLMAN

A Research Paper

Submitted to the Department of Geography

in Fulfilment of the Requirements

of Geography 4C6

McMaster University

April 1989

ABSTRACT

The analysis of six jack pine populations along a north-south transect through the MacKenzie River Valley in the Northwest Territories revealed no significant latitudinal trends in cone and seed morphometric measurements. In attempting to determine whether any variations may be environmentally induced, Radial Growth Rates were, 1) compared between sites, and 2), were correlated with morphometric measurements. No significant results were produced. In correlating trait measurements between sites and between one another in order to determine whether migration may be producing trends, again no significant relationships were obtained. A comparison of jack pine with the similar species lodgepole pine suggests that if the same factors controlling the migration of lodgepole pine also control jack pine migration, wing loading should be less in more recent populations. However, this study indicates no significant results in this respect. It is suggested, however, that a further sampling south along the latitudinal transect may produce significant results.

ACKNOWLEDGEMENTS

I would like to thank Dr. G. MacDonald for his guidance throughout this study, and for the opportunity to travel to the Northwest Territories and participate in the data collection. I would like, also, to thank Chris Hanks and our helicopter pilot for helping with cone collection at the sites. Finally, I wish to express my gratitude to Katherine McLeod for taking time to review and offer suggestions in my final paper, as well as my friends and family for being patient throughout this ordeal.

L.M.K. April, 1989.

TABLE OF CONTENTS

	Page
Title Page	i
Abstract	ii
Acknowledgements	iii
Table of Contents	iv
List of Figures	v
List of Tables	vi
Chapter 1 : INTRODUCTION AND LITERATURE REVIEW.....	1
1.1 Introduction	1
1.2 Literature Review	3
1.2.1 Introduction	3
1.2.2 Plant Migration and Climate	4
1.2.3 Invasion	6
1.2.4 Dispersal	7
1.2.5 Seed Characteristics	8
1.2.6 Lodgepole and Jack Pine	9
Chapter 2 : STUDY AREA.....	12
2.1 Introduction	12
2.2 Area History	12
2.3 Site Location and Description	15
Chapter 3 : DATA ANALYSIS.....	17
3.1 Introduction	17
3.2 Data Collection	17
3.3 Data Analysis	20
Chapter 4 : RESULTS.....	23
4.1 Correlation in Combined Data Set	23
4.2 Radial Growth Rate	25
4.3 Site by Site Correlations	28
4.4 Site by Site Trait Variations	28
Chapter 5 : DISCUSSION AND CONCLUSIONS.....	33
5.1 Discussion	33
5.2 Conclusion	36
References.....	38

LIST OF FIGURES

Page

Figure 1 : Geographical Locations of Sites.....13

Figure 2 : Site Location and Climatic Conditions....14

Figure 3 : Cone and Seed Measurement Points.....18

Figure 4 : Average Radial Growth Rates per Site.....27

Figure 5 : Cone Traits Plotted by Site.....30

Figure 6 : Seed Traits Plotted by Site.....31

LIST OF TABLES

Page

Table 1 : Correlation Coefficients for Traits from all Sites Combined	24
Table 2 : Correlation Coefficients for Radial Growth Rate Data versus Cone and Seed Traits	26
Table 3 : Site by Site Correlation Coefficients for Cone and Seed Traits	29

CHAPTER 1 : INTRODUCTION AND LITERATURE REVIEW

1.1 Introduction

In comparing the central versus marginal populations of a plant species geographical range, there are often significant differences with respect to morphology, physiology, and genetics. In examining morphological traits as is the objective in this study, variations may be genotypic (genetically fixed) or phenotypic (plastic response). In both cases, migration or the environment may be the selecting or imposing factor. In the former case, migration may cause differences between the central and marginal populations due to the extended period of time involved in the migration process or due to isolation of marginal populations. In the latter case, environmental conditions may produce stressful marginal conditions and natural selection may result.

Cwynar and MacDonald (1987) examined morphological and genetic differences in central and marginal populations of lodgepole pine (Pinus contorta) in western Canada in order to assess the relative importances of environmental and migrational factors in

producing variations. They concluded that the most important factor in central-marginal population variations was that of migration.

The present study will study morphological variation in Jack pine (Pinus banksiana) to determine if the geographical pattern of the variation is similar in lodgepole pine. The species jack pine and lodgepole pine are very similar in terms of their morphological characteristics, their population ranges, and population history. Both species have serotinous cones and both populations extend well into northern Canada; the northern extent of jack pine being in the western Northwest Territories, and that of lodgepole pine being slightly farther west in the Yukon Territory. If migration is truly the most important factor controlling differences in central-marginal populations of the Canadian pines, it is expected that the pattern of morphological variation in jack pine central-marginal populations should show the same trends as in lodgepole pine.

This study will examine morphological variations in jack pine (*Pinus banksiana*) along a north-south transect from the centre to the margin of the species distribution. By sampling the cones and seeds and analysing morphological variation both within and

between individual sites, it is hoped that 1), any significant relationships between any of these variables will be detectable, and 2), that any latitudinal changes in morphology will be detected, whether they be migrational or environmentally imposed. Tree growth rates will be estimated by studying tree ring cores. Relationships between the tree growth rates at each site and the morphological traits will be examined. It is hoped that a contribution can be made to the understanding of whether climate as it affects growth rates has an affect on the development of these morphological traits.

1.2 Literature Review

1.2.1 Introduction

In understanding and interpreting present distributions and characteristics of a plant species; it is important to fully understand the postglacial history not only of the species being considered (MacDonald and Cwynar, 1986). The postglacial history should be viewed in context with other studies of plant species range expansion that occurred at the end of the Pleistocene. Thus, in studying morphological variations in jack pine (*pinus banksiana*), it is important to be

familiar with the postglacial range expansion of the species, and seed characteristics and dispersability. In comparing jack pine to the similar species lodgepole pine, it is important to be aware of similarities and differences between the two species.

1.2.2 Plant Migration and Climate

Davis (1976), discusses interglacial and glacial periods and their impact on plant migration. She believes that glacial phases extend for much greater time periods than interglacial periods (glacials 50-100 000 years; interglacials 10-20 000 years) and that based on present interglacial records, floristic equilibrium is never attained before the next glacial phase arrives. Thus she introduces the idea that interglacials in the context of the Pleistocene, are unstable interruptions in the Pleistocene history. As evidence she discusses the fact that although the temperature maximum for the present interglacial phase (the Holocene) was reached approximately 5-8 000 years ago, and we are presently nearing the end of this interglacial phase, the fact that migration into unglaciated areas by plant species is still occurring, supports the idea that floristic equilibrium has not yet been reached in northern areas.

According to Davis (1976), plant migration is dependent on: 1) dispersal mechanisms, 2) the changing physical environment, and 3), the changing biotic environment. Therefore not only must a plant species have to contend with its own physical ability to expand, but also on its ability to adapt to changing environmental conditions, as well as its ability to successfully compete with other species. In the Quaternary the most important environmental factor controlling large scale plant distributions is climate. The most useful biological tool according to Wright (1984) in detecting climate change, are tree rings. In fact, Wright also states that the sensitivity of the rings is greatest near the species range limit. Davis (1984) also notes that with a warming trend, because adult trees are not there to compete with seedlings, movement of the tree line will be much more noticeable than changes within a forest community. Four processes are outlined by Prentice (1986) as being possibly related to the time in which it takes vegetation to respond to changes in the climate. The first of these processes is soil development. Secondly, migration may be important as the greater the distance needed for the species to attain a new equilibrium range is, the greater will be the time needed for the migrational

process. Thirdly, succession involves the birth, growth, and death of local species, and their dependence on the external environment and the present vegetation state. The fourth and final process is evolution and this encompasses the idea that many species of trees have a great deal of, or a great potential for, genetic variability within their present ranges. Species which are considered favourable in this respect include, plastic genotypes and species which are highly variable within their population (but for which this variation has a small geographical pattern). According to Ritchie (1986), there are very few general ecological theories existing and one of the primary reasons for this is that "many ecological problems are made up of multiple relationships controlled by multiple causes operating at varying scales of time and space".

1.2.3 Invasion

Watts (1973), selected a number of sites in order to observe long-scale trends of a number of species in accurate detail and concluded that: "invasion appears to be a gradual opportunistic process, the success of which depends on high competitive ability in seedling establishment of the invader while its population has a

low density." Also of importance and outlined in detail is the S-shaped population growth curve of an invader in which initial slow growth indicates initial establishment and maturation of a small number of the species, the sudden increase in growth rate is due to pollination (and therefore expansion of the species), and the final levelling off of the growth curve with time is a result of resistance. Watts (1973) believes the control in a species number to be a result of interspecific rather than intraspecific competition.

1.2.4 Dispersal

The dispersal mechanism of a species is of primary importance when dealing with competition. Howe and Smallwood (1982) outline three hypothesis^e regarding seed dispersal. Firstly, the 'Escape Hypothesis' indicates long distance dispersal due to seedling mortality near the parent. Secondly, the 'Colonization Hypothesis' assumes non-competitive environments will become available near the parent, and thirdly, the 'Directed Dispersal Hypothesis' involves the use of dispersal agents (ie birds and animals) to transport seeds. Harper et al (1970) believe that dispersal as an escape mechanism increases in importance as the frequency of

the invasion-colonization-suppression-extinction cycle increases.

According to Cwynar and MacDonald (1987), the act of post glacial migration of temperate plant species is likely to result in geographical variation of the species. As such, they expect that genetic variation will decrease in the direction of migration, and seeds of more recent populations will be more dispersable. In the case of lodgepole pine, data collected by Wheeler and Guries (1982) indicated a positive correlation between wing loading (seed mass divided by wing area) and the time since founding of the population. However, Cwynar and MacDonald (1987) note that it is very difficult to determine the relative importances of selection along the environmental gradient, and the process of migration.

1.2.5 Seed Characteristics

It is important to note that although variations in seed size and shape are mainly dispersal related, other factors which must also be considered include: features of shape due to conditions inside the ovary when developing (Harper et al; 1970), and relationships between individual seeds and environmental conditions in

which they are produced. With respect to the latter consideration, it has been shown that for a given species, seed weight decreases with elevation and latitude due to a decrease in temperature and moisture stress, and the shorter growing season (Baker, 1972). Baker also found a positive correlation between increased seed weight and increased light intensity.

According to Howe and Smallwood (1982), moisture availability is important in seed germination in that a greater quantity of water must be absorbed by the seed on the soil surface than is absorbed by the atmosphere from the seed. In this respect, larger seeds have a greater problem in retaining sufficient water to germinate. Dormancy in seeds is also important as it protects seeds from unfavourable growing seasons and environmental catastrophies through insulation over an extended time period (Harper et al, 1970). Howe and Smallwood (1982) conclude that even the slightest changes in seed shape and size have lasting effects when dealing with seed germination and establishment.

1.2.6 Jack and Lodgepole Pines

In a review of the late Quaternary history of lodgepole and jack pines, Critchfield (1985) suggests

that both lodgepole pine and jack pine likely evolved some time during the Pleistocene. He notes that jack pine appears to have travelled a farther distance and at a faster rate than lodgepole pine since the end of the Pleistocene, although lodgepole still occupies the greater range of the two species. Critchfield suggests that lodgepole pine has been modified to a much lesser degree by numerous glaciations than jack pine. The two pines are both attributed with rapid migration and population increases. However, in contrast to this idea, both have serotinous cones which are generally dependent on heat to expose the seeds. Of the two species, jack pine is the more fire dependent. With fire, regeneration is favoured as stored seeds are released, competition is reduced, and a suitable seed bed is produced. Critchfield (1985) notes that lodgepole pines have open cone phases, generally at less than 20-25 years of age and at greater than 30-35 years of age, while if jack pine has an open cone stage, it exists only for a few of its early years. Although the seed number of both species is very variable, the seed number is generally higher for jack pine than it is for lodgepole pine. Lodgepole pine and jack pines have overlapping regions and do hybridize, but the hybridization is limited due to differences in

ecological preferences, internal reproductive barriers,
and differences in flowering time (Critchfield, 1985).

Chapter 2 : STUDY AREA

2.1 Introduction

In studying morphological variations in Jack pine along its central-marginal population ranges, six sites were sampled along the MacKenzie River Valley in the Northwest Territories (Figure 1), all of which were located in the Boreal Forest (Figure 2). From each of these sites, trees were randomly sampled for cones and tree ring cores. The following will discuss the study area history and site locations.

2.2 Site History

The present interglacial, the Holocene, began about 10 000 years ago and reached its temperature maximum about 5-8000 years ago (Davis, 1976). MacDonald (1986) presents evidence that much of the plant cover of the MacKenzie Basin in the early Holocene was relatively sparse. The dominant vegetation progressed from herbs and gaminoids in well drained areas and sedges and willows in moister areas, to a dominant shrub birch vegetation about 10 000 years before present. By about 8500 years before present, *Picea* became the dominant

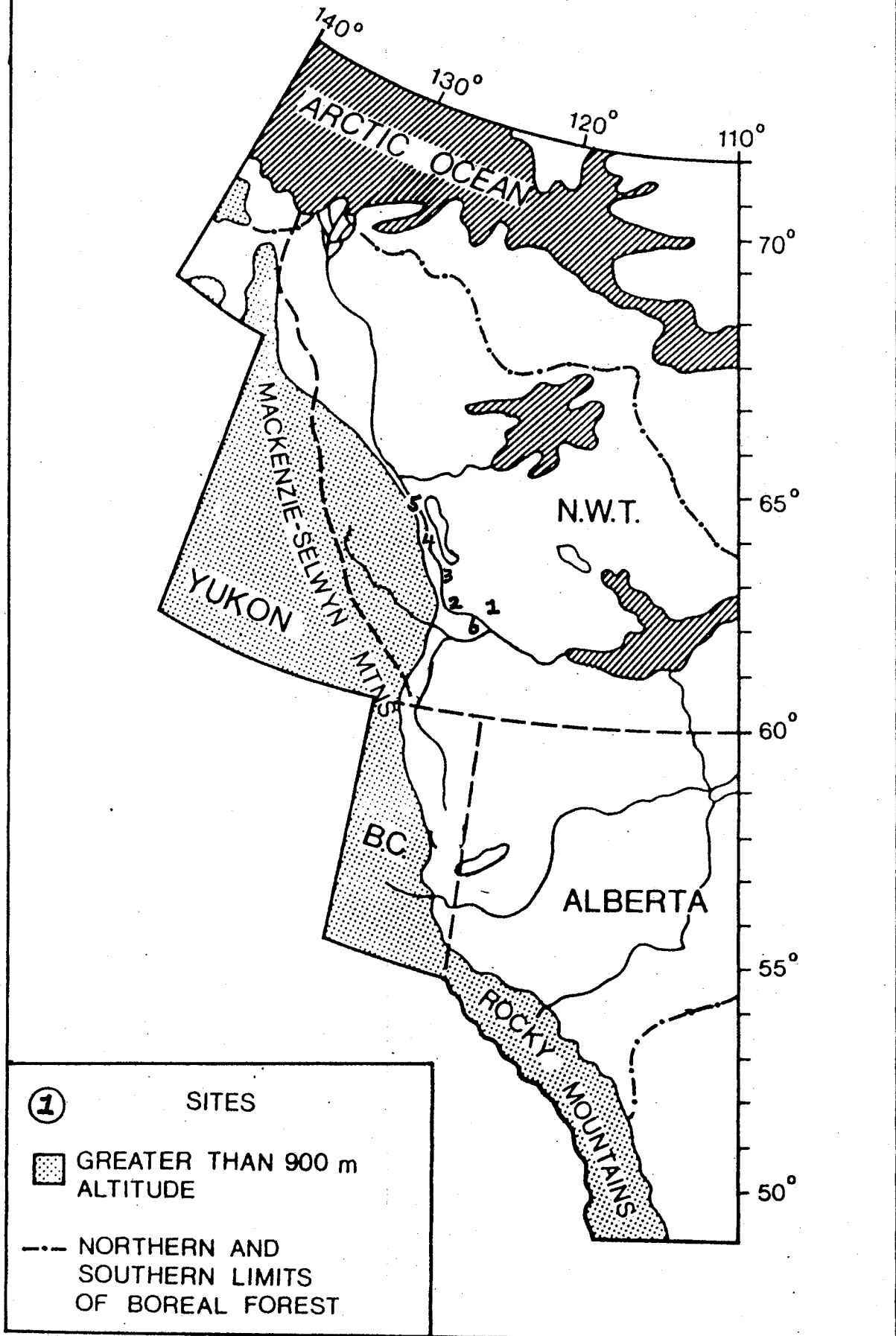


Figure 1 : Geographical Site Location

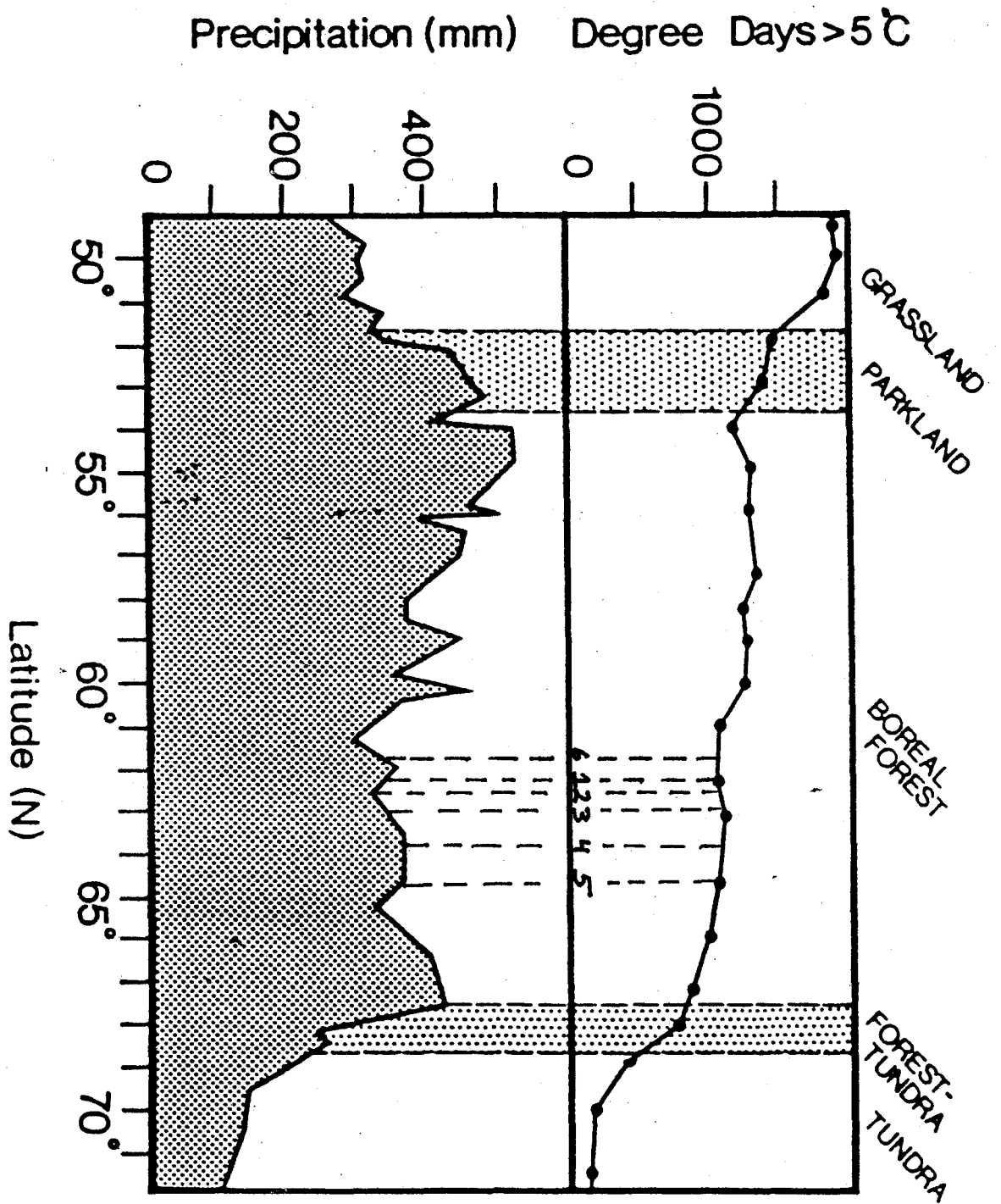


Figure 2 : Site Location and Climatic Conditions

vegetation. The rapid spread of *Picea* is partially attributed to long distance wind and water dispersal in the MacKenzie Basin (Ritchie and MacDonald, 1986). Lodgepole pine reached modern limits of its range about 5600 years ago, whereas jack pine reached the lower MacKenzie Basin about 6000 years ago, and modern limits about 2400 years ago (MacDonald, 1986). The pinus population as a whole took 2-3000 years to reach modern densities, this lengthy time being attributed to their serotinous cones and the poorly drained sites and shaded areas they invaded.

2.3 Site Location

In terms of the relative site positions, site six was the most southernmost site, site one was slightly north and west of site six, followed by sites two, three, four, and five, the most northernmost site. Sites two, four, and five were fairly similar stands of scattered pine on level ground and with essentially no overlying vegetation. Site six was the most diverse of all in that it consisted of a very dense, very mature stand of jack pine. Site one was located on the Horn Plateau, just to the west of the MacKenzie River. Vegetation in the vicinity of the collected samples

consisted of black spruce, poplar, and alder. The site was located on a level but slightly raised area, and the jack pine population was scattered. Site three was located on an esker. Surrounding vegetation consisted of mainly jack pine, mixed with some black spruce and located on level sites. The trees were scattered, but less so than those from sites one, two, four, and five.

Climate normals of Fort Simpson and Norman Wells, the approximate positions of the southern and northernmost sampled sites respectively, indicate the following. The mean annual temperature of Fort Simpson is -4.0 C, and that of Norman Wells -6.4 C. The mean annual precipitation of Fort Simpson is 216.5 mm while that of Norman Wells is slightly less at 188.3 mm. The mean annual wind speeds are 11.1 km/hr and 12.2 km/hr for Fort Simpson and Norman Wells respectively. Thus the northern sites would tend to be cooler, drier, and windier than the more southern sites.

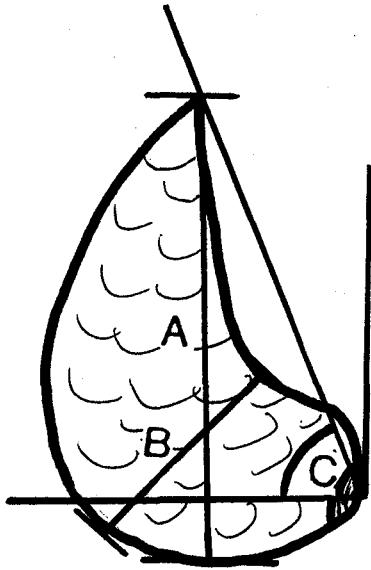
Chapter 3 : DATA ANALYSIS

3.1 Introduction

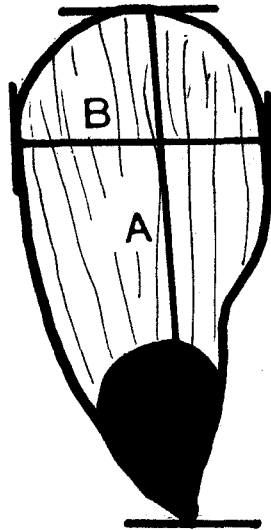
At each of the sampled sites, approximately sixty trees were randomly sampled for four to six cones. In addition to these cones, tree ring cores were obtained from the first ten suitable trees. A suitable tree constituted a tree from which a clear measurement of the rings could be made. Generally, the first ten trees were cored with little exception.

3.2 Data Collection

The data collection once the cones and tree ring cores had been obtained, was essentially divided into three sections: cone, seed and age analysis respectively. A sampling of twenty-five of the sixty sets of cones was made (including cones from the ten trees from which the tree ring cores were taken) for each of the six sites. From each of these cone sets, the four to six cones were measured for: cone length, cone width, cone weight, and cone curvature angle. Figure 3a illustrates the cone measurement points. The cone length and width measurements were made with a



- a) Cone Measurement Points:
A. cone length
B. cone width
C. cone curvature angle



- b) Seed Measurement Points:
A. seed length
B. seed width

Figure 3 : Cone and Seed Measurement Points

micrometer, and the widest section of the cone was consistently measured. The cone angle measurements were made with a protractor. The point at which the stem met the cone was consistently measured as the zero degree point in the measurement. Thus a perfectly straight cone would produce a measurement of zero degrees.

Once measurements of the cones was complete, two cones from each set were heated and opened in order to expose the seeds. These seeds were mixed, and a random sample of ten seeds from a minimum of twenty of the twenty-five trees from each site (including again the trees which were cored) were measured for seed length, width, area, and weight (see Figure 3b). Due to the small size of the seeds and the necessity for extremely accurate measurements, a digitizer was used in measuring seed length, width, and area. The digitizer was a device upon which a set of seeds could be put, their lengths and widths specified with a movable electronic device, and the values input directly into the computer. From the length and width measurements, a direct calculation of the seed area could also be made (ie the length was multiplied by the width). As was the case with the cone measurements, the widest part of the seed was measured for the width, and thus both the width and area values are maximum measurements. The corresponding seed weights

were also determined. Included in the seed measurements was a determination of the ratio of 'good' to 'bad' seeds. Good seeds were wings with large seeds whereas bad seeds were wings which had extremely small or no seeds. The two types were very easily distinguished from one another. Basically what this measurement entailed was quartering off the petri dish in which the seeds were contained, and counting the number of wings with and without seeds attached to them. The ratio was obtained by dividing the number of 'good' by the number of 'bad' seeds.

Sixty tree ring cores were set (a maximum of ten cores from each of the six sites) and age was determined by counting the number of rings on the core from the outermost to the central ring. A measurement of the distance between the center and outermost ring was made in order to determine the radial growth rate:

$$\text{Radial Growth Rate} = \frac{\text{core radius}}{\text{\# of rings}}$$

3.3 Data Analysis

Data obtained from the collection described above was put into a Lotus 123 spreadsheet for analysis. All

the data obtained for the cone and seed measurements was averaged so as to give a single value for each tree, and all further analysis used these single values. The data itself was analysed both as one complete set with no site distinctions (ie all sites combined), and was also analysed within each site and the site to site variations observed. Thus we are essentially looking to observe three things: 1) variations between traits for all the data combined, 2) variations in traits between sites, and 3), trait variations within each site.

In observing the data for all sites combined, the following analysis were made. The correlation coefficients (r^2) were determined for each cone trait versus cone trait, each seed trait versus seed trait, and each cone trait versus seed trait. There were 166 trees (at an average of 5 cones per tree for a total of approximately 830 cone measurements) from which cone traits were compared. For the seed traits, 126 trees (at an average of 10 seeds per tree for approximately 1260 seeds) were compared for traits. In comparing cone versus seed traits, 113 of the trees had corresponding cone and seed data.

The Radial Growth Rate (RGR) data were also observed for all sites combined. Correlation coefficients for RGR versus tree age, RGR versus each

cone variable, and RGR versus each seed variable were determined. There was a total of 50 trees for which corresponding cone data was available, and 49 trees for which corresponding seed data were available.

In order to make comparisons between sites of any given traits, bar graphs were made for each cone variable versus site, each seed variable versus site, and the RGR versus site.

Finally, in order to test for variations within each of the sites for a given set of variables, correlation coefficients were obtained for the cone versus cone, seed versus seed, and cone versus seed traits for each separate site.

Chapter 4 : RESULTS

4.1 Correlation in Combined Data Set

In testing for correlation between variables for the combined data as is shown in Table 1, there appears to be virtually no significant correlations. The exceptions are made only in the cone versus cone traits. The significant relationships exist only between the cone length and width (correlation coefficient= 0.6468, $p < 0.05$) and the cone width and weight (correlation coefficient =0.5995, $p < 0.05$). However, this is to be expected as with an increase in cone length or width you would also expect an increase in cone weight. The least significant relationships among the cone traits exists when cone curvature angle is one of the variables. The seed versus seed trait relationships show no significant correlations at all, not even not even between, for example, length and width or length and weight as one might expect to find. Thus long seeds are not necessarily wide seeds or heavy seeds. In correlating cone with seed traits, again no significant relationships were seen. Thus seed morphological characteristics are virtually unrelated to any cone characteristics.

TABLE 1 : Correlation Coefficients for Traits from all Sites Combined

Trait		Correlation Coefficient (r ²)	n
cone	length vs width	.2728	166
	length vs weight	*.6468	166
	length vs angle	.1978	166
	width vs weight	*.5995	166
	width vs angle	.0005	166
	angle vs weight	.0301	166
seed	length vs width	.2601	126
	length vs weight	.1759	126
	width vs weight	.1414	126
	area vs weight	.2102	126
cone vs seed	length vs width	.2161	113
	width vs length	.2313	113
	weight vs length	.3447	113
	angle vs length	.0012	113
	length vs width	.0492	113
	width vs width	.0084	113
	weight vs width	.1139	113
	angle vs width	.0219	113
	length vs area	.1636	113
	width vs area	.1612	113
	weight vs area	.2832	113
	angle vs area	.0039	113
	length vs weight	.1788	113
	width vs weight	.0679	113
	weight vs weight	.2384	113
	angle vs weight	.2510	113

* p < 0.05

4.2 Radial Growth Rate

No significant correlations or relationships were found between the Radial Growth Rate (RGR) and the cone and seed traits (Table 2). In order to ascertain that the radial growth rate was essentially the same for all tree ages, the correlation coefficient (correlation coefficient =0.154) was obtained for the RGR versus the tree age. The low correlation between the two variables allows us to be quite confident that the tree age did not bias these results. Therefore, the rate at which the tree grows has no effect on the measured morphological characteristics.

In plotting the Radial Growth Rates by site (Figure 4), there appears to be no clear directional trend. However, site six, the most southernmost site had by far the highest RGR, though this is not statistically significant. The other five sites though, show no clear trend. Because the distance between tree rings generally decreases exponentially with increased age of the tree, if anything the RGR of site six would be underestimated as the trees in this site are generally older than those of the other five sites.

TABLE 2 : Correlation Coefficients for Radial Growth Rate (RGR) Data versus Cone and Seed Traits

RGR vs Trait	Correlation Coefficient (r ²)
RGR vs cone	
length	.1645
width	.0357
weight	.1117
angle	.0291
RGR vs seed	
length	.0178
width	.0009
area	.0010
weight	.0458
weight/area	.0292
GB ratio	.1209

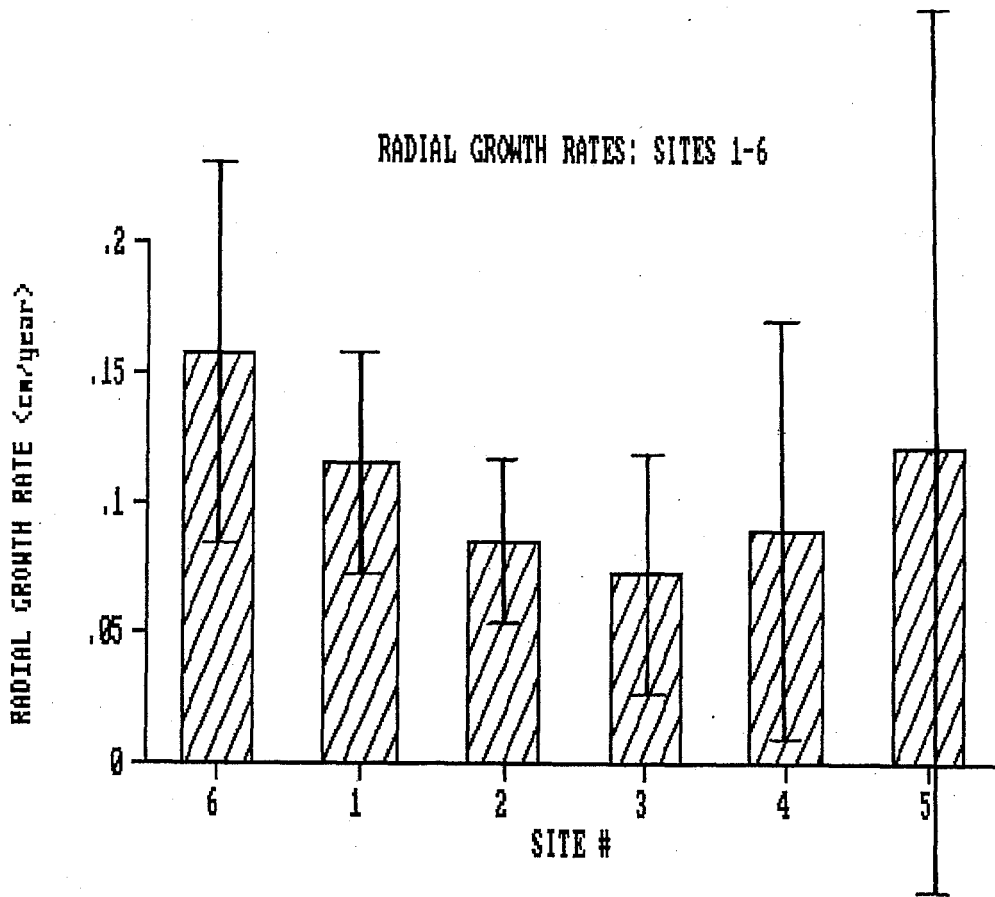


Figure 4 : Average Radial Growth Rates per Site

Note: Error bars indicate the 95% confidence interval which is calculated by $1.96 \times$ standard deviation.

4.3 Site by Site Correlations

The site by site correlation coefficients of the cone and seed traits are listed in Table 3. These figures show a great deal of variation between sites for any given combination of traits. As an example, cone width versus weight values vary from a correlation coefficient of 0.002 for site one, to a correlation coefficient of 0.872 for site two. Further interpretation of these data are beyond the scope of this thesis.

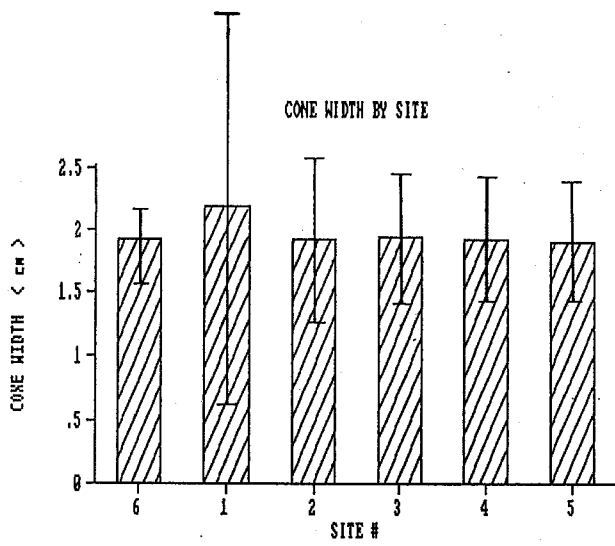
4.4 Site by Site Trait Variations

In comparing the measured traits between sites, (Figures 5 & 6), the following has been observed. Very little difference can be noted amongst the sites in the cone traits (Figure 5). Cone curvature angle appears to be extremely high in site six as compared to the others, however the variability in measurements of the cone analysis is also extremely high. Thus no significant trends can be observed in the cone traits. Seed length, width, area, and weight plots show very little difference amongst the sites (Figure 6), with only seed weight showing any possible, though insignificant

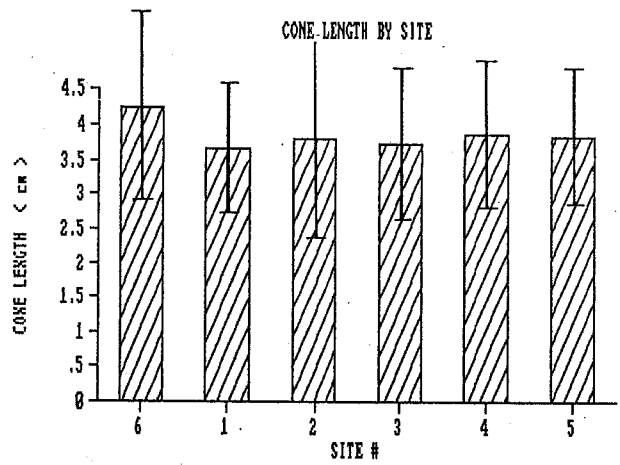
TABLE 3 : Site by Site Correlation Coefficients for Cone and Seed Traits

Trait	Correlation Coefficient (r^2)						
	Site 1	2	3	4	5	6	
cone	l vs w	.106	.403	.351	.595	.093	.245
	l vs wt	.647	.568	.800	.705	.569	.516
	l vs an	.213	.192	.020	.300	.142	.090
	w vs an	.250	.250	.006	.120	.180	.017
	w vs wt	.002	.872	.651	.803	.448	.486
	wt vs an	.002	.023	.022	.195	.000	.070
seed	l vs w	.002	.669	.160	.500	.472	.272
	l vs wt	.003	.497	.062	.459	.467	.138
	w vs wt	.195	.227	.115	.307	.274	.011
	a vs wt	.043	.431	.119	.419	.408	.069
cone	l vs l	.536	.476	.387	.417	.347	.140
	vs l vs w	.046	.521	.035	.352	.126	.003
seed	l vs a	.442	.555	.289	.426	.240	.030
	l vs wt	.012	.297	.010	.569	.105	.322
	l vs wt/a	.366	.001	.279	.183	.010	.043
	w vs l	.409	.392	.231	.549	.094	.213
	w vs w	.008	.427	.035	.439	.066	.019
	w vs a	.321	.465	.179	.537	.096	.033
	w vs wt	.117	.582	.002	.592	.222	.127
	w vs wt/a	.504	.040	.159	.138	.059	.001
	wt vs l	.587	.552	.372	.564	.369	.293
	wt vs w	.055	.515	.074	.672	.269	.035
	wt vs a	.530	.612	.313	.710	.368	.047
	wt vs wt	.034	.522	.013	.476	.415	.421
	wt vs wt/a	.470	.022	.324	.031	.033	.041
	an vs l	.059	.162	.054	.079	.105	.104
	an vs w	.023	.086	.004	.026	.127	.015
	an vs a	.069	.151	.034	.051	.150	.021
an vs wt	.055	.267	.003	.189	.002	.009	
an vs wt/a	.141	.054	.017	.104	.079	.086	

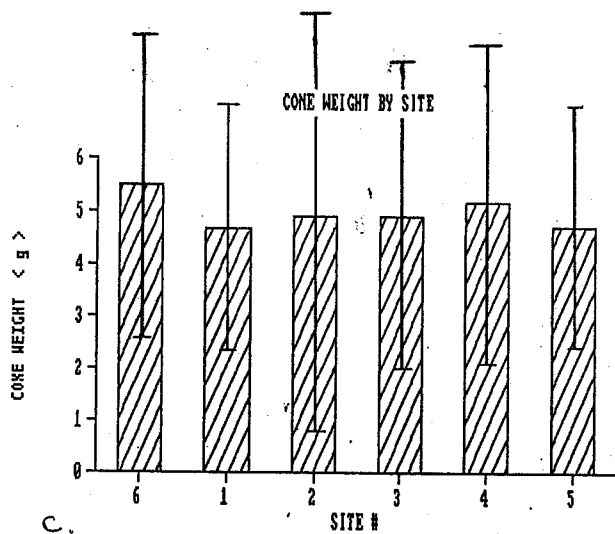
Note: l=length
w=width
wt=weight
an=curvature angle
a=area
wt/a=wing loading



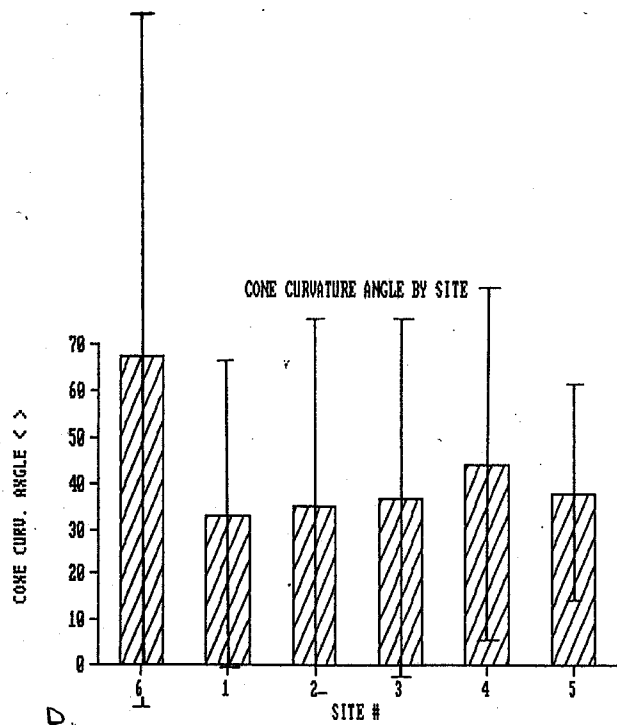
A.



B.



C.



D.

Figure 5 : Cone Traits Plotted by Site

Note: Error bars indicate the 95% confidence interval which is calculated by $1.96 \times$ standard deviation.

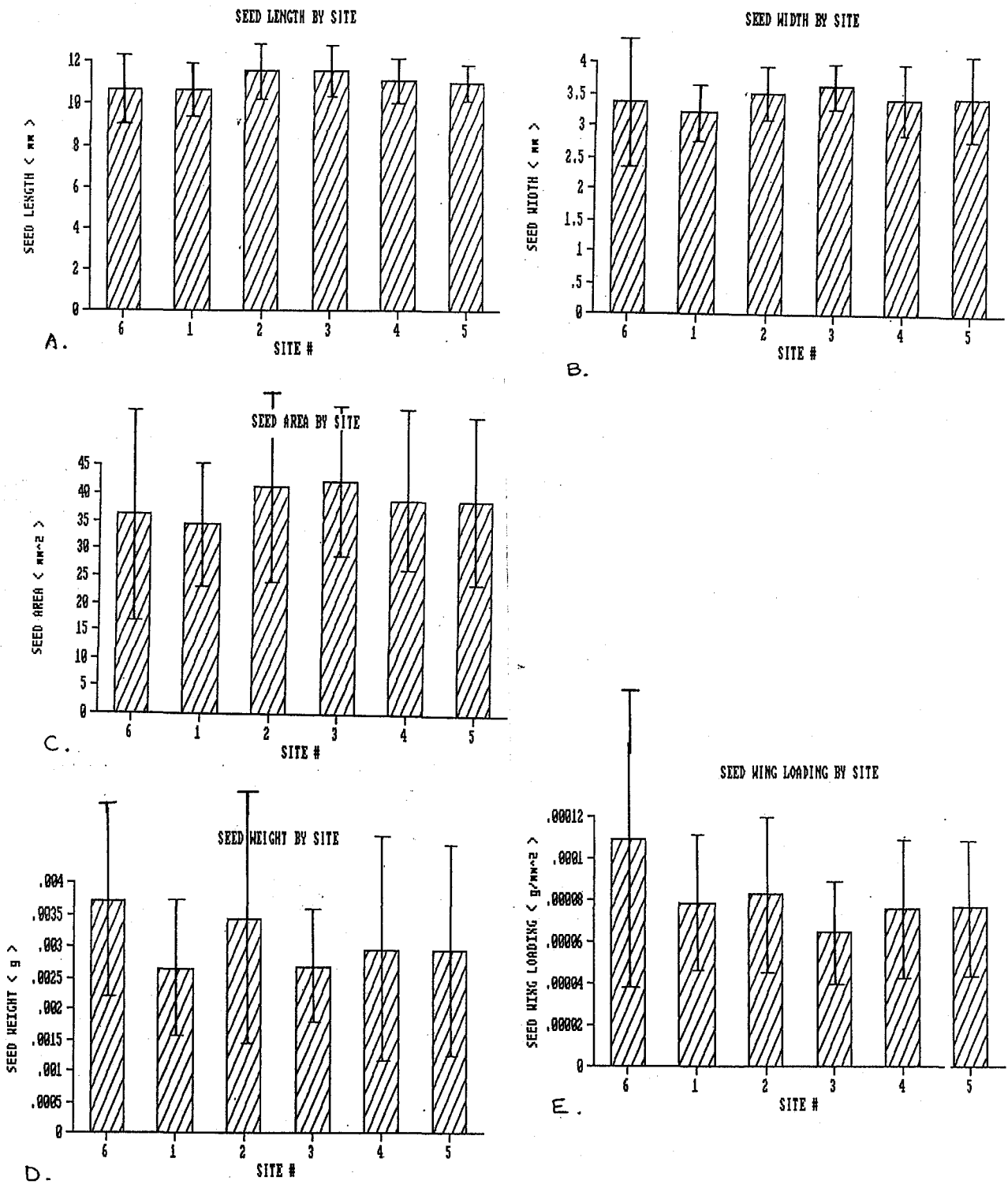


Figure 6 : Seed Traits Plotted by Site

Note: Error bars indicate the 95% confidence interval which is calculated by $1.96 \times$ standard deviation

differences. An interesting result was the lack of significant variation between sites for wing loading (weight/area), plotted by site (Figure 6e). It would be expected that with a decrease in time since founding of the population, the wing loading may show a significant trend. Although the most southern site, site six, shows a much higher value than the other five sites it is not significant and sites one through five show little variation.

Chapter 5 : DISCUSSION AND CONCLUSIONS

5.1 Discussion

The following will discuss the various results in relation to the objective of the study, and attempt to offer plausible explanations for them.

The aim in obtaining tree ring cores and determining the Radial Growth Rates (RGR) was to observe any central-marginal or south to north variations in tree growth which may suggest a climatic impact upon the growth rates of the sampled populations.

The RGR data averaged and plotted by site (Figure 4) has a great deal of potential error associated with a number of the sites, as is indicated by the error bars which specify the 95% confidence intervals. It is quite possible that if a larger sample of cores was obtained from each population, the error would be less and a latitudinal trend in growth rates may be evident. Of particular interest is site six which, as mentioned previously, shows a high rate of growth associated with it although the tree ages in the cored set are older than for the other sites and thus should act to reduce the RGR value. It is quite conceivable that, with a

larger north to south gradient, trends in growth rates may be more evident.

In correlating RGR with individual morphological traits in jack pine (Table 2), it appears that no relationships exist between the traits and the rate at which the trees grow. Again though, with a larger sample set and a larger gradient, trends may appear.

Correlation amongst traits both as a combined set (Table 1) and within individual sites (Table 3), is virtually insignificant. Not only are the variations high between the various sites for each correlation, but there appears to be no directional trend in correlations (ie. with a high degree of variability in correlation coefficients for each site, there is no clear increase in or decrease in the significance of the relationship in a given direction).

The site by site trait measurements (Figures 4 & 5) generally indicate little difference between sites and a relatively large error within each site. The significant correlation between wing loading and time since founding of the population found by Cwynar and MacDonald (1987) for lodgepole pine is not evident in this study of jack pine (time since founding in the present study decreasing northward with newer populations). However, the plotted values (Figure 6e) do suggest that there is

potential for a trend, particularly as site six, the southernmost site shows a large wingloading. This is, though, purely speculative.

Two possible explanations exist for the results obtained in this study. The dispersal along the sampled gradient must be considered, as well as the climate along the gradient. In their study of lodgepole pine, Wheeler and Guries (1982) sampled twenty-seven sites which spanned approximately 33 degrees of latitude. Cwynar and MacDonald (1987) used a subsample of these data that spanned 13 degrees latitude. In this study, six sites were sampled over approximately 4 degrees of latitude.

Because coniferous trees have a high capability for long distance dispersal, it would require a larger relative site to site distance to produce significant migratory induced changes than a species which did not have as great a potential for long distance dispersal. Variations observed between the sites may be locally induced. Therefore various local site specific microclimates, soil properties and competitors may be influencing traits at each site to the degree to which we have observed. Once a further sampling is done farther south, however, these fluctuations may just appear as a random noise in the overall trend.

Not only might dispersal be a factor in the results, but the climate change over the sampled area may not be conducive to the expected changes. Baker (1972) noted that seed weight of a given species tended to decrease with increased latitude and a shorter growing season. Therefore, working along a larger latitudinal gradient as is done in the lodgepole pine study, may have been a factor in producing their results. In addition, the conditions at the margins of the sampled jack pine population may not be stressful enough to induce changes, as compared to the southernmost site. However, once again, a sampling farther south may indicate such a change.

5.2 Conclusions

The following can be concluded in this study of morphological variations in jack pine along its central to marginal population ranges: 1) climate, as it is observed through tree growth rates, is not a factor, 2) very few significant relationships exist between and amongst measured cone and seed morphological traits, 3) directional changes in cone and seed morphological traits are not evident, and 4) morphological variations along the gradient of the sampled populations indicates

a great deal of variation.

There remains, however, a great deal of potential for future studies. A larger sampled latitudinal gradient might produce directional morphological changes which would incorporate the results of this study in the trends.

REFERENCES

- Baker, H.G. (1972) Seed Weight in Relation to Environmental Conditions in California, Ecology, Vol 53 : 997-1010.
- Bruhaler, L.B. (1986) Responses of Tree Populations to Climatic Change, Vegetatio, Vol 67: 119-130.
- Critchfield, W.B. (1985) Review: The Late Quaternary History of Lodgepole and Jack Pines, Can. J. For. Res., Vol 15: 749-772.
- Cwynan, L.C., MacDonald, G.M. (1987) Geographical Variations of Lodgepole Pine in Relation to Population History, American Naturalist, Vol 129: 463-469.
- Davis, M.B. (1976) Pleistocene Biogeography of Temperate Deciduous Forests, Geoscience and Man, Vol 13: 13-26.
- Davis, M.B., Community Ecology, Diamond, Jared and Case (eds), Harper and Row, New York, 1984, pp 269-284.
- Greene, D.F., Johnson, E.A. (1986) Dispersal Capacity and Seed Production in Anemochorous Plants, Oecologia, Vol 68: 629-631.
- Greene, D.F., Johnson, E.A., A Model of Wind Dispersal of Winged or Plumed Seeds from a Point Source, Ecology (in press)
- Harper, J.L., Lovell, P.H., Moone, K.G. (1970) The Shapes and Sizes of Seeds, Ann. Rev. Ecol. and Syst., pp 327-356.
- Howe, H.F., Smallwood, J. (1982) Ecology of Seed Dispersal, Ann. Rev. Ecol. Syst., Vol 13: 201-228.
- MacDonald, G.M., Cwynan, L.C. (1985) A Fossil Pollen Based Reconstruction of the Late Quaternary History of Lodgepole Pine (*Pinus contorta* ssp. *latifolia*) in the Western Interior of Canada, Can. J. For. Res., Vol 15: 1039-1044.

- MacDonald, G.M., Ritchie, J.C. (1986) Modern Pollen Spectra from the Western Interior of Canada and the Interpretation of Late Quaternary Vegetation and Development, New Phytologist, Vol 102: 245-268.
- MacDonald, G.M. (1987) Postglacial Vegetation History of the MacKenzie River Basin, Quaternary Research, Vol 28: 245-262.
- Prentice, C. (1986) Vegetation Responses to Past Climatic Variation, Vegetatio, Vol 67: 131-141.
- Ritchie, J.C. (1986) Climatic Change and Vegetation Response, Vegetatio, Vol 67: 65-74.
- Rudolph, T.D., Wheeler, N.C., Dhir, N.K. (1986) Cone Clusters in Jack Pine, Can. J. For. Res., Vol 16: 1180-1184.
- Teich, A.H. (1970) Cone Serotiny and Inbreeding in Natural Populations of *Pinus Banksiana* and *Pinus contorta*, Can. J. Bot., Vol 48: 1805-1809.
- Watts, W.A., Rates of Change and Stability in Vegetation in the Perspective of Long Periods of Time, Quaternary Plant Ecology, Birks and West (eds), 1975, Blackwells, Oxford, pp 195-206.
- Wheeler, N.C., Guries, R.P. (1981) Biogeography of Lodgepole Pine, Can. J. Bot., Vol 60: 1805-1814.
- Wheeler, N.C., Guries, R.P. (1982) Population Structure, Genetic Diversity and Morphological Variation in *Pinus contorta* Dougl., Can. J. For. Res., Vol 12: 595-605.
- Wright, H.E., Jr. (1984) Sensitivity and Response Time of Natural Systems to Climatic Change in the Late Quaternary, Quaternary Science Reviews, pp 91-127.
- Yeatman, L.W. (1967) Biogeography of Jack Pine, History, Can. J. For. Res., Vol 45: 2201-2211.