VARIATION IN VESSEL DIAMETER AND LEAF AREA OF WHITE BIRCH (*Betula papyrifera*) ALONG MOISTURE GRADIENTS IN CANADA.

By

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ABSTRACT

Kwiaton, L.O'N. 2010. Variation vessel diameter and leaf area of white birch (*Betula papyrifera*) along moisture gradients in Canada. 101 pp.

Key Words: white birch, vessel diameter, vessel area, total leaf area, moisture gradient, average annual rainfall, xeric regime, mesic regime, hydric regime

White birch (*Betula papyrifera* Marsh.) is one of the most widely distributed species in Canada, found in all forested regions and north to the tree line. It can be found in different soil, topographic and moisture regions. The genetic diversity of white birch has allowed it to adapt to several different environments, leading to the question of what hydraulic or water transportation characteristics allowed the species to evolve in this manner?

One of the key hypotheses of this research is that white birch that has evolved in wet areas will have larger vessels than those trees that evolved in dry areas. Since the wet areas are less likely to experience drought they can therefore produce larger vessels while dry areas produce smaller vessels to ward off any embolism that may occur during a drought. The second hypothesis is that birch trees in dry areas will produce lower sapwood to leaf area ratios then those in wetter environments. Trees in the wet areas can support higher leaf area per unit of sapwood area while trees in dry areas have made structural modifications to leaf area as a result of water stress.

In total thirty sites were sampled across Canada ranging from Ontario to B.C. Three trees from each site were selected for sampling and from each tree three branches were sampled at the base of the live crown. Each branch was sampled at the 1cm diameter mark and transported to the lab in coolers. Leaves were removed with the petiole and analyzed for total leaf area. Microscopic images were created from the branch samples and analyzed for total vessel area, average vessel area, vessel diameter and number of vessels. Climactic variables were measured including average annual rainfall and the sites were divided into three moisture regimes: xeric (dry), Mesic (moderate) and hydric (wet).

Vessel diameter and leaf area were both positively correlated with rainfall and total vessel area was also positively correlated with total leaf area in the mesic and xeric site, therefore we fail to reject the null hypothesis for xeric and mesic sites. Hydric sites had contradicting results, with smaller leaf areas and several negative relationships. It was assumed that yearly average rainfall would account for all rainfall in the growing season, as the rest of the sites experience precipitation mostly in the form of snow during the winter. The hydric sites receive rainfall all year round, with the majority falling in the winter months. This means that the trees in this site experience a more xeric environment during summer and are susceptible to water stress.

I recommend further sampling of white birch from areas of the natural distribution that were not sampled (i.e. Costal B.C., Alaska, east coast, Quebec) to further explore the hydraulic architecture. Also I recommend common garden tests and DNA testing to deduce whether the difference across moisture regimes is an ecotypic response to physical environments or a phenotypic response.

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CHAPTER 1. INTRODUCTION TO THE THESIS

1.1 INTRODUCTION

White birch (*Betula papyrifera* Marsh.) is one of the most widely distributed

species in Canada, found in all forested regions and north to the tree line (Farrar 1995).

It can be found in different soil, topographic and moisture regions. This includes

extreme dry, well-drained sites as well as very wet, poorly drained sites (Safford et. al

1990). The genetic diversity of white birch has allowed it to adapt to several different

environments, leading to the question of how did white birch adapt to such a wide range

of moisture gradients and what hydraulic or water transportation characteristics allowed

the species to evolve in this manner?

This research explores vessel and leaf features over different moisture gradients

and examines how white birch adapts to these environments in Canada. Examining the

evolution and adaptation of white birch to extremely varied site types will help us

further understand the possible responses of the species to climate change. With

increases or decreases in annual average rainfall and temperature evident in Canada

(Zhang et al. 2000, Environment Canada 2009, Atlas Canada 2009) , this is an

extremely important and relevant area of research and will provide information on how

white birch will react to climate change and provide insight into modifications in

hydraulic architecture and how they affect forest hydrology. Understanding the

hydraulic architecture of white birch from different sites in different moisture

conditions and how this architecture supports and modifies leaf area will give us a better understanding of how birch responds to climate change.

Trees react to variations within their habitat though physical adaptation, allowing different species to occupy a range of environments and resource conditions (Villar-salvador et. al 1997). The range to which different phenotypes can change their phenotypic characteristics is under genetic control but it is not known if the variation in phenotype is genetically coded or a by-product of selection (Aspelmeier and Leuschner 2004). For white birch, there are six different varieties of the species and the natural range is extensive; it is found in several different climatic regimes across a wide distribution of soil and site types (Farrar 1995, Safford et. al 1990).

One of the key hypotheses of this research is that white birch that has evolved in wet areas will have larger vessels than those trees that evolved in dry areas. Since the wet areas are less likely to experience drought they can therefore produce larger vessels while dry areas produce smaller vessels to ward off any damage (embolism) that may occur during a drought (Zimmerman 1983).

The second hypothesis is that birch trees in dry areas will produce lower sapwood to leaf area ratios then those in wetter environments. Trees in the wet areas can support higher leaf area per unit of sapwood area while trees in dry areas have made structural modifications to leaf area as a result of water stress (Mencuccini and Grace 1994). The growth and productivity of forests varies based on climate and site conditions (Carey et. al 1998, Medhurst and Beadle 2002) thus affecting the production of sapwood and leaf area. The more sapwood area per unit leaf area a tree produces the less susceptible it is to embolism or cavitation (interruption of the water column through

introduction of air into a vessel) as well as having an increase in water and nutrient storage capacity and mechanical stability (Villar-Salvador et. al 1997, Ewers et al. 2007).

The objectives of this study are: to examine the species fitness in terms of the hydraulic architecture of white birch across Canada; to predict how the species reacts to different climate regimes by comparing leaf area, weight and sapwood area to leaf area ratios at different locations across Canada; to map out the hydraulic architecture of white birch across Canada in terms of vessel size and number of vessels per unit of sapwood area and finally to examine the effects of mean annual precipitation and other climate factors (daily average temperature and potential evapotranspiration) on hydraulic architecture of white birch.

1.1.1 Silvics of White Birch

The extensive native range of white birch stretches from Newfoundland to British Colombia and extends southeast from North Carolina and southwest from the Washington state up to the northern limit for tree growth (Figure 1.1). There are six different varieties of white birch in Canada, based on different areas of geographical range (Safford et. al 1990). White birch can be found naturally in areas with short cool summers and long cold winters and has adapted to survive in extremely cold climates. The July isotherm of white birch in the northern borders is just 13^0C and it is rarely found naturally in southern environments that have a July isotherm of greater than 21^0C. White birch can also tolerate varying amounts of precipitation, with annual averages ranging from 200mm in Northern Saskatchewan and Alberta up to 3000mm in the Vancouver, B.C. area (Figure 1.2).

Figure 1.1. Natural distribution of white birch in North America.

Source: USGS 2007

White birch can be found on a variety of soil types and in a variety of topographic positions because of its genetic diversity as well as its large geographic distribution. White birch is most productive on deep, well-drained, sandy-loam sites while the poorest growth occurs on either very dry or very wet sites (Safford et. al 1990). White birch can be found in pure stands or mixed stands with trembling aspen (*Populus tremuloides* Michx.), white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill.) B.S.P.), jack pine (*Pinus banksiana* Lamb.), and balsam fir (*Abies balsamea* (l.) Mill.) (Safford et. al 1990).
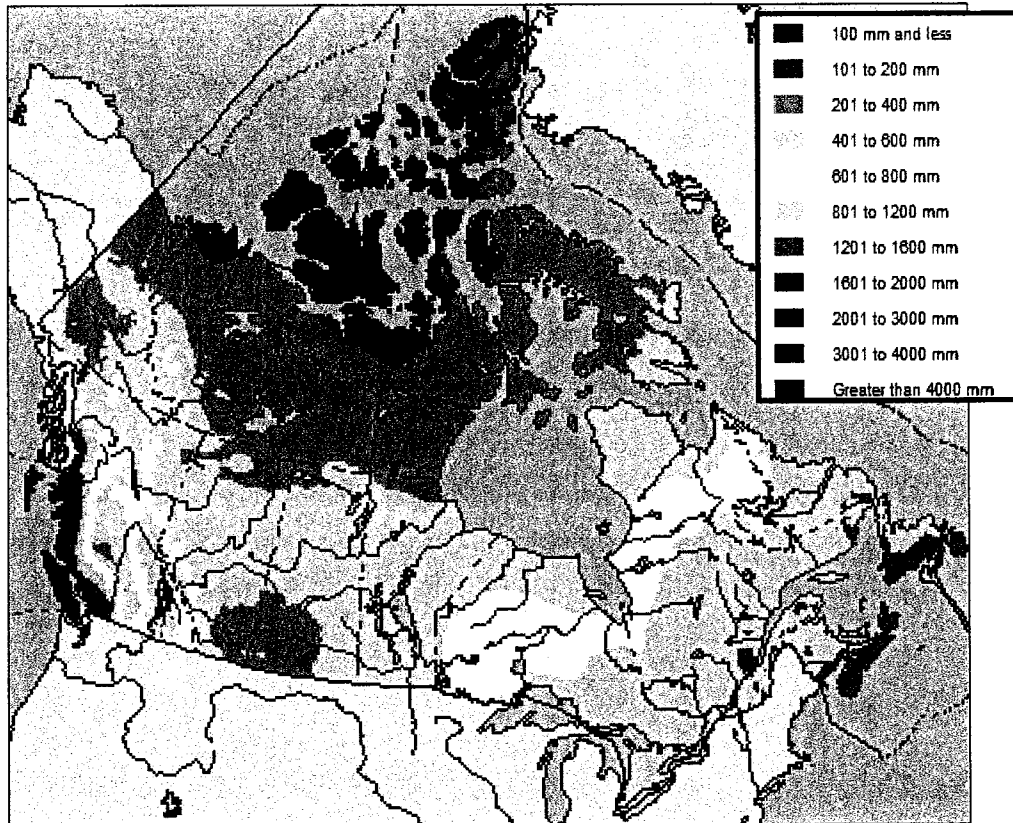
Figure 1.2. Annual mean total precipitation (mm) across Canada.

Source: Atlas Canada 2007

White birch is a monoecious species, which begins flowering in early April and

continues to flower until June, with seed dispersal from early August until mid-

September (Safford et. al 1990). The winged seeds are suited to wind transportation,

however, most seeds fall within the stand from which they originated. The seeds can

travel far distances but in undisturbed stand usually fall within 30 to 100m from the

origin. The seeds are extremely small and thus the resulting seedlings are very

susceptible to adverse growing conditions. Regeneration occurs the first year after a

disturbance, with the best growth on shaded sites with mineral soil and a humus layer

(Safford et. al 1990). Considered a short-lived species, white birch trees are fast-

growing when young (approx. first 30 years) and reach maturity in approximately 70

years, with a maximum life span ranging from 140-200 years. White birch begins height growth when the temperatures are just below freezing and has exhibited a long seasonal height growth when compared to its associated species. Diameter growth in white birch exhibits similar growing patterns, with growth beginning when temperatures are above freezing and continues later than most of the associated forest cover (Safford et. al 1990). This is consistent with a study by Heinrichs et. al (2007) that found the xylem production of white birch in the boreal region of Quebec began around mid-May and continued until late September, with latewood production beginning in early August.

1.2 RESEARCH METHODS

1.2.1 Site Location and Selection Criteria

The study sites were selected based on a stratified random sample design, in order to get a wide distribution of latitudes, longitudes and climate regimes (Figure 1.3). More sites were selected in Ontario and B.C. because these two provinces have the most diverse climate regimes. In total thirty sites were sampled across Canada ranging east-west from Kirkland Lake, Ontario to Vancouver, B.C. and north-south from Perry Sound, Ontario to Fort St. John, B.C. Requirements of candidate sites included: a minimum 70% of the site composition by stem density was white birch, an age range from thirty to sixty years and no damage or suppressed trees were sampled. All requirements were verified before sampling. Site position, slope, species composition, latitude and longitude were recorded for each sample site. All sample locations can be found in Figure 1.4.
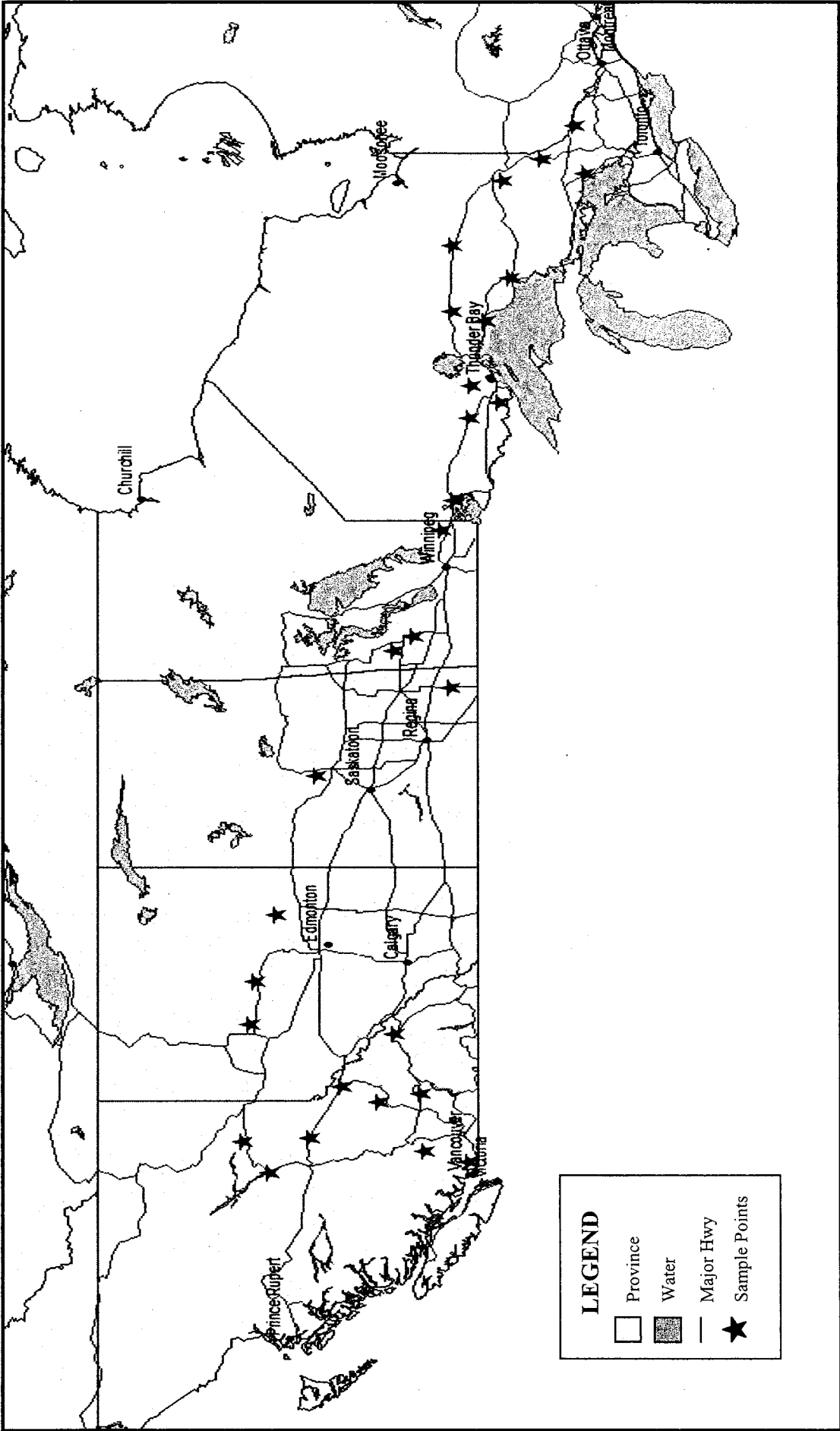
Figure 1.3. Location of sample sites across central and western Canada.

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Figure 1.4 Examples of study sites across Canada. Clockwose from top left: Alberta, northern British Colombia, southern British Colombia and Manitoba.

The birch sites were sampled in several different locations across the country in order to examine the effects of various climate regimes on the hydraulic architecture. Table 2.1 shows the range of climatic variables of the thirty sample sites. The latitude ranges from 47° to 55° N, while the longitude ranges from 78° degrees to 123° E (Table 1.1).

Average diameter at breast height (DBH) of sample trees at each site ranged from 15.07cm to 26.37cm while average height, age and crown length ranged from 10.73m to 20.20m, 35 years to 56 years and 4.53m to 15.37m, respectively. The average DBH for all sampled trees was 19.02cm, while the average height, age and crown length are 14.73m, 44.24 years and 9.95m respectively. There was also a good representation of different climatic variables, with daily average temperatures ranging from 0.14 degrees (in Longlac) to 9.60 degrees (in the Malcolm Knapp (MK) Research Forest). Average annual rainfall ranged from 294.20mm in Winnigami to 2130.90mm in the MK Research Forest (Table 1.1).

Table 1.1. Average DBH, height, age, crown length, annual precipitation, daily average temperature, PET and locations of all sample plots.

SITE		Latitude	Longitude	Average DBH (cm)	Average Height (m)	Average Age (years)	Average Crown Length (m)	Daily Average Temp. (^{0}C)	Annual Average Rainfall (mm)	PET	Moisture Regime
Winston Churchill	LA1	N54°49'	W111°59'	21.63	13.23	42.00	9.34	1.90	352.05	2	x
Slave Lake	LA2	N55°29'	W114°51'	26.37	18.67	49.33	13.87	1.66	384.40	2	x
Winnagami	LA3	N55°37'	W116°40'	17.60	15.63	45.00	10.83	1.20	294.20	2	x
Morberly Lake	LB1	N55°48'	W121°41'	18.13	17.57	44.67	12.80	3.00	318.40	2	x
Tudyah Park	LB2	N55°03'	W123°01'	23.03	17.40	37.33	13.33	2.30	358.30	2	x
Sugarbowl	LB3	N53°52'	W121°32'	17.43	14.77	40.00	11.57	4.00	418.90	2	m
Mount Robson	LB4	N52°58'	W119°21'	26.73	18.43	56.00	13.70	3.50	372.30	2	x
Wells Grey	LB5	N51°52'	W120°00'	23.00	19.70	51.60	14.66	6.92	365.10	3	x
Lillooet	LB6	N50°35'	W122°05'	20.57	16.63	37.67	12.93	9.20	297.10	1	x
MKRF	LB7A	N49°16'	W122°34'	16.17	14.57	35.00	9.93	9.60	2132.90	4	h
MKRF	LB7B	N49°16'	W122°34'	18.76	18.41	35.00	11.34	9.60	2132.90	4	h
Penticton	LB8	N50°39'	W119°38'	20.20	15.24	32.20	12.56	7.65	334.00	3	x
Donald	LB9	N51°26'	W117°05'	24.05	15.40	23.33	12.60	3.15	463.90	1	m
Whiteshell	LM1	N50°03'	W95°31'	15.07	10.83	45.00	4.53	2.30	445.50	3	m
Riding Mtn.	LM2	N50°52'	W100°03'	17.47	13.00	45.33	5.97	2.00	370.60	3	x
Duck Mtn.	LM3	N51°41'	W100°42'	15.96	14.55	47.50	9.88	1.68	399.70	3	x
Kenora	LO1	N49°41'	W94°14'	15.57	12.43	45.33	5.53	2.70	514.40	3	m
Marathon	LO2	N48°47'	W86°35'	15.77	11.77	53.00	6.07	1.44	581.60	2	m
Wawa	LO3	N48°04'	W84°45'	19.53	12.47	41.67	8.07	1.70	727.40	2	m
Grundy Lake	LO4	N45°52'	W80°21'	16.60	14.03	49.00	8.93	4.75	690.30	3	m
Petawawa	LO5	N46°10'	W78°18'	20.57	20.20	54.67	15.37	3.75	611.55	3	m
Temagami	LO6	N47°09'	W79°43'	19.10	11.73	44.33	7.63	2.30	553.90	3	m
Kirkland Lake	LO7	N48°17'	W80°39'	17.13	12.37	46.33	7.30	1.65	589.70	2	m
Mattice	LO8	N49°45'	W83°22'	17.87	10.73	43.33	6.43	0.14	521.20	2	m
Longlac	LO9	N49°46'	W86°12'	19.27	14.53	50.67	9.83	0.33	546.40	2	m
Armstrong	LO10	N49°10'	W89°21'	20.00	16.10	52.33	9.67	2.00	571.15	3	m
Upsala	LO11	N49°15'	W90°45'	17.47	12.23	49.33	8.13	2.05	563.65	3	m
Thunder Bay	LO12	N48°23'	W90°05'	16.67	12.57	48.33	6.73	2.50	559.00	3	m
Prince Albert	LS1	N53°41'	W106°02'	16.20	15.70	42.67	10.60	0.90	323.70	3	x
Moose Mountain	LS2	N49°49'	W102°16'	16.77	10.90	39.33	8.27	2.60	330.50	2	x

x = xeric, m = mesic, h = hydric

CHAPTER 2. VESSEL DIAMETER AND FREQUENCY ACROSS THREE
MOISTURE REGIMES IN CANADA

2.1 INTRODUCTION

The xylem is one of the most integral parts of any plants hydraulic architecture.

Vessels are the key structure in the transportation of water in white birch trees. The size

and number of these vessels affect not only the amount of water a tree can transport but

also can determine how vulnerable a tree is to damage. Vessels with larger area are

more prone to embolism than smaller vessels, which cause the vessels to cease

functioning and therefore cease transporting water (Zimmerman 1983). Increased

number of vessels per unit of area also creates a situation where if vessels do cavitate,

the percentage of conductance lost is less than if the sample had lower number of

vessels per unit area (Villar-Salvador et al. 1997). One of the main causes of embolism

is lack of available water, or drought situations, so plants can vary their structure to

maintain fitness under a variety of environmental conditions, including xylem variation

(Villar-Salvador et al. 1997).

White birch can maintain fitness under an ample range of environmental

conditions, including both wet and dry areas. This chapter serves to address our first

hypothesis, that white birch which has evolved in wet areas will have larger vessel sizes

than those trees that evolved in dry areas. Since the wet areas are less likely to

experience drought they can therefore produce larger vessels while dry areas produce smaller vessels to ward off any damage (embolism) that may occur during a drought.

2.2 LITERATURE REVIEW

2.2.1 Wood Anatomy and Transportation Processes

The wood of white birch is classified as diffuse porous, which refers to the even size and distribution of the vessels between growth rings (Figure 2.1) (Pansin and Zeeuw 1980). Diffuse porous vessels occupy more total volume than vessels of ring porous trees (vessels that are concentrated around the growth rings) (Siau 1984). The vessels are the cells responsible for transportation of water from roots to leaves. Vessels are composed of vessel elements, a group of individual cells with no end walls as they are partially dissolved during cell maturation (Zimmerman 1983). The openings left from the holes in the end walls are known as perforations. Thus the end walls shared by adjacent vessel elements are known as perforation plates. White birch exhibits scalariform perforation plates that consist of multiple openings parallel to one another that form narrow strips, known as bars (Figure 2.1) (Pansin and Zeeuw 1980).
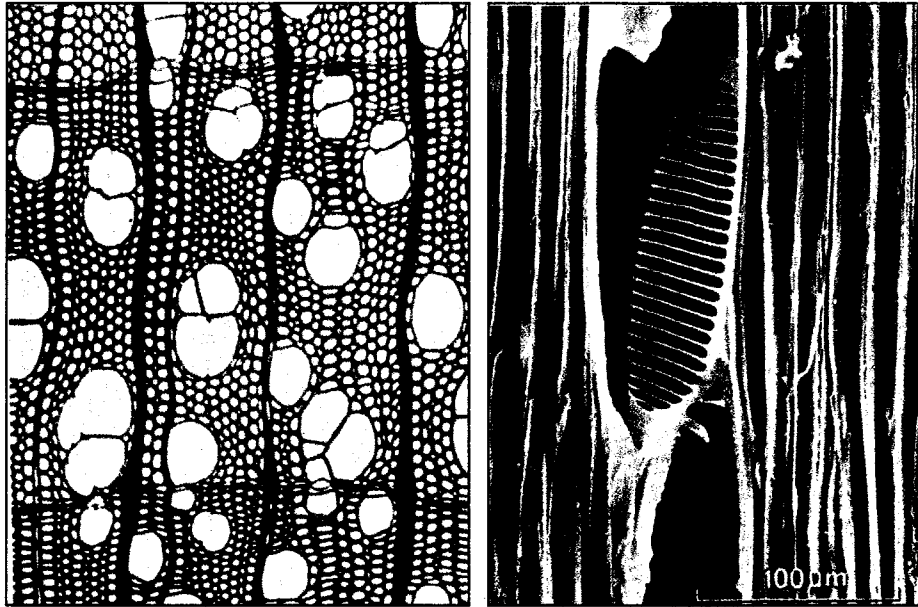
Figure 2.1. Diffuse porous vessel distribution (left) and scalariform plating (right) in white birch.

Source: Zimmerman 1983, Pansin and Zeeuw 1980

Pitting on vessel walls and intervessel pitting are other species-specific characteristics that appear in the anatomy of various hardwoods. Pit pairs between vessel walls are usually bordered, but when they occur between parenchyma and vessels they can be bordered, half bordered or simple (Pansin and Zeeuw 1980). Intervessel pitting also occurs in three different forms, opposite pitting (horizontal arrangement), alternate pitting (diagonal arrangement) and scalariform pitting (linear arrangement of long single pits). *Betula* spp. exhibit very small, alternate intervessel pits and are easily identified by a lack of spiral thickening of vessel walls common in diffuse porous trees (Pansin and Zeeuw 1980).

Vessel diameter varies depending on the age or location of the vessel within the tree. This variation continues when comparing the roots, stem and branches within the same tree. Root vessels are generally larger than those in the stem while vessels in the branches are smaller than those in the stem, creating an increase in vessel diameters in a

basipetal direction (top to bottom) (Zimerman 1983, Leitch 2001). In white birch, the branch vessels are approximately 30-50% smaller than those in the stem, however, branches contain less fibre and more vessels then those found in the stem (Safford et. al 1990). De Micco et al. (2008) suggest that studying the hydraulic architecture of juvenile structures is relevant as the most distal part of the tree is the branch and thus they play an important role in water flow.

It is important when examining specific vessel attributes (i.e. number of vessels and/or diameter) and relating to habitat or climate to measure samples from different trees with the same criteria (i.e. branches less then 1cm in diameter) to ensure that the variation in vessel diameter between roots and leaves are not affecting the size or distribution of the vessels being tested (Zimmerman 1983, Wang 2005).

2.2.2 Hydraulic Architecture

Hydraulic architecture is defined as "the relationship of the hydraulic conductivity of the xylem in various parts of a tree and the amount of leaves it must supply" (Cruiziat et. al 2002). Zimmerman (1983) defines conductivity as "the reciprocal value of resistivity, i.e. the resistance to flow expressed per transverse-sectional area (of wood for example)". Hydraulic conductivity is in reference to the entire plant part being examined, for example branch, stem or root (Cruiziat 2002).

Water transportation in trees is based on the cohesion-tension theory, which states the driving force of water movement is the transpiration of water from the leaves, which causes a water potential gradient that pulls water from the soil and creates a passive movement through the xylem (vessels or trachieds) to the leaves (Cruiziat et. al 2002, Zimmerman 1983). The solar radiation that causes transpiration also creates a

negative pressure or less then atmospheric pressure gradients within the xylem. This theory has some criticisms based on the fact that some species do exhibit positive pressure (Zimmerman 1983). However, several studies have shown that transpiring leaves cannot perform their task without uptake of water from the soil and that negative pressure gradients within the xylem do exist (Zimmerman 1983). The vascular system of trees is made up of several different pathways, where any root can connect with any branch and is not limited to just one. This means that water can travel vertically up the tree but can also pass laterally through the pit membranes of the vessels (Cruiziat et. al 2002).

The Hagen-Poiseuille law calculates the flow of water in vessels as a function of the vessel diameter raised to the 4th power. Hagen and Poiseuille in 1839 and 1840, respectively, discovered that liquid is stationary along the capillary wall with flow increasing towards the centre of the capillary (Zimmerman 1983, Cruiziat 2002). This means that small vessels transport much less water than large vessels. For example, if the three vessels in Figure 2.2 represent a vascular bundle, the smallest would only carry 0.04% of the water when compared to the larger vessels which would carry 5.9% and 93.7%.

Relative Diameter	1	2	4
Relative TS Area	1	4	16
Relative Flow Rate	1	16	256
% Flow Rate	0.4	5.9	93.7
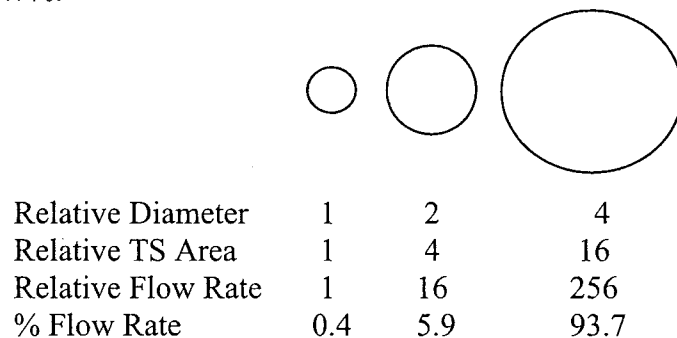
Figure 2.2. Relative transverse-sectional (TS) areas and relative flow rates in capillaries with different diameters.

Hagen-Poiseuille law states that conductivity should increase if the number of vessels or average vessel diameter increases within the cross-sectional area of the branch. It is important to remember that there is no simple correlation between the total cross section of a branch and the area of the vessels, as they change along the branch (Cruiziat 2002). Vessels will not be proportional to the fourth power because vessels differ greatly from capillaries. To begin there is both lateral and vertical movement of water between vessels as well as the perforation plates that separate the vessel elements (Zimmerman 1983,Cruiziat 2002). Other irregularities within the vessels themselves, including rough vessel walls and pits, create inefficiencies in transport when compared with perfect capillaries. The scalariform perforation plates of the *Betula* species (specifically *B. pubescens* Ehr.) showed vessels are only 34-38% as efficient as perfect capillaries (Zimmerman 1983). However, inside vessel diameter is still an important factor for hydraulic conductivity, as any increase in vessel diameter means a significant increase in the conductivity and flow rates of the tree (Zimmerman 1983, Cruiziat 2002). Assuming pressure gradients are the same, trees with larger vessels have a larger flow, for example gymnosperms (evergreens) transport through trachieds and have a lower specific conductivity (conductivity divided by sapwood area) when compared to angiosperms (hardwoods), which transport water through the larger vessels (Wang 2005, Siau 1984). Not all trees have evolved to have extremely large vessel diameters. This is because larger vessels are more prone to embolism and cavitation, while the smaller vessels have less vulnerability to embolism (Villar-Salvador et al. 1997, Wang et. al 1992). Embolism is defined as "the abrupt change from liquid water under tension

to water vapour" (Cruiziat et. al 2002). This can be caused by injury to the tree (via boring beetle, wind damage etc) or from drought. Drought induced embolism occurs when a water filled vessel draws in air bubbles from adjacent air filled spaces or cells (Schenk et. al 2008). This changes the pressure to atmospheric (or positive) from negative and the cell becomes embolised or no longer capable of transportation (Cruiziat et. al 2002, Zimmerman 1983). Essentially it is a breakage in the water column caused by the infiltration of air into the vessel from a change in xylem pressure (Sperry and Pockman 1993, Schenk et. al 2008).

There are different pressure levels that cause cavitation in different species, ranging from −1.0 MPa in a tropical species to −10.0 MPa in the chaparral species (Sperry and Pockman 1993). Pressures within an individual species critical level therefore reduce or eliminate water transportation and it is clear that drought (or water stress within the tree) is the main cause of summer embolism. It is important to note that several months of drought are required to damage enough vessels via embolism to cause serious harm to the tree (Sperry and Pockman 1993, Cruiziat et. al 2002). The cause of drought-induced embolism is debated among the scientific community. The most popular explanation is based around the air-seeding theory. The air bubble enters into the water filled vessel via the pit pores, which causes water to evaporate into it, increasing its size. This causes a change in pressure and seals the air inside the vessel until the entire vessel is filled with the air vapour. Thus it is the size of the pit pores, not the vessel diameter that causes the embolism of conduits in the summer time (Zimmerman 1983, Cruiziat 2002).

Freeze-thaw cycles of northern climates have also been found to induce embolism (known as winter embolism) and a loss in hydraulic conductivity, which can result in delayed leaf out in the spring (Wang 2005, Wang et. al 1992). Ring porous trees in these northern or temperate climates are much more susceptible than their diffuse porous neighbours, for whom winter embolism is more gradual, occurring after several frost events. Unlike summer embolism, winter embolism is a direct relation to the size of the conduits, where the larger the conduit the more susceptible the vessels are to winter embolism (Cruiziat et. al 2002). Wang et. al (1992) found, when studying 43 north-temperate species, that angiosperms exhibit more vulnerability to winter embolism then gymnosperms. Wang (2005) also found that pioneer species, including white birch, with high conductivity also were more prone to winter embolism.

The explanation for winter embolism is based about the frost-thaw theory (Cruiziat et al. 2002). Air bubbles of different sizes form during sap freezing at temperatures below zero, when ice forms. When the temperatures are above freezing the sap thaws and the bubbles either expand or collapse, depending on their size. The larger vessels are more prone to embolism of this manner simply because the initial sizes of the bubbles are larger (Cruiziat et al. 2002, Zimmerman 1983). In fact, it has been suggested that the scalariform perforation plates in white birch are a defence mechanism against the spreading of air bubbles by trapping them (Zimmerman 1983). Zhu et al. (2002) found that yellow birch seedlings were susceptible to frost-thaw events after 12 days of exposure to thawing, which de-hardened seedlings enough to cause cavitation damage. The damage from these events created a lower stem increment, shoot length and leaf area when compared to non-thawed seedlings.

It has been found that there is some embolism occurring throughout the year known as residual embolism. This can result from poorly formed vessels, bad weather events that cause injury, and any pathogens (insect or fungi) that may attack the tree even in well-watered areas (Cruiziat et. al 2002).

2.2.3 Effect of Climate on Wood Anatomy

There have been several studies done trying to relate specific weather factors to wood anatomy because trees react to variations within their habitat through physical adaptation, allowing different species to maintain their fitness in an ample range of environments and resource conditions (Villar-Salvador et. al 1997). The degree to which the adaptation occurs depends on both the genetic diversity within the species as well as the ability of the individual tree to change its phenotypic makeup (Aspelmeier and Leuschner 2004). The range to which an individual tree can change its phenotypic characteristics is under genetic control but it is not known if the variation in phenotype is genetic code or a by-product of selection (Aspelmeier and Leuschner 2004).

A study done by Henrichs et. al (2007) found a significant effect of weather patterns on the production of xylem (vessels) for white birch in boreal Quebec. The onset of xylem production was positively correlated with an increase in soil and air temperatures. White birch also responded greatly in radial growth to high levels of precipitation in June.

It has also been suggested that xylem structure within a species can be manipulated by differences in aridity and low temperatures. Three species of *Quercus* were sampled along a climate gradient in North-eastern Spain to test the climatic factors limiting growth: summer drought and winter cold. One ring porous species, *Q. faginea*

(Lam.) and two diffuse porous evergreen species, *Q. coccifera* (L.) and *Q. ilex* (L.) were studied (Villar-Salvador et. al 1997). Hagen-Posieuille law states that *Q. faginea* should have a higher hydraulic conductivity then the diffuse porous *Quercus* spp., which should exhibit limited rates of flow. Villar-Salvador et. al (1997) found that the ring porous species with large vessels was found in deeps soils with constant water supply and the diffuse porous species with smaller vessels were found in dry and shallow soils. These results correlated with the ecological distribution of the three *Quercus* species studied. While none of the species responded significantly to changes in winter temperatures, the diffuse porous evergreen species did react to changes in precipitation. This may not apply to white birch in Canada as winter temperatures here are much colder than those of the Mediterranean. Both species reduced their average vessel diameter when the growing environment became more arid (Villar-Salvador et. al 1997). The decrease in average vessel diameter could be a response to the scarcity of available water in an effort to reduce water consumption. The authors found that water availability was the most important factor influencing the development and variation of vessels and that species with similar phenotypic characteristics can adopt different strategies even within the same climate gradient (Villar-Salvador et. al 1997).

Certain anatomical features of trees, shrubs and climbers have been associated with macroclimate. In Europe, trees from boreal sites tend to have scalariform perforation plates, and solitary vessels while trees from warmer Mediterranean climates have simple perforation plates, vascular trachieds and different vessel size classes (Baas and Schweingruber 1987). In relation to dry (which includes wet saline) to mesic sites, the occurrence of scalariform plating increases greatly, as does that of differing vessel

sizes. Spiral thickening decreases, as does the presence of vascular trachieds. There is no correlation between ring porosity and moisture availability (Baas and Schweingruber 1987).

2.3 METHODS

2.3.1. Data collection and branch sampling

Three trees were randomly selected at each site and measured for diameter at breast height, total height, age, crown length, crown form and microsite position. From each tree, three branches with a one centimetre diameter were sampled at the base of the live crown, a total of nine branches per site (Figure 2.3). The base of the live crown was selected because, as mentioned above, the vessel decrease as tree height increases, thus the most variation would be found in lower branches. Also this created a standardization of sampling that limits bias. The branches were cut using a pole clipper, measured for length, labelled and stored in plastic bags (Figure 2.3). They were transported from the site to the lab in coolers and stored in the lab refrigerator.
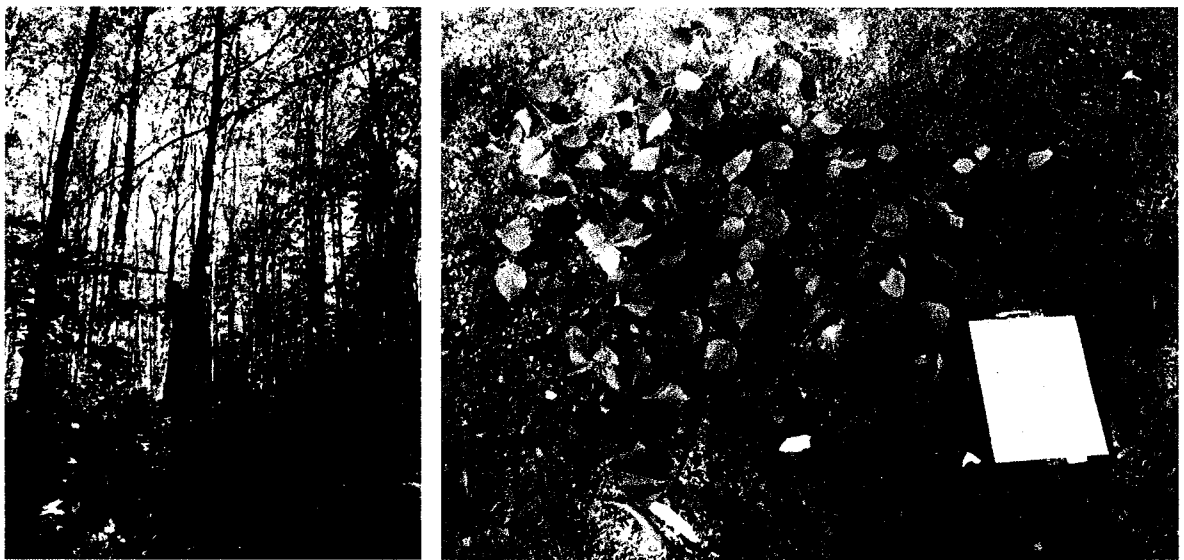
Figure 2.3. Left: Sampling branches with the pole clipper. Right: Three branch samples from one tree before the leaves were removed

2.3.2 Microscope Slide Preparation

The branches were cut into approximately 7 cm pieces with the cross sectional face at the one centimetre diameter mark. The sample blocks were then immersed in distilled water in a beaker and allowed to soak for two days to prepare them for the microtome (Figure 2.4). The microtome was used to slice the branch sections for the slides. The edges of the branches were slightly bevelled, which eases the microtome blade into the sample and helps to create better sections. Each branch was fastened into place with the cross-sectional plane facing upwards and adjusted so that the face was parallel with the knife (Figure 2.4).

The microtome knife was set to cut 20 micrometer thick sections and was manually operated. The sections were very thin and fragile, thus a fine, wet paintbrush was used to transfer the cut section into a glass holding plate filled with distilled water to ensure that air would not re-enter the sections. The next step in the microscopy was to create temporary slides of each sample. Two sections were selected and placed in a temporary mount using distilled water and a slide cover (Figure 2.4).

Figure 2.4. Clockwise from top left: branch sample blocks soaking is distilled water, all equipment used in slide preparation, branch sample block on the microtome, branch segments stored in water and a temporary slide.

2.3.3 Microscopy and Image Analysis

Once the slides were created, they were examined under a microscope at 16x magnification. Three digital pictures were taken from each section (Figure 2.5), making a total of six images per branch. Each image represented $1.75mm^2$ of area on the cross sectional plane of the branch.

The digital pictures were analysed using the WinCell© program (Regent Instrument Inc.) to count the number of vessels, determine each vessel width and diameter, average vessel area, and total vessel area (Figure 2.6). Examples of images from all sample sites can be found in Appendix I. All of the analysis was done in the outermost ring, to ensure that there is no bias introduced in sampling from different years within the sapwood area, as well as to ensure the tissues being examined were juvenile sapwood and therefore also actively conducting water.

Along with vessel variables derived from the WinCell© analysis, climate variables were collected from the National Climate Data and Information Archive (Environment Canada 2008). Data were taken from the nearest weather station and were calculated as a yearly average totalled from 1971 until the year 2000. The variables extracted were average annual rainfall and daily average temperature. Based on the climate data, four average annual potential evapotranspiration (PET) ranges were established for site classification. PET for each site was categorized into the following four ranges: 0 - 40.6cm, 40.7 - 50.8cm, 50.9 - 61.0 cm and > 61.1cm.
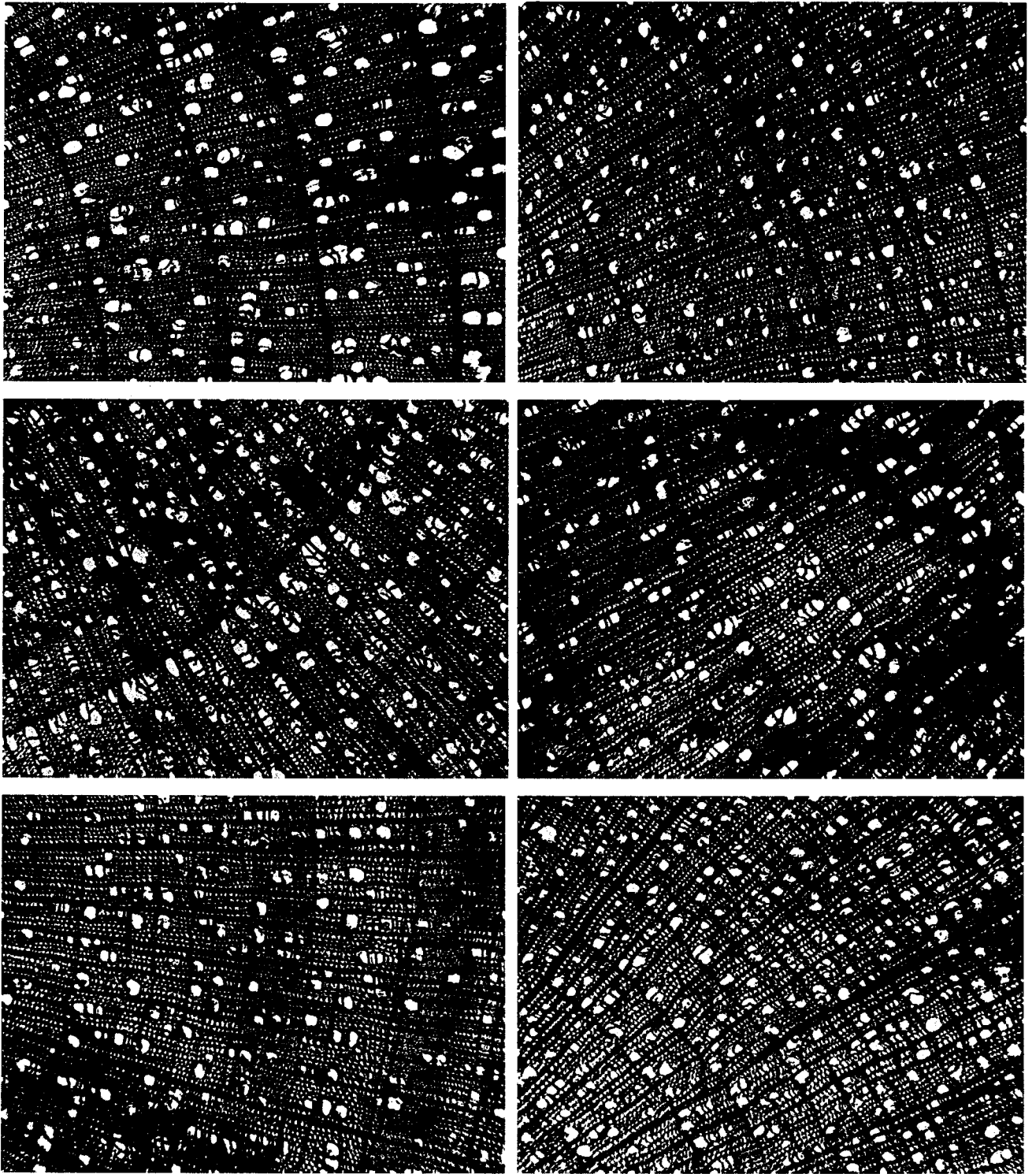
Figure 2.5. Example of vessel images. Clockwise from top left: a site in northern Ontario (LO2), Sask. (LS2), Alberta (LA1), southern Ontario (LO7), Manitoba (LM2), and B.C. (LB4)

2.3.4 Data Analysis

The data were categorized into three rain regimes. Sites with less than 400mm of average annual rainfall were considered xeric. Sites with greater than 400mm of average annual rainfall, up to 750mm were considered mesic. The hydric category represents two sites in costal B.C., which exhibited over 2100mm of average annual rainfall and created outlier issues in the data set and were examined separately.

A Pearsons Product-Moment Correlation (Data Desk©) was performed on all variables to deduce any significant positive or negative relationships between variables at the branch, tree and site level. Any variables exhibiting extremely high correlations (0.90 or greater) were screened to ensure the variable in question did not account for similar variance in subsequent statistical analyses. The level of significance for the branch data set at the alpha 0.10 level is $\pm$ 0.112 for 241 degrees of freedom, which creates a significant r^2 value of 1.25%. The level of significance tree data set at the alpha 0.10 level is $\pm$ 0.173 (df = 90) with a significant r^2 value of 2.99%, while the level of significance for the site data set at the alpha 0.10 level is $\pm$ 0.306 (df= 28) with a significant r^2 value of 9.36%.

Frequency distributions were created for vessel diameter for each moisture regime using all vessel data. A one-way analysis of variance (ANOVA) was used to test for significant differences among mean vessel diameter between moisture regimes at the alpha 0.10 level.

Significant correlations of interest at all levels were plotted in a simple regression to examine the data distribution between variables. Extreme outliers were removed to examine the impact on the simple regression result. A t-test (Zar 1996) was

run between mesic and xeric sites in each simple regression to determine if the models were significantly different. If the slopes were not significantly different then a t-test was run on the respective y-intercepts.

Stepwise multiple regression analyses were conducted on three different dependent variables – average number of vessels within $1.75mm^2$, average vessel diameter and total vessel area – at the site level, where:

$$y = b_o + b_1x_1 + b_2x_2 \ldots + b_ix_i$$

Where $_i$ is the number of variables.

Independent variables included site variables (latitude, longitude, average height, and average DBH) and climactic variables (average annual rainfall, daily average temperature and PET). Best fit model was determined using stepwise multiple regression at the alpha 0.10 level. Models were developed to examine the influence of independent variables on the dependent variables, not as a prediction equation.

2.4 RESULTS

The summary of average vessel area, diameter, number of vessels and average total vessel area for each site can be found in Table 2.1. The site with the smallest average total areas was in northern Saskatchewan (LS1), while LO12 in southern Ontario had the highest average total area. The site with the smallest vessel area and diameter was northern B.C. (LB1) while LO2 in northern Ontario had the highest vessel area and diameter. LB4 exhibited the lowest number of vessels, while the highest number of vessels occurred at LO7. The overall average for total vessel area was 123,101.09 μm^2, while the total average for vessel area, diameter and number of vessels was 467.59 μm^2, 26.42 μm and 268.22, respectively.

A Pearsons Product-Moment Correlation was performed at the branch, tree, and site level for all variables (Tables 2.2, 2.3 and 2.4, respectively). Total vessel area was significantly correlated with average vessel area, average vessel diameter, number of vessels and daily average temperature and negatively correlated with latitude at both the tree and site level. Both average vessel area and vessel diameter were significantly correlated with each other as well as total vessel area, daily average temperature and average annual rainfall at the tree and site levels. Both variables were negatively correlated with latitude at the tree and site levels and negatively correlated with number of vessels, however, only at the tree level. Number of vessels was correlated only with total vessel area at the site level, while at the tree level was significantly correlated total vessel area and negatively correlated with average vessel area and diameter. The branch level Pearsons Product-moment test produced the same relationships at the tree and site level but also produced more significant relationships with average annual rainfall and vessel area, width and length as well as more significant relationships with latitude and vessel variables.

Table 2.1. Average total vessel area, average vessel area and diameter and average number of vessels for each sample site.

Site	Avg. Total Vessel Area (μm^2)	Avg. Vessel Area (μm^2)	Avg. Vessel Diameter (μm)	Avg. No. Vessels
LA1	108523.89	429.91	25.36	257.44
LA2	122084.88	445.04	25.88	279.87
LA3	115525.38	421.22	25.23	278.06
LB1	120710.42	414.15	25.08	295.48
LB2	128457.20	461.43	26.42	283.13
LB3	112502.48	463.51	26.50	245.22
LB4	111459.57	486.83	27.03	233.06
LB5	123763.71	480.98	26.82	265.44
LB6	133068.95	476.67	26.69	283.07
LB7A	129134.16	486.21	27.10	269.50
LB7B	128718.90	521.39	27.88	250.59
LB8	132800.43	503.09	27.19	267.66
LB9	138984.84	499.51	27.08	282.87
LM1	128354.92	453.83	26.06	287.76
LM2	122621.66	483.87	26.71	256.69
LM3	123795.44	475.86	26.59	266.69
LO1	129314.32	469.18	26.54	282.13
LO2	128330.19	533.94	27.90	245.74
LO3	110118.66	466.05	26.33	241.45
LO4	120031.65	434.35	25.63	280.67
LO5	130135.08	477.58	26.82	276.04
LO6	131029.16	456.72	26.22	292.57
LO7	123809.95	422.26	25.26	298.37
LO8	116419.13	446.08	25.88	266.76
LO9	105929.39	462.86	26.19	233.78
LO10	129652.70	486.95	26.75	272.06
LO11	129408.78	514.29	27.49	256.28
LO12	148687.65	504.15	27.14	297.30
LS1	104536.13	433.16	25.55	244.88
LS2	105123.08	416.73	25.27	256.13

Table 2.2. Pearsons Product-Moment correlations of variables measured at the site level. Significant values (R>0.306) at alpha 0.10 (df = 28) level in bold.

Site	Latitude	Longitude	DBH	Height	Age	Crown Length	Total Weight	Total Leaf Area	SLA	Sapwood Area	Total Vessel Area	Avg Vessel Area	Avg Vessel Length	Avg Vessel Width	Avg Vessel Diameter	No. vessels	Daily Avg Temp	Rainfall
Latitude	1																	
Longitude	**0.726**	1																
DBH	**0.387**	**0.401**	1															
Height	**0.372**	**0.541**	**0.623**	1														
Age	-0.161	-**0.490**	0.017	0.091	1													
Crown Length	**0.432**	**0.605**	**0.719**	**0.909**	-0.091	1												
Total Weight	-**0.377**	-**0.340**	0.234	-0.240	0.043	-0.057	1											
Total Leaf Area	-0.202	-0.247	**0.395**	-0.068	0.174	0.070	**0.886**	1										
SLA	**0.421**	0.264	-0.098	0.191	0.020	-0.003	-**0.845**	-**0.644**	1									
Sapwood Area	-**0.473**	-**0.402**	-0.202	-**0.307**	-0.080	-0.273	**0.569**	**0.328**	-**0.622**	1								
Total Vessel Area	-**0.353**	-0.018	-0.001	0.052	-0.178	-0.040	**0.341**	0.282	-0.290	**0.375**	1							
Avg Vessel Area	-**0.353**	0.032	0.008	0.106	-0.059	0.007	0.187	0.096	-0.149	0.177	**0.544**	1						
Avg Vessel Length	-**0.366**	0.108	-0.036	0.176	-0.117	0.082	0.061	-0.013	-0.106	0.128	**0.449**	**0.908**	1					
Avg Vessel Width	-0.303	0.019	0.048	0.103	-0.017	0.001	0.192	0.118	-0.131	0.142	**0.548**	**0.969**	**0.796**	1				
Avg Vessel Diameter	-**0.353**	0.068	0.006	0.148	-0.072	0.045	0.134	0.055	-0.125	0.144	**0.525**	**0.990**	**0.949**	**0.946**	1			
Nvessels	-0.084	-0.070	-0.009	-0.036	-0.115	-0.066	0.208	0.245	-0.169	0.262	**0.649**	-0.280	-**0.307**	-0.246	-0.293	1		
Daily Avg Temp	-0.156	**0.529**	0.088	**0.403**	-**0.393**	**0.394**	-0.113	-0.124	-0.066	-0.049	**0.370**	**0.363**	**0.500**	0.288	**0.418**	0.074	1	
Rainfall	-**0.356**	0.096	-0.211	0.067	-0.251	-0.065	-0.162	-0.237	-0.024	0.229	0.264	**0.371**	**0.448**	**0.352**	**0.422**	-0.035	**0.567**	1

Table 2.3. Pearsons Product-Moment correlations of variables measured at the tree level. Significant values (R>0.173) at alpha 0.10 level (df = 90) in bold.

Tree	Latitude	Longitude	DBH	Height	Age	Crown Length	Total Weight	Total Leaf Area	SLA	Sapwood Area	Total Vessel Area	Avg Vessel Area	Avg Vessel Length	Avg Vessel Width	Avg Vessel Diameter	No. vessels	Daily Avg Temp	Rainfall
Latitude	1																	
Longitude	**0.706**	1																
DBH	**0.311**	**0.317**	1															
Height	**0.327**	**0.496**	**0.538**	1														
Age	-0.108	**-0.384**	**0.262**	0.140	1													
Crown Length	**0.395**	**0.573**	**0.620**	**0.866**	-0.018	1												
Total Weight	**-0.315**	**-0.291**	0.167	**-0.224**	0.110	-0.037	1											
Total Leaf Area	-0.165	**-0.219**	**0.231**	-0.086	0.160	0.045	**0.826**	1										
SLA	**0.363**	**0.222**	-0.095	0.180	-0.013	-0.018	**-0.744**	**-0.383**	1									
Sapwood Area	**-0.405**	**-0.330**	**-0.227**	**-0.308**	**-0.180**	**-0.266**	**0.385**	**0.209**	**-0.413**	1								
Total Vessel Area	**-0.207**	0.011	-0.098	0.053	-0.182	-0.007	0.176	**0.204**	-0.048	**0.203**	1							
Avg Vessel Area	**-0.237**	0.068	-0.102	0.110	-0.150	0.053	0.131	0.129	-0.033	**0.192**	**0.512**	1						
Avg Vessel Length	**-0.241**	0.127	-0.102	**0.179**	-0.165	0.118	0.050	0.074	-0.012	0.147	**0.473**	**0.933**	1					
Avg Vessel Width	**-0.203**	0.048	-0.106	0.085	-0.127	0.031	0.129	0.128	-0.009	**0.180**	**0.507**	**0.967**	**0.831**	1				
Avg Vessel Diameter	**-0.232**	0.093	-0.108	0.139	-0.153	0.079	0.092	0.105	-0.011	0.171	**0.512**	**0.992**	**0.959**	**0.954**	1			
Nvessels	-0.038	-0.052	-0.021	-0.025	-0.060	-0.058	0.095	0.137	-0.018	0.065	**0.711**	**-0.233**	**-0.224**	**-0.212**	**-0.228**	1		
Daily Avg Temp	-0.136	**0.572**	0.088	**0.388**	**-0.324**	**0.397**	-0.118	-0.134	-0.047	-0.039	**0.232**	**0.295**	**0.394**	**0.231**	**0.329**	0.009	1	
Rainfall	**-0.349**	0.110	**-0.177**	0.072	**-0.209**	-0.064	**-0.179**	**-0.227**	0.022	**0.180**	0.158	**0.270**	**0.328**	**0.254**	**0.305**	-0.044	**0.538**	1

Table 2.4. Pearsons Product-Moment correlations of variables measured at the branch level. Significant values (R>0.112) at alpha 0.10 level (df = 241) in bold.

Site	Latitude	Longitude	DBH	Height	Age	Crown Length	Total Weight	Total Leaf Area	SLA	Sapwood Area	Total Vessel Area	Avg Vessel Area	Avg Vessel Length	Avg Vessel Width	Avg Vessel Diameter	No. vessels	Daily Avg Temp	Rainfall
Latitude	1																	
Longitude	**0.729**	1.00																
DBH	**0.327**	**0.32**	1															
Height	**0.334**	**0.49**	**0.54**	1														
Age	-0.121	**-0.38**	**0.279**	**0.147**	1.0													
Crown Length	**0.412**	**0.57**	**0.624**	**0.875**	-0.006	1												
Total Weight	**-0.274**	**-0.29**	**0.139**	**-0.224**	**0.125**	-0.085	1											
Total Leaf Area	**-0.122**	**-0.20**	**0.191**	-0.08	**0.157**	0.011	**0.824**	1										
SLA	**0.353**	**0.26**	-0.053	**0.22**	-0.038	0.078	**-0.644**	**-0.219**	1									
Sapwood Area	**-0.308**	**-0.25**	**-0.184**	**-0.248**	**-0.148**	**-0.223**	**0.299**	**0.177**	**-0.281**	1								
Total Vessel Area	**-0.154**	0.01	-0.095	0.041	**-0.152**	-0.006	**0.179**	**0.173**	-0.057	**0.162**	1							
Avg Vessel Area	**-0.177**	0.07	-0.077	0.093	**-0.124**	0.051	**0.157**	**0.164**	-0.013	**0.176**	**0.556**	1						
Avg Vessel Length	**-0.171**	**0.13**	-0.068	**0.164**	**-0.138**	**0.119**	0.097	**0.139**	0.004	**0.154**	**0.499**	**0.918**	1.00					
Avg Vessel Width	**-0.15**	0.04	-0.083	0.061	-0.104	0.023	**0.135**	**0.137**	0.012	**0.151**	**0.558**	**0.959**	**0.79**	1.00				
Avg Vessel Diameter	**-0.17**	0.09	-0.08	**0.118**	**-0.127**	0.075	**0.123**	**0.146**	0.008	**0.162**	**0.558**	**0.991**	**0.95**	**0.95**	1.00			
Nvessels	-0.032	-0.054	-0.04	-0.023	-0.055	-0.053	0.084	0.074	-0.049	0.042	**0.717**	**-0.171**	**-0.174**	**-0.136**	**-0.163**	1		
Daily Avg Temp	-0.096	**0.576**	0.068	**0.398**	**-0.316**	**0.393**	**-0.177**	**-0.175**	0.043	-0.039	**0.174**	**0.244**	**0.339**	**0.182**	**0.275**	-0.005	1	
Rainfall	**-0.337**	**0.113**	**-0.2**	0.057	**-0.206**	-0.083	**-0.201**	**-0.227**	0.085	**0.122**	0.104	**0.216**	**0.268**	**0.197**	**0.245**	-0.06	**0.551**	1

White birch trees from xeric sites (762 total samples) had the highest percentage

of vessels in the 23-24 μm diameter class, while trees from mesic sites (810 total

samples) had the highest percentage of vessels in the 24-25 μm diameter class. The

hydric (120 total samples) regime is skewed to the right, with the highest percentage of

samples in the 26-27 μm vessel diameter class (Figure 2.7).
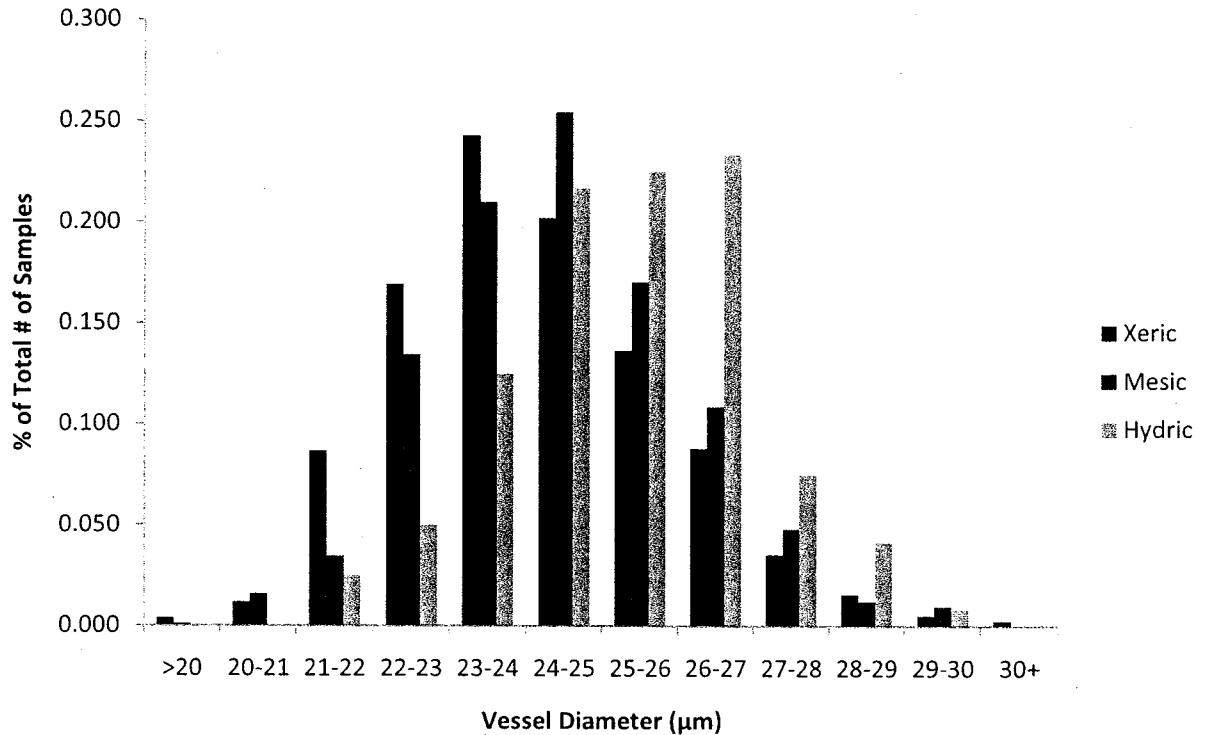
Figure 2.6. Vessel diameter frequency distribution across xeric, mesic, and hydric rain regimes.

One-way ANOVA showed that mean vessel diameter was significantly different

from xeric, mesic to hydric ($p = 0.05$) (Figure 2.8). The p values were 0.0001, 0.0168,

and 0.0001 for hydric, mesic, and xeric sites respectively. Outliers shown for mesic and

xeric sites were non-influential and remained in the dataset.
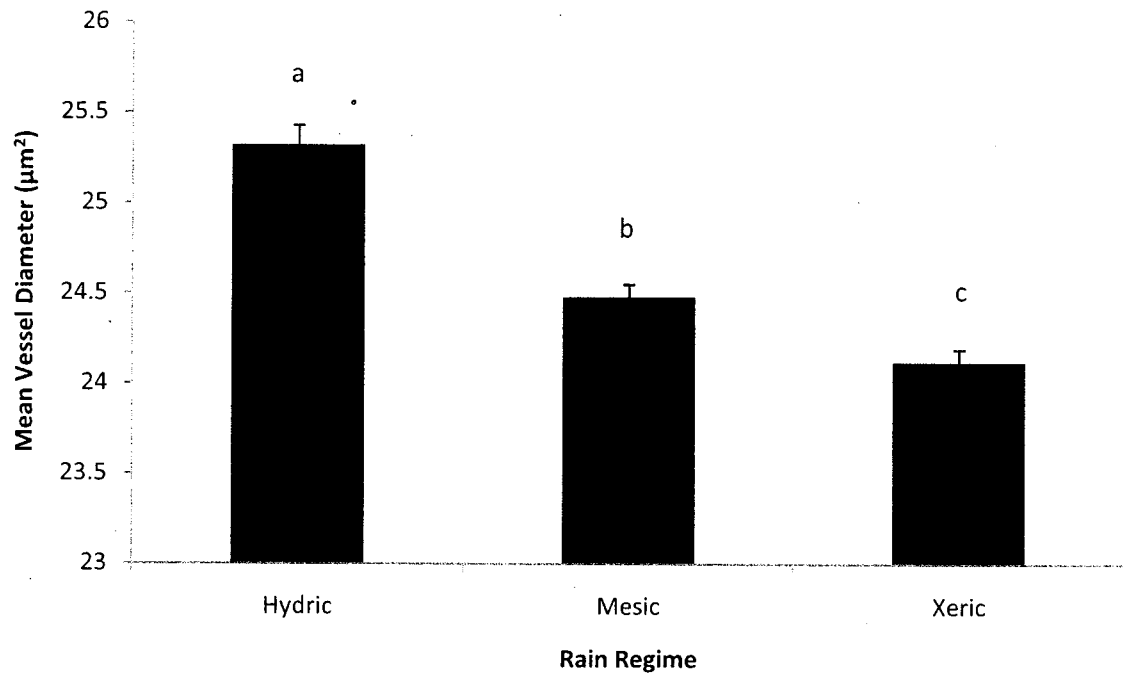
Figure 2.7. Mean vessel diameter for each rain regime with standard errors, where, a, b, and c display significant differences between each rain regime

Average vessel diameters are somewhat positively related to average annual rainfall of the sample sites (Figure 2.9). As average rainfall increases, average vessel diameter increases. The r^2 of 17.82% exhibits at the alpha 0.10 level a positive significant, as it is higher than the 9.36% level.
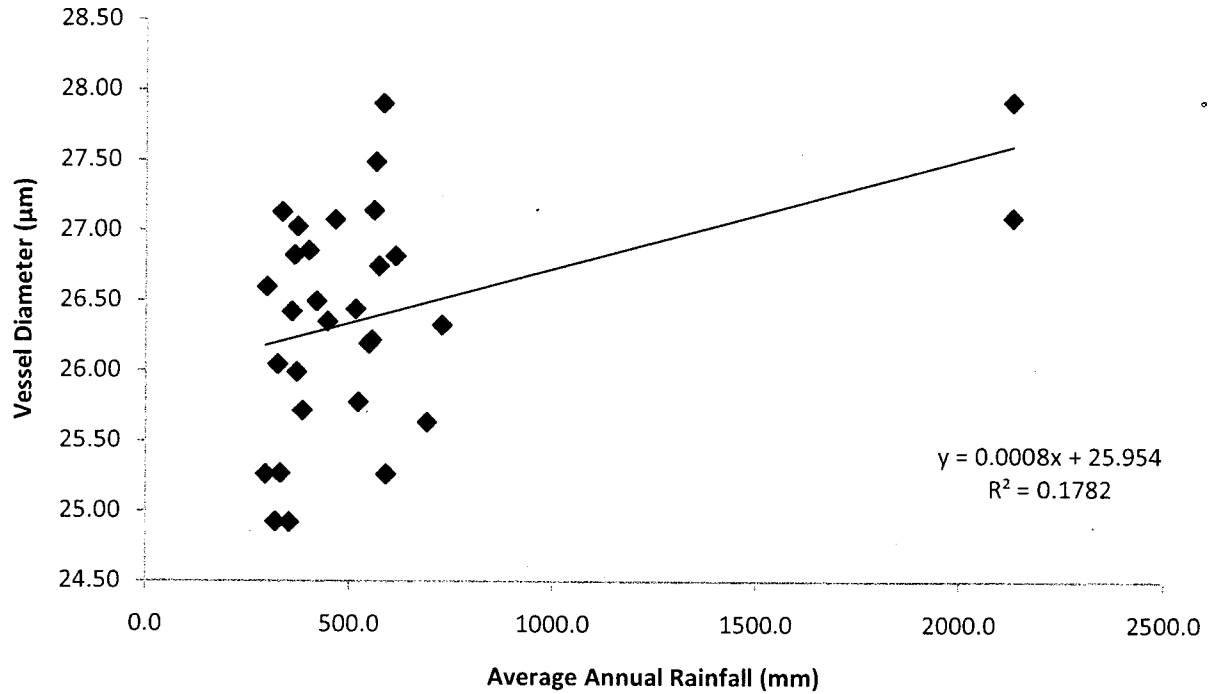
Figure 2.8. Relationship between average vessel diameter and average annual rainfall at the site level.

The relationship between average vessel diameter and number of vessels can be found in Figure 2.10. As expected, the model showed a negative trend indicating that average vessel diameter decreases as the number of vessels increases per unit of sapwood area. The model accounted for 2.66% of the variability at the branch level, which seems low, however due to the large sample size the result is significant as the minimum degree of significance at degrees of freedom = 241 is 1.25% at the alpha 0.10 level.
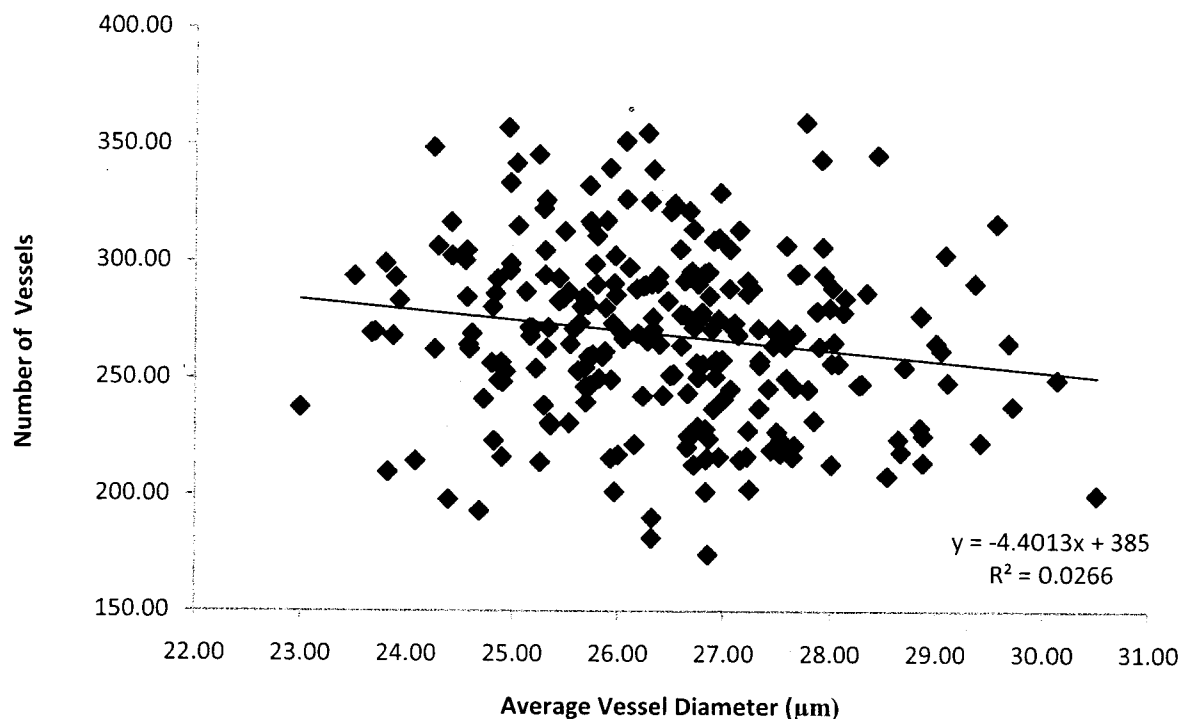
Figure 2.9. Relationship between average vessel diameter and average number of vessels at branch level for all sampled sites.

The relationship between average vessel diameter and number of vessels was further examined at the branch level by moisture regime (Figure 2.11). Both the xeric and mesic sites show a negative trend consistent with Figure 2.10, while the hydric sites show a slight positive trend. The r^2 for the xeric and mesic regressions are low, 3.49% and 2.53% respectively, but are above the significant level of 2.86% and 2.37% respectively. The hydric model displays an extremely poor fit with an r^2 value of 0.17% and is not significant. While the slopes of the two significant regressions appear to be similar a t-test between the xeric and mesic sites shows they are significantly different (t= 3.08, p=0.002).
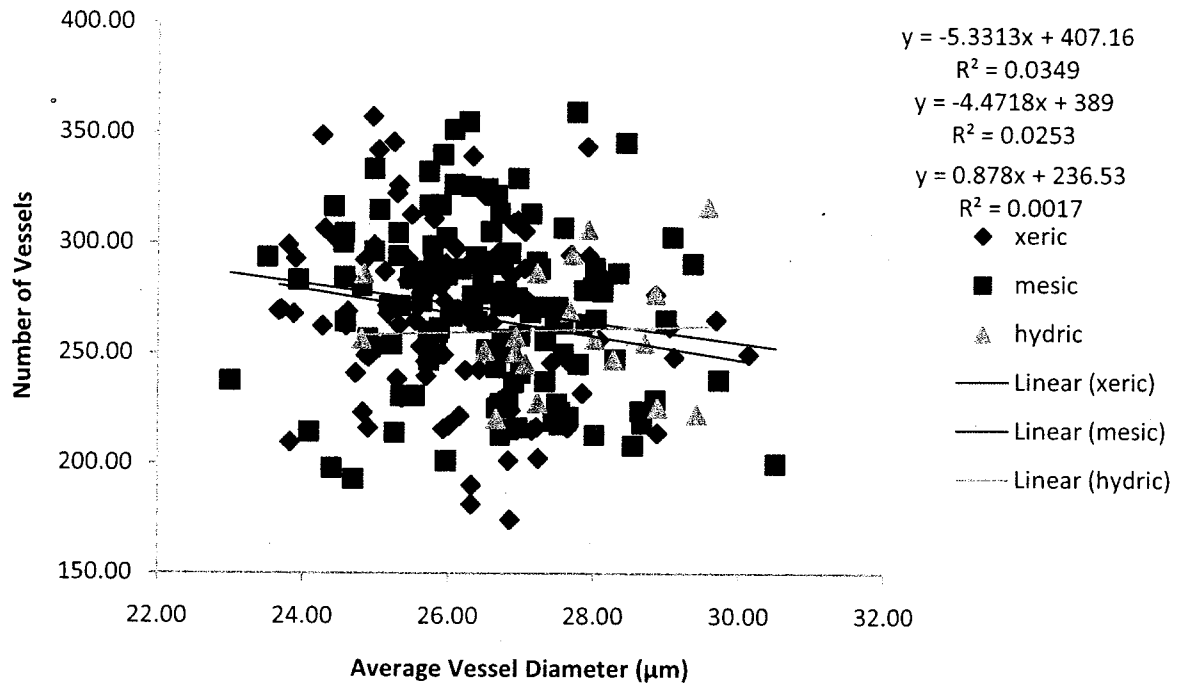
Figure 2.10. Relationship between average vessel diameter and number of vessels at the branch level. Xeric and mesic site significantly different, $p = 0.002$.

The stepwise multiple regression for dependent variable total vessel area against number of vessel and the site and climactic variables is shown in Table 2.5. The three models produced a good fit with an r^2 value of 60.4%. The significant predictors were number of vessels, latitude, and longitude.

Table 2.5. Predictor variables and their corresponding coefficient values for regression models of total vessel area. Model 1 = $b_o + b_{nv}X_{nv}$, Model 2 = $b_o + b_{nv}N_{nv} + b_{lat}+N_{lat}$, Model 3 = $b_o + b_{nv}N_{nv} + b_{lat}+N_{lat} + b_{lon}X_{lon}$.

Model		Unstandardized Coefficients		Standardized Coefficients		
		B	Std. Error	Beta	T	Sig.
1	(Constant)	29427.738	21935.433		1.342	0.191
	NVessels	349.238	81.585	0.629	4.281	0.000
2	(Constant)	88342.109	34854.883		2.535	0.017
	NVessels	337.267	77.233	0.607	4.367	0.000
	LAT	-1096.110	521.613	-0.292	-2.101	0.045
3	(Constant)	123461.869	33385.617		3.698	0.001
	NVessels	344.067	68.774	0.620	5.003	0.000
	LAT	-2485.703	673.896	-0.663	-3.689	0.001
	LONG	327.462	115.121	0.511	2.845	0.009

Where nv = number of vessels, lat = latitude, lon = longitude.

The number of vessels was used as the dependent variable against total vessel area, site and climatic variables. The model displayed good fit with a total r^2 45.2%. The significant predictors were total vessel area and rainfall (Table 2.6).

Table 2.6. Predictor variables and corresponding coefficients values of regression models for Number of vessels. Model 1 = $b_o + b_{tva}X_{tva}$, Model 2 = $b_o + b_{tva}X_{tva} + b_r X_r$

Model		Unstandardized Coefficients		Standardized Coefficients		
		B	Std. Error	Beta	t	Sig.
1	(Constant)	128.793	32.686		3.940	0.000
	TotalVesselArea	0.001	0.000	0.629	4.281	0.000
2	(Constant)	124.221	31.825		3.903	0.001
	TotalVesselArea	0.001	0.000	0.676	4.653	0.000
	Rainfall	-0.010	0.006	-0.241	-1.661	0.108

Where tva = Total vessel area, r = rainfall

The stepwise regression for dependent average vessel diameter against independent site and climatic variables yielded one model and thus one predictor. The model exhibited a less than desirable fit with an r^2 value of 17.3%, which is somewhat low, however, due to the variability in ecological data is still showing the influence of the predictors on the dependent variable. The single predictor was rainfall, with p of 0.022 (Table 2.7).

Table 2.7. Predictor variable and corresponding coefficient values of the regression model developed for average vessel diameter. Model 1 = $b_o + b_r x_r$

Model		Unstandardized Coefficients		Standardized Coefficients		
		B	Std. Error	Beta	t	Sig.
1	(Constant)	25.998	.218		119.267	0.000
	Rainfall	0.001	0.000	0.416	2.423	0.022

Where r = rainfall

2.5 DISCUSSION

Several significant results regarding vessel attributes of white birch sampled were observed in this chapter. To begin, the frequency distribution of vessel size and one-way ANOVA, showed a significant difference between moisture regimes, where xeric sites had the highest percentage of small vessels creating a left skew in the distribution, and mesic sites had a more normal distribution, while the hydric sties were skewed to the right. This result confirmed our hypothesis that trees in drier areas would have smaller vessel diameters than those with more moisture.

There was a distinct negative relationship between average vessel diameter and number of vessels, meaning as the number of vessels increases the average diameter decreases, consistent with results found by Aloni and Zimmerman (1984). Since the

conductivity of vessels is proportional to the fourth power of the diameter (Hagen-Poiseuille law) any decrease in vessel size should automatically result in an increase in vessel numbers to compensate the loss of conductivity (Schenk et al. 2008). This law also means that the larger the vessel the more water it is able to transport, however the larger the vessel the more prone it is to cavitation, as they embolise at lower level of water stress than vessels with smaller diameters (Zimmerman 1983, Tyree et al. 1994, Mitchell et al. 2008). Conductivity may become more efficient in two ways: by either producing more cross-sectional xylem or by altering anatomical features, such as vessel diameter and length (February et al. 1995).

The results of this study exhibit a trade off between the safety of smaller vessels in the more drought prone xeric sites for efficiency of larger vessels in the mesic regime, which receives more average annual rainfall. While larger vessels provide more efficient transport they also require less carbon to be invested in wood creation, as they occupy more space (Tyree et al. 1994). Westoby and Wright (2006) discuss the trade-off triangle where the efficiency of water conductance is sacrificed for resistance to cavitation and mechanical strength. Eder et al. (2009) also found that trees vary cell size to optimize water transport and mechanical stability. In addition to being more prone to cavitation lager vessels also exhibit a loss of pathway redundancy. Pathway redundancy is "provided by the sharing of walls and pits in common between adjacent conduits" (Tyree et al. 1994). Therefore, wide and long vessels with low redundancy can be considered the most cost effective way of transporting water when compared to narrow and short vessels with high redundancy. Again the trade-off between efficiency and safety is evident, as wide vessels reduce the mechanical strength of wood, where narrow

vessels increase strength properties but cost more in terms of carbon and may decrease the amount of water being transported to the leaves (Ewers et al. 2007).

Vessel diameter has been positively associated with vessel length, thus generally the larger a vessel diameter the greater the vessel length (Bass et al. 1983, Aloni and Zimmerman 1984). There is additional safety in producing shorter (and therefore more narrow) vessels as they can prevent any cavitations from spreading (Bass et al. 1983). There is a size limit, however, on how small a vessel can be because if it got too small more wood would have to be constructed than the vessel could support (Tyree et al. 1994). Again this reflects what our research found, as vessels in the xeric moisture regimes exhibited smaller vessels than those in the mesic moisture regimes.

In the Pearsons Product-Moment correlations, simple regression and multiple regression vessel diameter was influenced by rainfall. All three statistical methods showed a positive trend, indicating that vessel diameter increases in white birch as average annual rainfall increases. This positive trend between vessel diameter and rainfall is clearly a response to the increased threat of cavitation of vessels in drought prone areas or areas with extremely low amounts of rainfall and is consistent with several other studies that also showed increased vessel diameter as rainfall increases (Villar-salvador et. al 1997,Giantomasi et al. 2009, Zimmerman 1983, De Micco et al. 2008, February et al. 1995). All previous studies have been interspecific, where this study focused on the intraspecific trend of white birch. White birch is defined as a pioneer species, and in general pioneer species are extremely plastic and show great variability in responses to the physical environment (Sobrado 2003). Eder at al. (2009) suggests that trees vary their vessel size to optimize water transport and mechanical

stability. From these results we can deduce that white birch is showing a response to the physical environment by changing vessel diameter.

To further distinguish the relationship between vessel diameter, number of vessels and rainfall, we grouped the sites into three different moisture regimes and examined the relationship between the number of vessels and average vessel diameter for each regime. The mesic and xeric moisture regimes displayed significant negative trends. The hydric site experienced a slightly positive trend which was not significant and these sites will be further discussed in Chapter four. The two negative trends for the mesic and xeric sites also proved to be significantly different from one another, again, allowing us to deduce that white birch is showing a response to the physical environment, specifically available moisture.

All vessel size variables were significantly negatively correlated with latitude. This corresponds with several global trends that show that both trees and shrubs have decreasing vessel diameter and length with increasing latitude (Fisher et al. 2007). Once again this can be related to the efficiency of water transport versus safety trade-off. While cavitation can occur during a drought, cavitation can also occur during winter freeze-thaw events. Mayr et al. (2006) also found that several species of coniferous trees experienced greater drought stress and higher winter embolism with increasing altitude, which we can relate to latitude as the temperature decreases with increasing altitude. Diffuse porous trees can survive better in cold climates than ring porous trees as the increase in winter cavitation is more gradual. Again the trend shows that vessels with larger diameter are more susceptible to winter embolism than vessels with smaller diameters (Cruiziat et al. 2002). Since temperature gradually decreases with latitude, we

can assume that the negative relationship of vessel diameter with latitude is also negatively correlated with temperature. When temperatures are below zero it is believed that during thawing xylem tensions introduce air bubbles into the vessels. Air bubbles are believed to be bigger in vessels with larger diameters, making them more vulnerable to winter cavitation (Cruiziat et al. 2002). While ring porous trees generally have much larger vessels than diffuse porous trees, this study shows the intraspecific variation in vessel diameter of white birch in Canada with latitude.

We tested all measured parameters at the 0.10 alpha level instead of the commonly used 0.05 level due to expected less variation within the same species. We are interested in the difference of white birch from different environments in order to select the populations to better adapt to climate change (Morris 2009). Very few studies have examined the within-species differences of vessel diameter and its relation to leaf area over a wide range of moisture gradient features. Even a small significant difference at the alpha 0.10 level demonstrates room for selection and indicates a significant response within the white birch species to different moisture regimes.

CHAPTER 3. LEAF AREA AND SAPWOOD AREA VARIATONS ACROSS THREE MOISTURE REGIMES

3.1 INTRODUCTION

It is imperative to tree growth and survival to maintain an adequate supply of water to the leaves. This occurs as water is taken up from the roots and moves through the xylem under negative pressure up to the leaves (Ambrose et al. 2009). The amount of leaf area a tree can support depends on the amount of water that is available. The more sapwood area per unit leaf area a tree produces the less susceptible it is to embolism or cavitation (breaking of the vessel) as well as having an increase in water and nutrient storage capacity and mechanical stability (Villar-Salvador et. al 1997, Ewers et al. 2007). The growth and productivity of forests varies based on climate and site conditions (Carey et. al 1998, Medhurst and Beadle 2002) thus affecting the production of sapwood and leaf area.

It is the purpose of this chapter to address the hypothesis that birch trees in dry areas will produce lower sapwood to leaf area ratios then those in wetter environments. Trees in the wet areas can support higher leaf area per unit of sapwood area while trees in dry areas have made structural modifications to leaf area as a result of water stress (Mencuccini and Grace 1994). Also, plants in more arid environments tend to have smaller and thicker leaves as well as increased layers of mespohyll (spongy leaf tissue)

and they also allocate less carbon to the production of leaves further decreasing leaf area (Smith and Smith 2001).

3.2 LITERATURE REVIEW

3.2.1 Leaf Area

Leaf area is an important factor when considered hydraulic architecture, as leaf area has significant effects on water loss of individual plants. This is because plants with large leaf areas transpire more than plants with smaller leaf areas (Kozlowski and Pallardy 1997). Transpiration is the loss of water through small openings known as stomata as carbon dioxide diffuses through these openings (Smith and Smith 2001). Plants can regulate the opening and closing of the stomata to maintain the leaf water potential when the water potential gradient driving the ascension of water from roots to leaves becomes very steep as soil water becomes limited. Short term responses to water stress in leaves can result in the curling, rolling, or wilting of leaves, or in extreme cases results in shedding of the leaves (Kozlowski and Pallardy 1997). Long term exposure to water stress can result in specific adaptations of the leaves to avoid the stresses of reduced moisture availability. Plants in more arid environments tend to have smaller and thicker leaves as well as increased layers of mesophyll (spongy leaf tissue) and they also allocate less carbon to the production of leaves further decreasing leaf area (Smith and Smith 2001).

3.2.2 Sapwood to Leaf Area Ratio

Leonardo da Vinci first began exploring the hydraulic architecture of trees, stating:

> "all the branches of a tree at every stage of its height when put
> together are equal in thickness to the trunk (below them). All the

branches of a water (course) at every stage of its course, if they are of equal rapidity, are equal to the body of the main stream. Every year when the bow of a plant (or tree) have made an end of maturing their growth, they will have made, when put together, a thickness equal to that of the main stem; and at every stage of its ramification you will find a thickness of the said main stem; as i k, g h, e f, c d, a b, will always be equal to each other; unless the tree is pollard – if so the rule does not hold good " (Zimmerman 1983).

This concept of conductance is known as the pipe model, and has been studied since the late 1800s. In 1928 Huber expanded this vision by measuring the fresh weight of the leaves and expressing the transverse-sectional area of xylem of branches or stem as a ratio to leaf area and is known as the Huber Value (HV) (Zimmerman 1983, Cruiziat 2002). There are two main criticisms of the Huber value measure, the first being that the conducting surface being measured is a variable portion of the entire section which can't be measured. Secondly the distribution of the vessel elements can experience large ranges of flux even if the pressure gradient and cross-section of wood are the same (Zimmerman 1983, Cruiziat et. al 2002).

Zimmerman (1983) proposes to use leaf specific conductivity, which is measured by dividing hydraulic conductivity by the leaf area distal to the branch segment and is designed to calculate the pressure gradients along an axis of the tree. The factors that leaf specific conductivity depends on are the leaf surface and hydraulic conductivity (Cruiziat et. al 2002). In fact, leaf specific conductance can be calculated by:

$$K_l = HV \times K_s$$

Where K_l is the leaf specific conductivity, HV is the Huber value and K_s is the specific conductivity (hydraulic conductivity divided by sapwood cross section)

(Cruiziat et. al 2002). This is a useful tool in determining the amount of water a branch transports to support the leaves. The higher the leaf specific conductivity the lower the pressure gradient needed in the branch (Cruiziat et. al 2002). *Betula* shows a distinct decrease of leaf specific conductivity in the distal direction (Figure 3.1). Zimmerman (1983) states that "leaf specific conductivities of lateral branches are consistently smaller than those of the main stem"
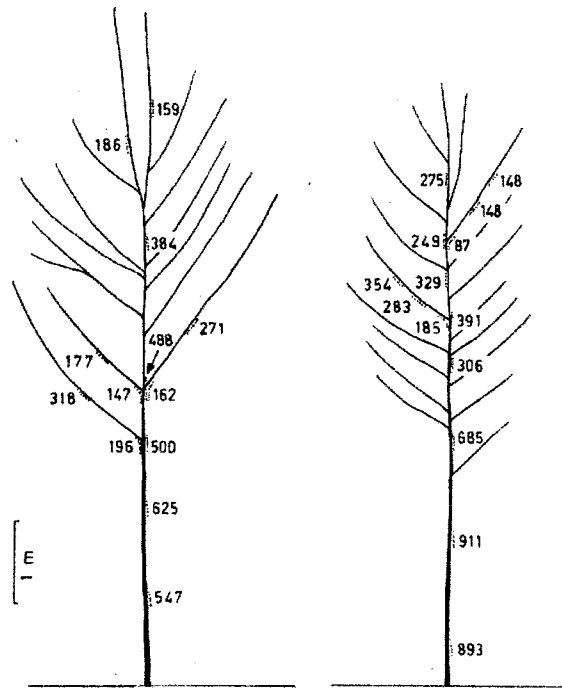

Figure 3.1. Leaf specific conductivities along the axes of two open-grown white birch.
Source: Zimmerman 1983

Villar-Salvador et al. (1997) found that in *Q. coccifera*, a diffuse porous oak tree in dry, arid environments, had a foliage area almost four times that of the two other oak species studied. The higher HV value means that *Q.coccifera* produces more wood per unit leaf area, which has shown to be a factor in the reduction of xylem embolism as well as a facilitator for increase water transportation (Villar-Salvador et. al 1997).

A study involving the crown of silver birch (*B. pendula* Roth) measured both the leaf area to sapwood area ratio (1/HV) and specific leaf area of closed-canopy species (Aspelmeier and Leuschner 2004). Results showed that the Huber value not only decreased basipetally within a crown, but also decreased according to branch order, which is consistent with several other studies. The authors conclude that HV increases in basal direction, which alleviates the effects of xylem transport between lower and upper branches. Specific leaf area (SLA), defined as the ratio between leaf area and leaf mass was also found to decrease basipetally within the crown (Sellin and Kupper 2006, Medhurst and Beadle 2002).

The crown and leaf structure of trees can be adjusted to avoid damage and/or water loss in adverse environmental conditions (Sellin and Kupper 2006). Wang et. al (1992) found that the loss of hydraulic conductivity of diffuse porous trees in the winter was significantly less than that of semi-ring porous or ring porous trees (17%, 26% and 55% respectively). An increased loss of conductivity during winter months has an adverse effect on the timing of leaf out. Essentially, "within deciduous hardwoods, the greater the winter loss of hydraulic conductivity, the later a tree will leaf out in the spring" (Wang et. al 1992). For diffuse porous trees, such as white birch, that naturally have less winter hydraulic conductivity loss due to smaller vessels, this means that they are less likely to experience the unfavourable delay in leaf out (Wang et. al 1992). Wang (2005) found increase specific conductivity values for hardwoods in the spring, as the trees require more water at the time of bud flush. Increased transpiration rates and high photosynthetic rates may also account for an increase in xylem activity and the fast growth of pioneer species, such as white birch.

Another species that has a wide geographic range in North America is ponderosa pine (*Pinus ponderosa* Doug. Ex P. & C. Laws.). The difference between the hydraulic architecture of trees in the desert and montane regions in western USA is great (Maherali et. al 2002). The authors proposed a study on how the climate affects the water relations in ponderosa pine stands in the above-mentioned environments. The desert pine was found to exhibit a lower leaf area to sapwood area ratio then the montane variety, thus receiving the benefit of increased leaf-specific hydraulic conductivity and transpiration (Maherali and DeLucia 2001). Another study examined whether the difference in hydraulic architecture between different populations of ponderosa pine in the desert and montane environments was based on ecotype or based on phenotypic characteristics. The seedlings grown in a common garden did not exhibit any ecotypic variations and showed no difference in vulnerability of the xylem to summer embolism. The significant effects of the induced drought on the leaf to sapwood ratio and leaf specific conductivity are more likely a phenotypic difference (Maherali et. al 2002). Carey et. al (1998) surmised that because the desert trees exhibit lower leaf to sapwood ratios and thus allocate more carbon to the sapwood than the montane trees that they will exhibit poorer growth then the montane trees. The authors found, however, that increased carbon allocation to sapwood does not always reduce the growth of the trees. Mencuccini and Grace (1994) tested the leaf area to sapwood area ratio of Scots pine (*Pinus sylvestris* L.) in different climates. They examined the effects of water vapour at different sites on the leaf area to sapwood area ratio. Despite climatic differences, the two stands examined experience a similar water potential gradient as the leaf to sapwood ratio adjusted to maintain the pressure gradient (Mencuccini and

Grace 1994). As shown by the above studies, information on the leaf area to sapwood area ratio and hydraulic conductivity is an important factor as it measures the amount of sapwood required to support the canopy.

3.3 METHODS

3.3.1. Leaf sample collection

Three trees were randomly selected at each site and measured for diameter at breast height, total height, age, crown length, crown form and microsite position. From each tree, three branches with a one centimetre diameter were sampled at the base of the live crown, a total of nine branches per site. The leaves from each branch were removed at the petiole and stored in labelled plastic bags (Figure 3.2). The samples were transported from the site to the lab in coolers and stored in the lab refrigerator for measurement.

Figure 3.2. An example of collected leaf samples.

3.3.2. Leaf Preparation and Analysis

A random subsample of 15-25 leaves that represent the range of leaf sizes was taken from each branch and scanned into the computer as an image file (Figure 3.3). The leaves with their petioles were measured for total area using the WinFolia© analysis program (Regent Instrument Inc). The scanned leaves and petioles were placed in a paper envelope, while the remaining leaves from the branch were placed in a paper bag and all were dried at 70 °C for 48 hours. Once dried, the samples were allowed to cool briefly and both the subsample and sample leaves were immediately measured for total dry weight. Using a leaf area to dry weight ratio from the subsample we calculated the total leaf area once we had the dry weight of the remaining leaves.

3.3.3. Sapwood area

Diameter inside bark (DIB) was measured at the one centimetre diameter mark of the branch samples before they were prepared for vessel analysis. Mayer et al. (2006) found - through dye experiments during the summer - that twig cross sections were all actively conducting water. Therefore, branches were sampled at such a small diameter under the assumption that the entire area was juvenile sapwood and thus actively conducting water. Sapwood area was calculated using the following formula:

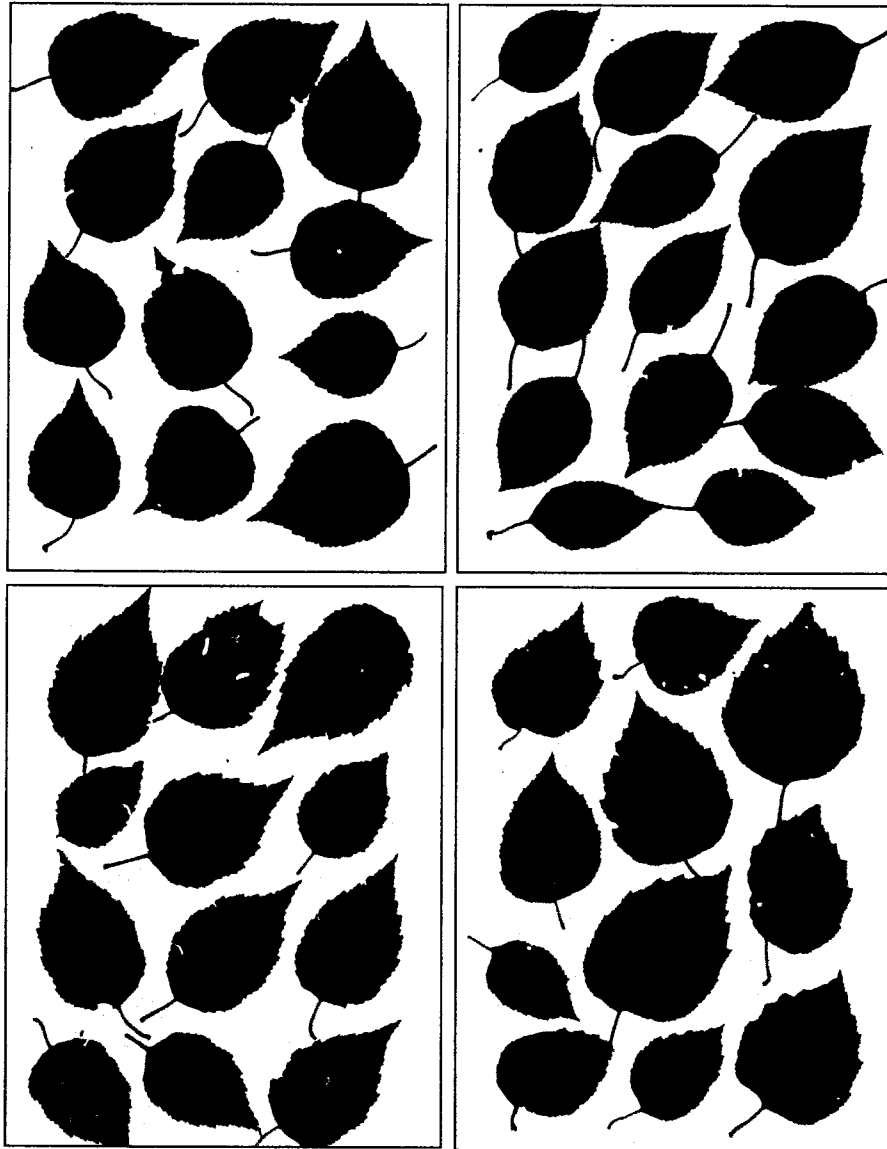$$\text{Sapwood area} = (DIB/2)^2 * \pi$$

Figure 3.3. An example of leaf images used for analysis in the WinFolia© program.

3.3.4 Data Analysis

The variables derived from the WinFolia© analysis program – total leaf weight

and total leaf area were used to calculate specific leaf area (SLA) for each branch using

the following formula:

$$SLA = \text{total area } (cm^2)/\text{total oven dry weight(g)}$$

Averages were then calculated for total leaf area, total leaf weight, SLA and

sapwood area at the site and tree levels. The data was categorized into three moisture

regimes – xeric was classified for sites with less than 400mm of average annual rainfall, while mesic was any site with greater than 400mm of average annual rainfall, up to 750mm. The hydric category represents only two sites from costal B.C., which exhibited over 2100mm of average annual rainfall and often created outlier issues in the data analysis and was therefore examined separately.

A Pearsons Product-Moment Correlation was performed on all variables to deduce any significant positive or negative relationships between variables. Any variables exhibiting extremely high correlations (0.90 or greater) were screened to ensure the variable in question did not account for similar variance in following statistical analyses. The level of significance for the branch data set at the alpha 0.10 level is ± 0.112 for 241 degrees of freedom, which creates a significant r^2 value of 1.25%. The level of significance tree data set at the alpha 0.10 level is ±0.173 (df = 90) with a significant r^2 value of 2.99%, while the level of significance for the site data set at the alpha 0.10 level is ± 0.306 (df= 28) with a significant r^2 value of 9.36%. This chapter will focus on the correlation between leaf variables and site and climactic variables. Frequency distributions were created for leaf area in each moisture regime using all branch data. A one-way analysis of variance (ANOVA) was used to test for significant differences among mean total leaf area between moisture regimes at the alpha 0.10 level

Significant correlations of interest at all levels were plotted in a simple regression to examine the data distribution between variables. Extreme outliers were removed to examine the impact on the simple regression result. A t-test (Zar 1996) was run between mesic and xeric moisture regimes in each simple regression to determine if

the models were significantly different. If the slope was not significantly different than a t-test was run on the y intercept.

Multiple regression analyses were conducted on three different dependent variables – total leaf area, total SLA and sapwood area – at the site level, where:

$$y = b_o + b_1x_1 + b_2x_2 \ldots + b_ix_i$$

Where $_i$ is the number of variables.

Independent variables included site variables (latitude, longitude, average height, and average DBH) and climactic variables (average annual rainfall, daily average temperature and PET). Best fit model was determined using stepwise multiple regression at the alpha 0.10 level. Models were developed to examine the influence of independent variables on the dependent variables, not as a prediction equation.

3.4 RESULTS

The average total leaf weight, area, specific leaf area (SLA) and sapwood area for each site can be found in Table 3.1. LM2 in Manitoba exhibited the lowest leaf area and weight, while LO12 in northern Ontario showed the highest leaf weight and LB4 in B.C. had the highest leaf area. LA2 in northern Alberta had the lowest sapwood area while LO12 in Ontario had the largest sapwood area. Again, LO12 had the lowest specific leaf area while LM2 had the highest SLA. The overall average for SLA was 218.90, while the overall average for leaf area, weight and sapwood area was 2749.04 cm^2, 14.12 g and 0.46 cm^2, respectively.

Table 3.1. Average total leaf area and weight, average SLA and average sapwood area for each sample site.

Site	Avg. Total Leaf Weight (g)	Avg. Total Leaf Area (cm^2)	Avg. Total SLA	Avg. Sapwood Area (cm^2)
LA1	13.51	3029.85	237.74	0.41
LA2	8.87	3008.47	343.61	0.36
LA3	10.97	2556.24	227.90	0.39
LB1	10.08	2437.31	248.14	0.48
LB2	12.15	3006.46	245.65	0.43
LB3	10.20	2042.37	207.73	0.42
LB4	20.35	4205.14	205.64	0.41
LB5	12.45	2442.65	202.04	0.42
LB6	15.24	3519.41	230.55	0.40
LB7A	6.46	1409.91	246.57	0.48
LB7B	9.62	2198.75	222.87	0.49
LB8	19.26	3141.96	170.31	0.54
LB9	23.54	3544.70	172.40	0.49
LM1	9.54	2269.84	247.75	0.39
LM2	2.33	806.96	346.93	0.45
LM3	2.48	870.52	343.59	0.43
LO1	10.84	2681.54	242.82	0.47
LO2	13.44	2965.60	229.02	0.40
LO3	17.79	3165.56	178.53	0.46
LO4	19.67	3450.20	176.29	0.44
LO5	13.62	2831.54	207.36	0.45
LO6	17.57	2817.34	162.55	0.57
LO7	17.14	3579.29	228.43	0.54
LO8	23.28	3814.95	163.68	0.53
LO9	16.10	2535.22	158.95	0.55
LO10	17.04	3214.20	196.79	0.55
LO11	24.81	4072.27	175.47	0.55
LO12	25.15	3234.92	128.69	0.57
LS1	4.79	1246.57	261.91	0.41
LS2	15.37	2371.52	156.97	0.45

A Pearson's product-moment correlation was performed at the branch, tree and site levels for all variables (Table 2.2, 2.3, 2.4). At the branch and tree levels, total leaf area was positively correlated with diameter at breast height (DBH), sapwood area, total leaf weight, and rainfall and was negatively correlated with longitude. At the site level total leaf area was significantly correlated with DBH , total leaf weight and sapwood area and negatively correlated with SLA. Total leaf weight was significantly correlated with total leaf area, and sapwood area and negatively correlated with latitude, longitude and SLA at all levels.

The frequency distribution of total leaf area across three moisture regimes produced some unexpected results (Figure 3.4). Both xeric and mesic sites show a similar distribution pattern, with the highest percentage of samples for both moisture regimes in the 2000-3000 cm^2 total leaf area class. The two regimes appear to differ in the division above and below the 2000-3000 cm^2 total leaf area class, as mesic sites had more samples in the ranges with higher area, while xeric sites had more samples in the ranges of lower area. Hydric sites had the most unexpected results with the highest percentage of samples in the 1000-2000 cm^2 range, lower than both xeric and mesic sites and also had fewer samples in the ranges with greater leaf area and no samples greater than 5000 cm^2. This pattern for the hydric sites will be discussed in chapter four. Overall mean total leaf area was different between the moisture regimes, thus the frequency distributions are also different. The values were significantly different at the alpha 0.10 level (Figure 3.5).
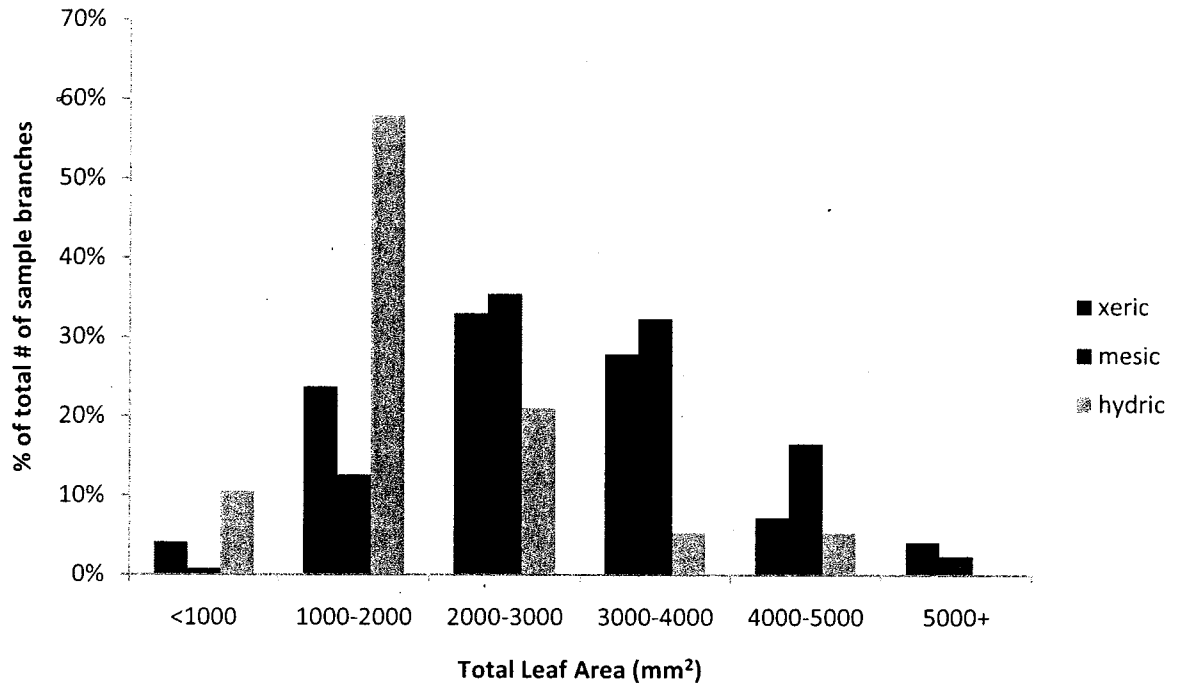
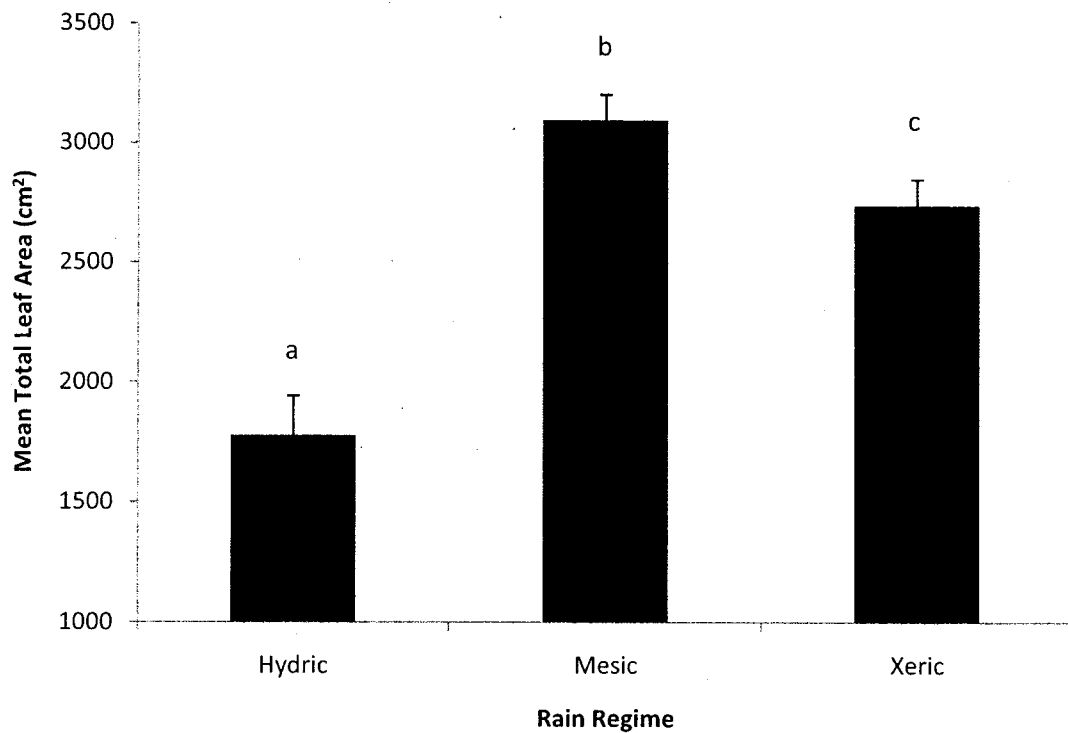Figure 3.4. Total leaf area frequency distribution across all rain regimes.

Figure 3.5. Mean total leaf area for each rain regime with standard errors, where a, b, and c display significant differences between each rain regime

Not surprisingly, there was a strong positive relationship between total leaf area

and total leaf weight at the branch level (Figure 3.6). The general trend across all

moisture regimes is the increase in leaf weight as leaf area increases, however the rate is

different across each moisture regimes. All regressions had very strong r^2 values –

66.8%, 65.6% and 85.6% for xeric, mesic and hydric sites, respectively. The slopes

proved significantly different with a p value of 0.0001 and a t value of 6.43.
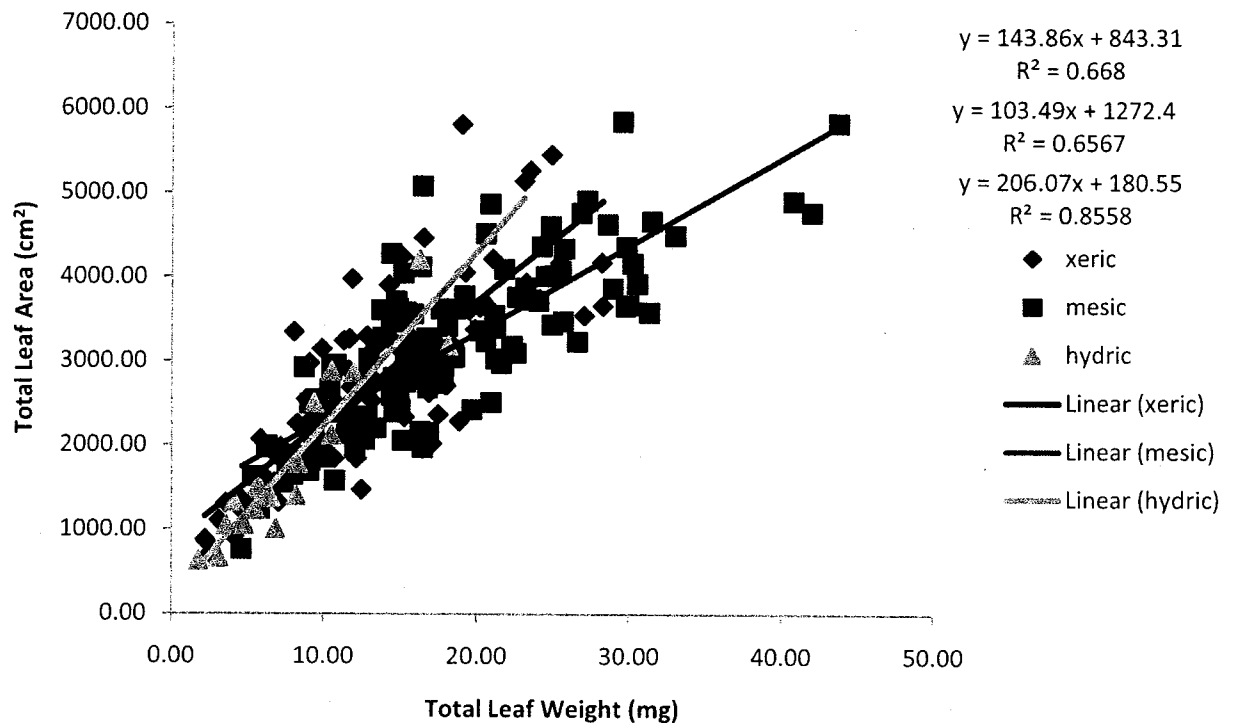
Figure 3.6. Relationship between total leaf area versus total leaf weight for all sampled branches across xeric, mesic, and hydric rain regimes.

There was a positive relationship between average total leaf area and rainfall at

the tree level (Figure 3.7). Hydric sites were considered outliers because the annual

rainfall greatly exceeded any of the xeric and mesic sites and were therefore removed

from this analysis. While the r^2 shows a somewhat weak relationship of 9.3% it is still a

significant trend at the alpha 0.10 level, as the r^2 is above the 2.99% required for data

sets with 90 degrees of freedom.
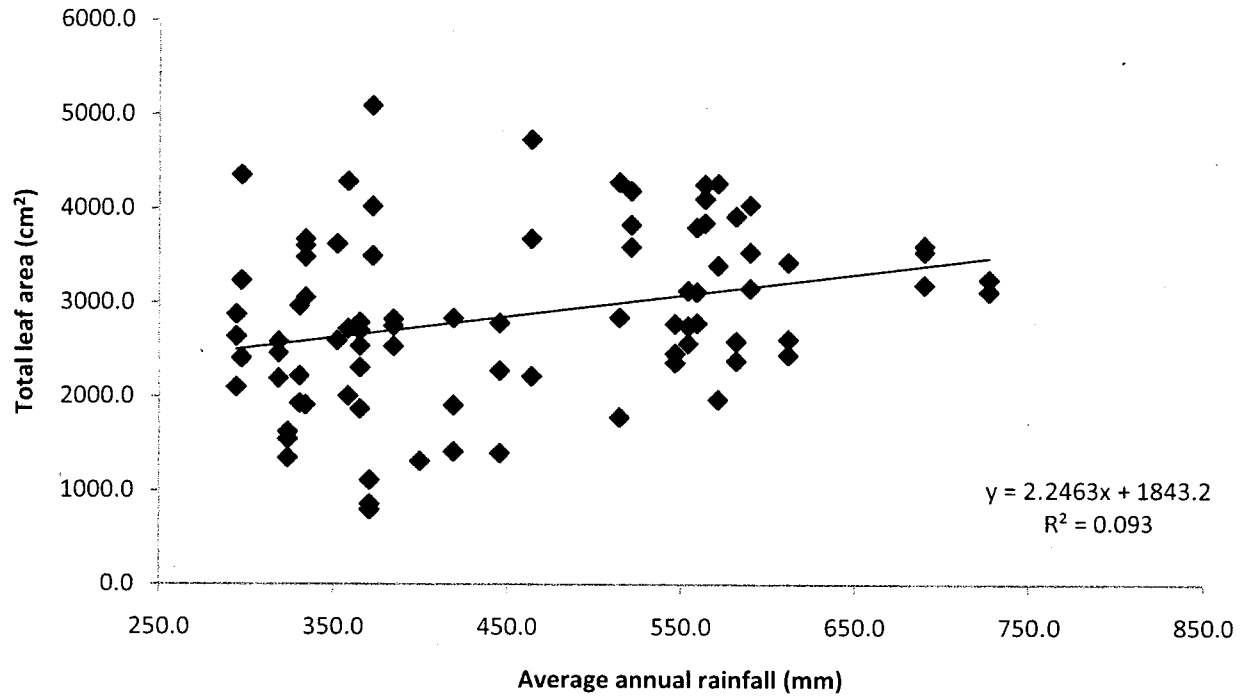
Figure 3.7. Relationship between average total leaf area versus average annual rainfall for all sampled trees, except trees from coastal site LB7.

There is also a positive relationship between average total leaf area and sapwood

area at the site level (Figure 3.8). The positive trend explains a significant amount of

variability (r^2 = 10.93%), where an increase in sapwood area corresponds to an increase

in average total leaf area.
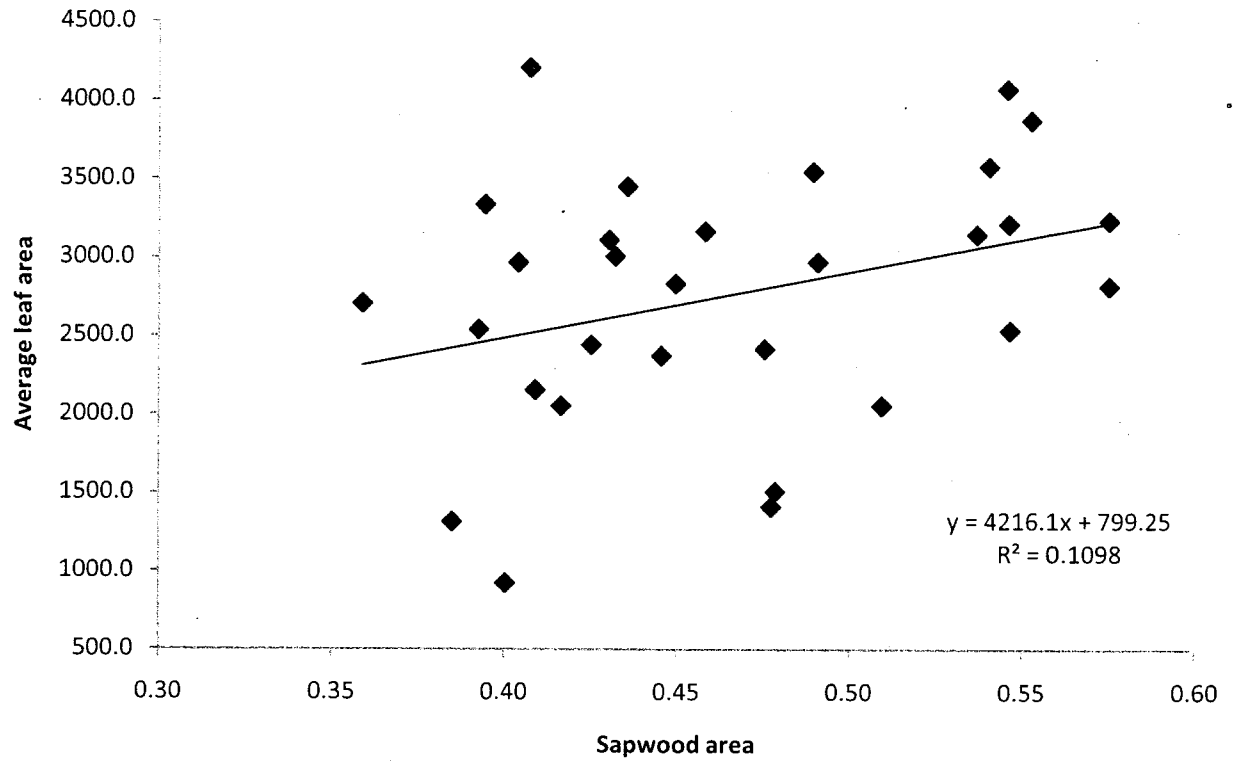
Figure 3.8. Total leaf area versus total sapwood area at site level.

The stepwise regression for total leaf area produced four models (Table 3.2).

Variables that were found to predict leaf area in the four significant models were PET,

sapwood area, DBH, and latitude. All predictors were significant at the alpha 0.10 level.

The r^2 value is very high at 57.6%, indicating a strong influence of the full model on

total leaf area.

Table 3.2. Predictor variables and corresponding coefficients of the regression models for total leaf area versus climatic and site variables. Model 1 = $b_o + b_{pet}x_{pet}$, Model 2 = $b_o + b_{pet}x_{pet} + b_{sap}x_{sap}$, Model 3 = $b_o + b_{pet}x_{pet} + b_{sap}x_{sap} + b_{dbh}x_{dbh}$, Model 4 = $b_o + b_{pet}x_{pet} + b_{sap}x_{sap} + b_{dbh}x_{dbh} + b_{lat}x_{lat}$

Model		Unstandardized Coefficients		Standardized Coefficients		
		B	Std. Error	Beta	T	Sig.
1	(Constant)	3949.707	489.819		8.064	0.000
	PET	-473.963	188.299	-0.430	-2.517	0.018
2	(Constant)	1469.705	914.961		1.606	0.120
	PET	-610.916	171.020	-0.554	-3.572	0.001
	SAPWOODAREA	6054.011	1972.207	0.476	3.070	0.005
3	(Constant)	-674.853	1337.323		-0.505	0.618
	PET	-472.822	174.093	-0.429	-2.716	0.012
	SAPWOODAREA	6510.862	1871.323	0.512	3.479	0.002
	DBH	83.306	39.709	0.327	2.098	0.046
4	(Constant)	5404.074	2880.114		1.876	0.072
	PET	-547.422	163.982	-0.496	-3.338	0.003
	SAPWOODAREA	4711.106	1892.729	0.370	2.489	0.020
	DBH	105.776	37.926	0.415	2.789	0.010
	LAT	-107.858	46.160	-0.374	-2.337	0.028

Where sap = sapwood area, lat = latitude

Stepwise regression indicated there were five significant models to predict SLA. The final r^2 value of 66.0% indicates that the predictors strongly account for the variance. The significant predictors were very similar to those identified for total leaf

area – sapwood area, PET, latitude – but also included crown length and total height (Table 3.3).

Table 3.3. Predictor variables and corresponding coefficients of the regression models for total SLA versus climatic and site variables. Model 1 = $b_o + b_{sap}x_{sap}$, Model 2 = $b_o + b_{sap}x_{sap} + b_{pet}x_{pet}$, Model 3 = $b_o + b_{sap}x_{sap} + b_{pet}x_{pet} + b_{lat}x_{lat}$, Model 4 = $b_o + b_{sap}x_{sap} + b_{pet}x_{pet} + b_{lat}x_{lat} + b_{cl}x_{cl}$, Model 5 = $b_o + b_{sap}x_{sap} + b_{pet}x_{pet} + b_{lat}x_{lat} + b_{cl}x_{cl} + b_h x_h$

Model		Unstandardized Coefficients		Standardized Coefficients		
		B	Std. Error	Beta	t	Sig.
1	(Constant)	466.319	61.268		7.611	0.000
	SAPWOODAREA	-530.679	130.261	-0.610	-4.074	0.000
2	(Constant)	437.989	57.943		7.559	0.000
	SAPWOODAREA	-608.340	124.896	-0.699	-4.871	0.000
	PET	25.814	10.830	0.342	2.384	0.024
3	(Constant)	62.781	198.367		0.316	0.754
	SAPWOODAREA	-499.961	130.870	-0.575	-3.820	0.001
	PET	32.118	10.782	0.426	2.979	0.006
	LAT	6.079	3.087	0.309	1.969	0.060
4	(Constant)	27.172	190.838		0.142	0.888
	SAPWOODAREA	-520.844	125.767	-0.599	-4.141	0.000
	PET	31.146	10.333	0.413	3.014	0.006
	LAT	7.962	3.127	0.404	2.546	0.017
	CROWNLENGTH	-4.808	2.614	-0.259	-1.840	0.078
5	(Constant)	-57.696	185.123		-0.312	0.758
	SAPWOODAREA	-451.704	123.670	-0.519	-3.652	0.001
	PET	18.282	11.675	0.242	1.566	0.130
	LAT	7.865	2.954	0.399	2.663	0.014
	CROWNLENGTH	-16.875	6.498	-0.908	-2.597	0.016
	HEIGHT	14.239	7.094	0.701	2.007	0.056

Where sap =sapwood area, lat = latitude, cl = crown length, h = height

The final stepwise regression was performed on all leaf, site and climatic variables, however since the previous leaf variables all had similar significant predictors

in the separate regressions, only sapwood area and total leaf area were chosen for this analysis. The regression resulted in three models, with a total r^2 value of 57.7%, again showing that the predictors - total weight, PET and total area – have a significant influence on the dependent variable, sapwood area (Table 3.4).

Table 3.4. Predictor variables and corresponding coefficients of the regression models for sapwood area versus climatic and site variables. Model 1 = b_o + $b_{tw}x_{tw}$, model 2 = b_o + $b_{tw}x_{tw}$ + $b_{pet}x_{pet}$, Model 3 = b_o + $b_{tw}x_{tw}$ + $b_{pet}x_{pet}$ + $b_{ta}x_{ta}$

Model		Unstandardized Coefficients		Standardized Coefficients		
		B	Std. Error	Beta	T	Sig.
1	(Constant)	0.382	0.025		15.292	0.000
	TOTALWEIGHT	0.006	0.002	0.566	3.636	0.001
2	(Constant)	0.256	0.042		6.091	0.000
	TOTALWEIGHT	0.007	0.001	0.714	5.147	0.000
	PET	0.042	0.012	0.480	3.462	0.002
3	(Constant)	0.323	0.056		5.748	0.000
	TOTALWEIGHT	0.012	0.003	1.134	4.062	0.000
	PET	0.034	0.012	0.393	2.738	0.011
	TOTALAREA	-3.963E-5	0.000	-0.504	-1.715	0.098

Where tw = total weight, ta = total area

3.5 DISCUSSION

There were several relationships found between leaf variables, site variables and climatic variables. Total leaf area, weight, and specific leaf area (SLA) were all found to have significant positive relationships with potential evapotranspiration (PET), diameter at breast height (DBH), latitude, and sapwood area. SLA was also correlated with crown length and tree height.

Similar to vessel diameter, total leaf area also displayed a positive relationship with rainfall, so as rainfall increased total leaf area also increased. The above relationship is consistent with a global trend that showed leaf area shifts along both

temperature and rainfall gradients (Westoby and Wright 2006). Other studies have shown leaf area to be positively related to water availability in Eucalypts (Zeppel and Eamus 2009). Plants in more arid environments tend to have smaller and thicker leaves as well as increased layers of mespohyll (spongy leaf tissue) and they also allocate less carbon to the production of leaves further decreasing leaf area (Smith and Smith 2001).

We know that tree water use is influenced by leaf area and that increasing leaf area requires a greater amount of conducting tissue to support it (Zeppel and Eamus 2008, Medhust and Beadle 2002). Sobrado (2003) suggests that in order to maintain the homeostatic balance between water transport and leaf area in moisture stress, plants adjust the leaf area to keep the homeostatic level of leaf specific conductivity consistent. Ackerly (2004) also found that reduced specific leaf area in combination with increased nitrogen enhanced water use in dry environments, and "across broad climate gradients leaf size is associated with water availability". The sample sites in this study occur across an extremely broad range of moisture regimes as well as a large geographic distribution and show that white birch alters leaf size according to water availability.

There are several studies examining biomass allocation of ponderosa pine (*Pinus ponderosa*) in different climate regimes. Callaway et al. (1994) found that trees in hot dry desert environments allocated more biomass to sapwood production than leaves when compare to trees in cooler, moist montane environments and concluded that "a phenotypic acclimation or genotypic change in response to xeric climate occurred". In my results, as latitude increased, total leaf area and weight decreased and sapwood area increased. This high allocation of biomass to sapwood area as opposed to leaf area is

likely a trade-off of hydraulic efficiency for safety. Having more sapwood may reduce the impact of cavitation in the xeric environments and improve water storage capacity (Callaway et al. 1994). Maherali and DeLucia (2001) found that difference between biomass allocations of ponderosa pines in desert and montane environments were highly correlated with differences in water transport efficiencies and concluded that increased allocation to sapwood over leaf area was to increase leaf specific conductance. I show that leaf area to sapwood area increased as rainfall increased, therefore we can deduce that the same trends mentioned above are occurring for white birch across Canada.

PET is defined as "the potential water loss by evaporation and transpiration from ground and plant surfaces where there is a continuous vegetation cover and sufficient soil moisture for plant use" (Atlas of Canada 1974). Leaf area was negatively correlated with PET, indicating that areas with higher PET also have lower leaf areas. Areas with high PET are usually associated with drought, explaining the negative relationship between leaf area and PET. Again, this correlates to available water supply and water stress, as leaves can control the opening and closing of the stomata (the amount of transpiration) based on water stress. If the stomata are not controlled in times of water stress excessive cavitation can occur and severely damage the hydraulic architecture of the trees. The result is a trade-off between minimizing water loss and maximizing carbon gain, as photosynthesis is constrained by the opening or closing of stomata (Ambrose et al. 2009)

Several studies have been done examining the effects of tree size and foliar attributes. Along a rainfall gradient, the relationship between DBH and sapwood area

was the same within sites, but was found to be different among sites (Zeeple and Eamus 2008). There is a direct positive relationship between sapwood area and leaf area (Figure 3.8) and would explain the effect of DBH on leaf area and weight. Calvo-Alvarado (2008) also found that DBH was the best predictor of leaf area and leaf mass in a non-linear regression for three species of trees in Costa Rica. The linear models in that study were rejected as they were not significant at the alpha 0.05 level. As the linear models in this study were specifically to examine which variables were influencing the dependant variable and not to create an allometric relationship, we can consider DBH a significant variable affecting both leaf area and weight.

As trees increase in height the ascension of water becomes more difficult due to gravity and friction (Ambrose et al. 2009). To account for this several adjustments are made including increasing sapwood area relative to leaf area and reducing leaf specific conductance and stomatal conductance. Taller trees also have higher leaf mass per unit area (Ambrose et al. 2009), which is consistent with the positive relationship found between SLA and tree height in this study. Calvo-Alvarado et al. (2008) found leaf area increased with tree size and that as trees increase in height and diameter they trade-off leaf conductance for larger leaf areas, as maximizing leaf area increases photosynthesis. As height was significantly correlated with total leaf area and SLA we can assume similar relationships are occurring in white birch across Canada.

CHAPTER 4. LEAF AND VESSEL REALTIONSHIPS IN THREE DIFFERENT MOISTURE REGIMES

4.1 INTRODUCTION AND LITERATURE REVIEW

The hydraulic architecture of trees is very complicated, involving the extraction of water from soil into roots and transportation of this water through the stem and into the leaves. Most of the water is lost through transpiration which is an essential process that takes place in leaves and allows for intake of carbon dioxide which is used in photosynthesis (Raven et al. 2003). In the previous chapters I examined the various features pertaining to xylem and leaves separately but in this chapter I will examine the relationship between vessel and leaf characteristics of white birch from a wide range of environmental conditions.

The leaf-xylem relationship is extremely important as the cohesion-tension theory states that water is pulled up from the soil through the xylem and into the leaves by negative pressure created by transpiration in the stomata, which are responsible for regulating the pressure and flow rate (Raven et al. 2003, Sperry et al. 2002). The pipe model of hydraulic architecture describes the relationship between xylem and leaves as a series of pipe units which each supports a certain amount of leaves, where "the amount of leaves existing in and above a certain horizontal stratum in the plant community is directly proportional to the amount of the stems and branches existing in that horizon" (Cruiziat et al. 2002). This relationship can be applied at several different

ecological levels, such as the branch level, tree level and/or community levels. The relationships described by the pipe model have been used for predicting canopy leaf mass and area from stem cross sections (leaf area to sapwood area ratios) and have also been used in tree growth and biomass allocation models (Cruiziat et al. 2002).

The soil-plant-atmosphere continuum (SPAC) is the relationship between available moisture in soil, plant functions in transportation and transpiration of water into the atmosphere. The xylem is an integral part of this continuum with the main function being to "provide a low resistance pathway for water transport" (Loepfe et al. 2006), while stomatal regulation and the cohesive strength of water preserves hydraulic contact between the soil and canopy (Sperry et al. 2002).

Transpiration is extremely variable and differs according to several environmental factors including temperature, humidity, carbon dioxide concentration, light, water availability in the soil, atmospheric conditions, as well as plant specific features and functions (Raven et al. 2003, Mitchell et al. 2008).

In order for the xylem to provide a low resistance pathway to transport water, the leaves in turn regulate the amount of transpiration via the stomata to constrain leaf water potential and avoid excess tension in the xylem which may cause embolism and disrupt the water column (Meinzer et al. 2008). The hydraulic limitation caused by stomatal closure may prevent runaway embolism. Runaway embolism occurs when a vessel becomes embolised and increases the tension on remaining vessels which have to maintain the same amount of water to the leaves, which generates additional embolisms creating a cycle of cavitation. The only way to stop runaway embolism is when the entire xylem has been completely compromised or by stomatal closure which will

reduce transpiration and thus decrease the water potential in the xylem (Cruiziat et al. 2002).

Wang et al. (1992) also found a strong correlation between leaf phenology and xylem vulnerability to cavitation. We know that plants with large leaf areas transpire more than plants with smaller leaf areas (Kozlowski and Pallardy 1997), and that total leaf area is closely related to the amount of conducting tissue in the sapwood. Plants with larger vessels also have the ability to transport greater amounts of water and support a larger total leaf area, however, are more susceptible to cavitation than plants that exhibit smaller vessels (Wang 2005). It is the purpose of this chapter to examine the hydraulic relationships between vessel size and frequency and the amount of leaf area.

4.2 METHODS

4.2.1 Data Analysis

A Pearsons Product-Moment Correlation was performed on all variables to deduce any significant positive or negative relationships between variables. Any variables exhibiting extremely high correlations (0.90 or greater) were screened to ensure the variable in question did not account for similar variance in subsequent statistical analyses. The level of significance for the branch level data set at the alpha 0.10 level is ± 0.112 for 241 degrees of freedom, which has a significant r^2 value of 1.25%. The level of significance for the tree level data set at the alpha 0.10 level is $+ 0.173$ (df = 90) with a significant r^2 value of 2.99%, while the level of significance for the site level data set at the alpha 0.10 level is ± 0.306 (df= 28) with a significant r^2 value of 9.36%. This chapter will focus on the correlation between leaf variables, vessel variables, site and climactic variables at site and tree level.

Significant correlations of interest at all levels were plotted in a simple regression to examine the data distribution between variables. Extreme outliers were removed to examine the impact on the simple regression result. A t-test (Zar 1996) was run between mesic and xeric moisture regimes in each simple regression to determine if the models were significantly different. If the slope was not significantly different than a t-test was run on the y intercept.

4.2.2 Hydric Site Data Analysis

A frequency distribution of total leaf area was created for the hydric sites, as well as a simple regression between total leaf area and vessel diameter. A chart showing the average rainfall and daily average temperature for each month to compare amount of rain received during growing season and dormant season was created to help explain the differences on the hydric coastal sites.

4.3 RESULTS

A summary of all variables can be found in Tables 2.1 and 3.1. The Pearson Product-Moment correlation showed that there were several significant relationships between the leaf and vessel variables (Tables 2.2, 2.3, 2.4). At all levels there were significant correlations between total vessel area and total leaf weight. Total vessel area was also significantly correlated with sapwood area and total leaf area at the tree level. Sapwood area was also significantly correlated with average vessel area and number of vessels at tree level. At branch level, total leaf area was significantly correlated with total vessel area, average vessel area, vessel diameter and vessel width, as was total leaf weight. Sapwood area also showed an increase in correlations, showing significant

relationships with total vessel area, average vessel area, vessel diameter and vessel width.

Total leaf area was positively related to total vessel area at all levels of the Pearson Product-moment tests Figure 4.1). The general trend is a statistically significant positive trend, as the r^2 of 2.99% is above the critical r^2 value of 1.25% for 241 degrees of freedom.
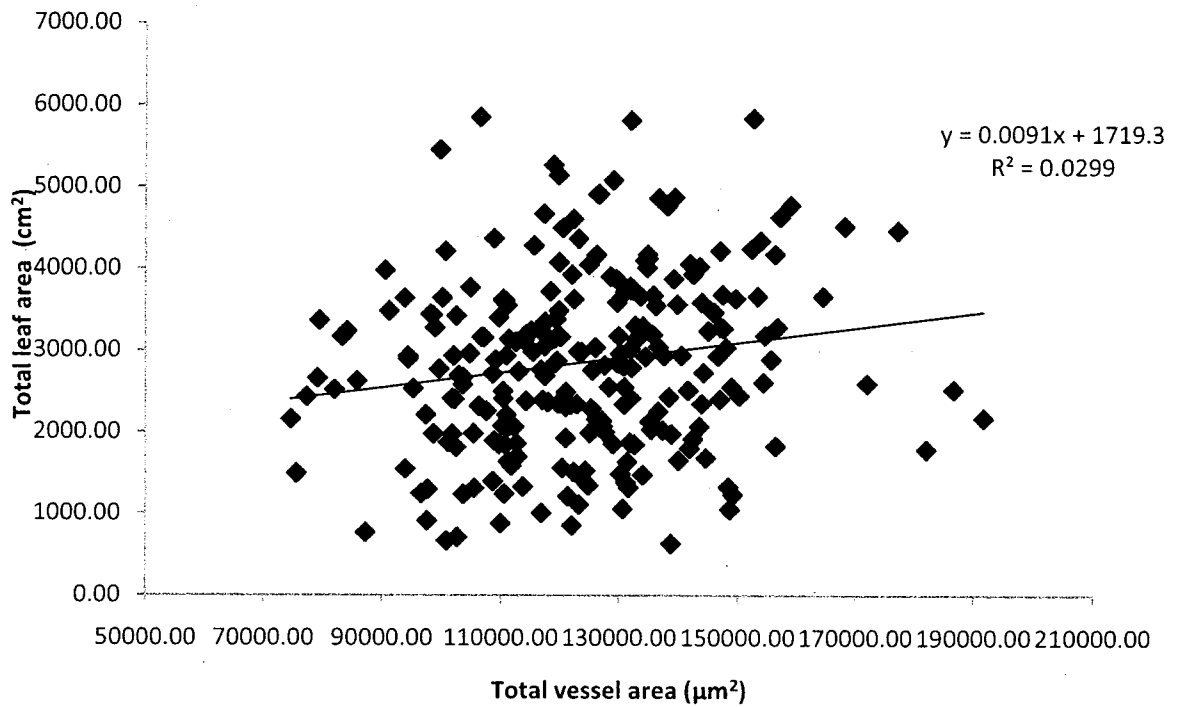
Figure 4.1. The relationship between total vessel area and total leaf area for all sampled branches.

This relationship between vessel size and total leaf area was further explored in Figure 4.2, comparing average vessel diameter and total leaf area. Both mesic and xeric sites exhibit a positive trend, thus as vessel diameter increases leaf area also increases.

Both sites showed significantly positive r^2 values, 3.54% and 8.77%, respectively. The

t-test showed that these regressions are also significantly different from one another at

the 95% confidence level (t = 7.15, p = 0.0001). The hydric site differed greatly from

the other two sites, and showed a slightly negative trend. The regression did have a

significant r^2 value of 2.22%.
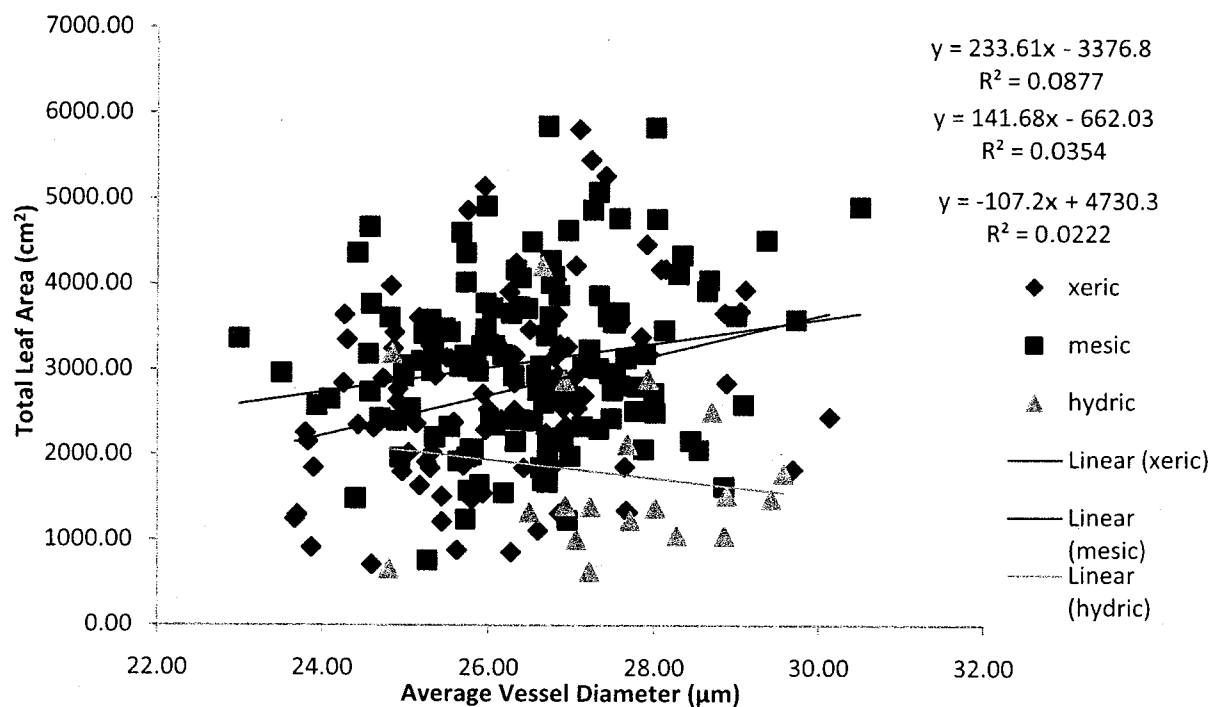
Figure 4.2. The relationship between average vessel diameter and total leaf area for all
sampled branches.

As shown in Chapter three (Figure 3.8), there is a positive relationship between

leaf area and sapwood area. Leaf area to sapwood ratio was plotted against average

vessel diameter to further explore the effects of conducting tissues on leaf area (Figure

4.3). Both xeric and mesic sites showed significant positive trends, with r^2 values of

7.33% and 1.28%, respectively. A t-test showed the regressions are also significantly different from one another at the alpha 0.05 level (t=49.89. p=0.0001). Again hydric sites showed very different results, with a negative trend. The regression is significant with an r^2 value of 11%.
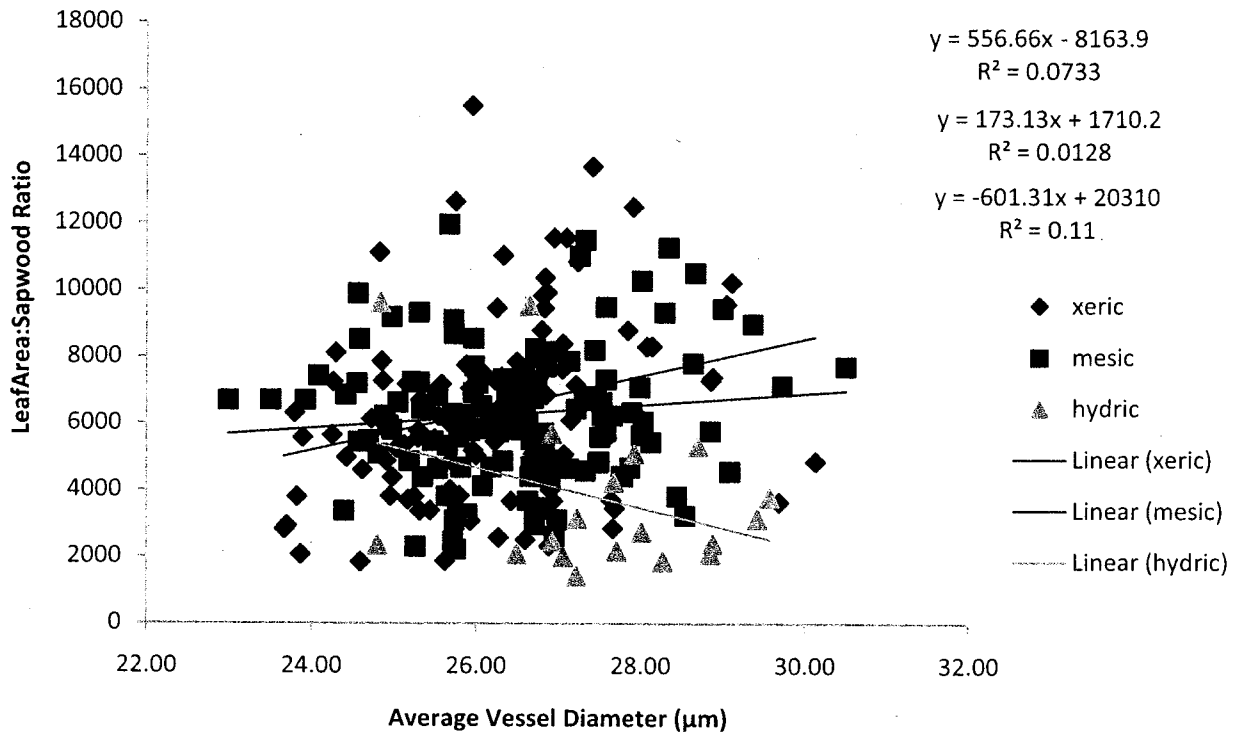
Figure 4.3. The relationship between the leaf area to sapwood area ratio and average vessel diameter for xeric, mesic and hydric sites.

4.3.1 Results for hydric sites

The relationships between leaf area and vessel diameter for the hydric sites were further examined. Figure 4.9 shows the leaf area distribution for the hydric sites. As mentioned previously, the highest percentage of samples falls in the 1000-2000 cm^2 total leaf area range. This was lower than both mesic and xeric sites. With over 2100mm of average annual rainfall, one would expect for leaf area to be relatively high.

The relationship between average vessel diameter and total leaf area was presented as an insert in Figure 4.9. This relationship also contradicts to the general trend that was found for mesic and xeric sites.
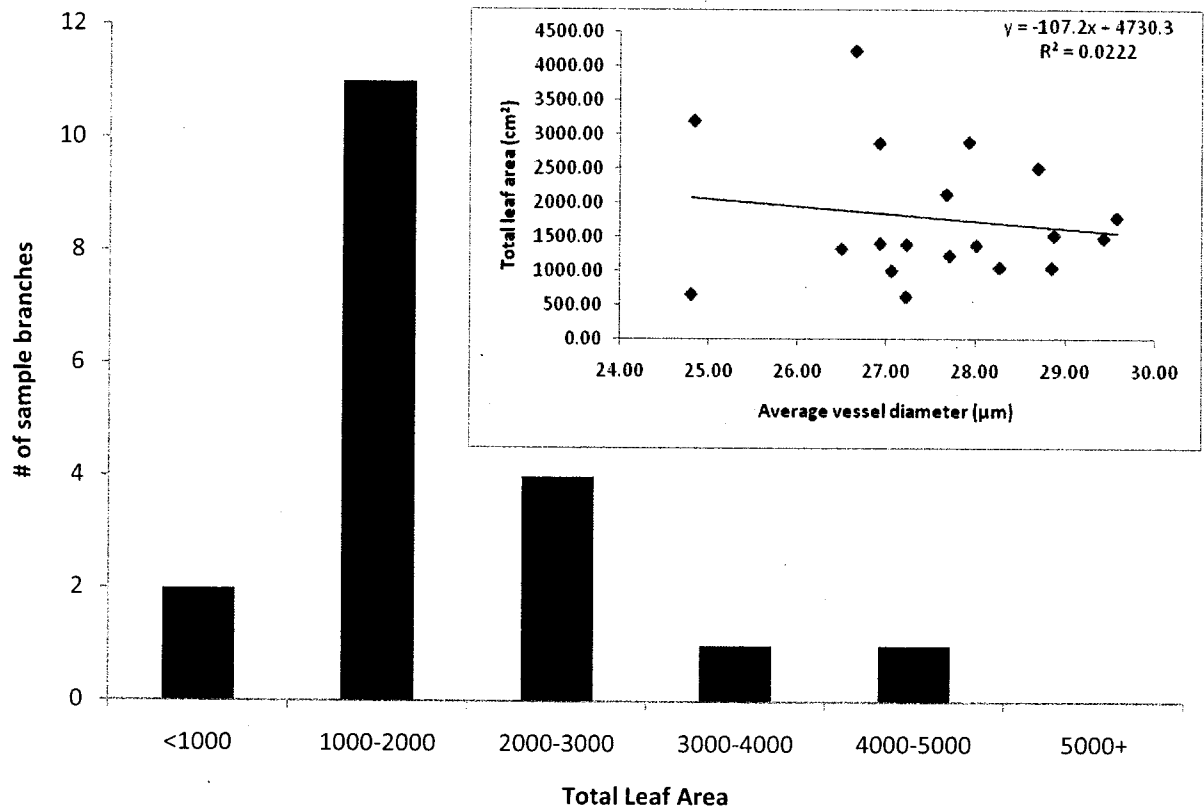
Figure 4.9. Leaf area distribution for hydric sites. Inlay: relationship between average vessel area and total leaf area.

To explain why white birch from these two hydric sites that receive ample amounts of rainfall had lower total leaf area, I examined the distribution of rainfall and temperature throughout the year. Figure 4.10 presents daily average temperature and average rainfall on a monthly basis. During the growing season from April to August, monthly average rainfall decreases significantly when compared to the winter months. It reaches the lowest in August decreasing well below 100mm of rainfall a month, where in November it triples to approximately 325mm a month. To coincide with this decrease

in rainfall there is also an increase in daily average temperature, which in combination with decreased rainfall might cause drought during the peak of growing season for white birch. Therefore total annual rainfall is not a good indicator for predicting leaf area of white birch for the hydric sites I studied.
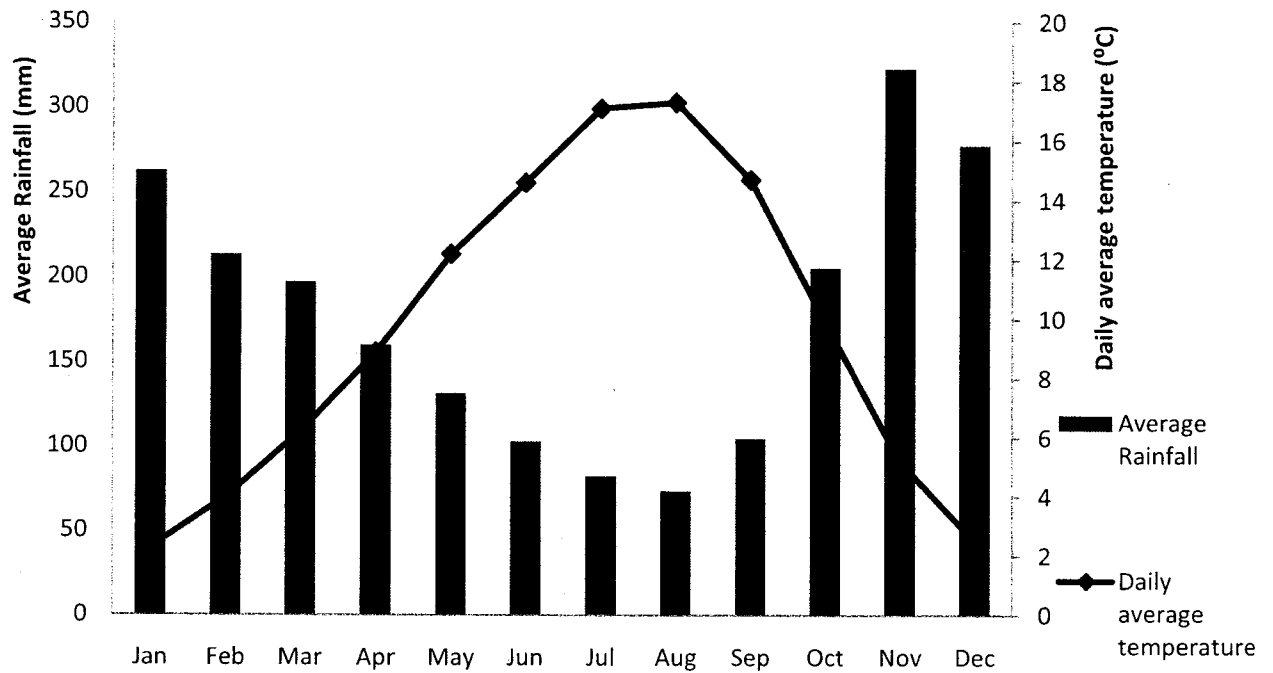
Figure 4.10. Average rainfall and daily average temperature by month for hydric sites in costal B.C. with an average annual rainfall 2132.9mm.
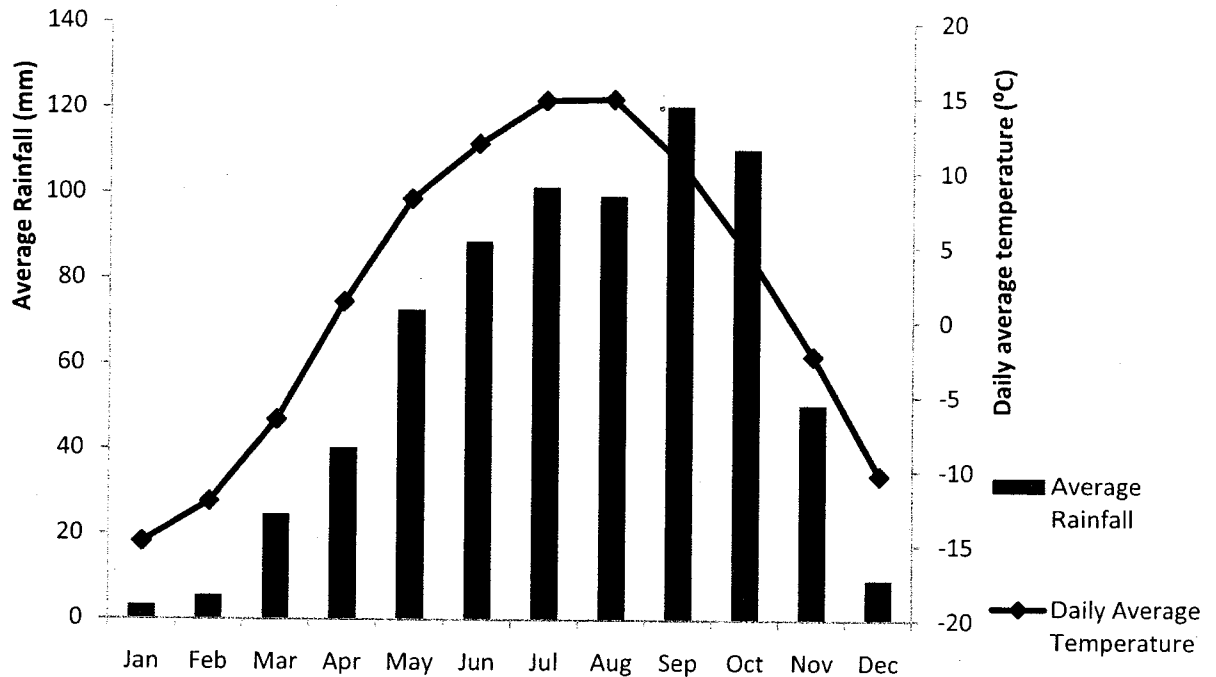
Figure 4.11. Average rainfall and daily average temperature by month for LO3 in Wawa, Ontario with an average annual rainfall 727.4mm.

In contrast, the site with the next highest average annual rainfall in Wawa, Ontario has different pattern of rainfall (Figure 4.11). The rainfall pattern in Wawa indicates that during the growing season (April to August) rainfall increases, as does temperature creating a good growing environment. This climate regime does not exhibit the same gap in the growing season that the hydric sites do.

4.4 DISCUSSION

Availability of water is crucial to the development of leaf anatomy and the results showed that total leaf area was positively correlated with total vessel area, meaning that the more vessel area is conducting water, the more leaf area the tree can support. This strategy has several benefits, including increase transpiration resulting in increased photosynthesis. I found significant positive relationships between vessel area and total leaf area for white birch trees from xeric and mesic sites, which also proved to

be significantly different from one another. In contrast, a negative relationship was found between average vessel area and total leaf area of white birch on hydric sites. As vessel diameter increases total leaf area increases and the rate at which this occurs differs amongst xeric and mesic sites. Villar-Salvador et al. (1997) also found that two species of *Quercus* had decreased theoretical specific leaf conductivity (which corresponds to a lower leaf area) when the mean vessel diameter decreased. These results are consistent with the trends explored in previous chapters, and suggest that the xylem and foliar structures of white birch trees vary in response to different climate conditions.

It is clear from the results in Chapters two, three and four that white birch is modifying both vessel and leaf features along different moisture gradients. A study on montane and desert populations of Ponderosa pine found that the difference in hydraulic architecture and biomass allocation was in fact a phenotypic variation within the species, and not an ecotypic differentiation (Maherali et al. 2002). A common garden test showed that there was no difference between the montane and desert populations in terms of growth, biomass allocation or hydraulic variables including conductivity. Genetic testing also revealed that differentiation between the two populations was not associated with distance or climate regime, and found that phenotypic plasticity may be responsible for any differences between the two populations (Maherali et al. 2002). The next step in the research regarding the hydraulic architecture of white birch should also follow this direction, testing if the difference along the climate gradient were ecotypic or could be attributed to phenotypic plasticity using common garden experiment as well as genetic testing. It would also be beneficial to sample white birch trees from Alaska,

Quebec and the east coast, to further explore how white birch differs across the entire range of its natural distribution.

The most surprising results were in the hydric sites, as the trees sampled exhibited contradictory results to those found in the mesic and xeric sites. Not only did these sites tend to have lower total leaf area they also had negative relationships between; vessel diameter and total leaf area, total leaf area and total vessel area, and vessel diameter and leaf area to sapwood area ratio. The sample size for the hydric sites was very small and should be taken into consideration when exploring these results.

It was assumed that yearly average rainfall would account for all rainfall in the growing season, as the rest of the sites experience precipitation mostly in the form of snow during the winter, and rain in the summer (Figure 4.11). The hydric sites in costal B.C., however, receive rainfall all year round, with the majority falling in the winter months when deciduous trees like white birch have no leaves and become dormant (Figure 4.10). This means that the trees in this site experience a more xeric environment during summer and are susceptible to water stress. Deciduous species have a high demand for water in the spring for bud flush and a xylem that is efficient for transporting water may allow for increased transpiration rates (Wang 2005). The low amount of rainfall in the spring may decrease the leaf area of white birch on hydric sites as there is increased competition for water and a depleting moisture resource. Wang et al. (1992) found that evergreen species have no loss in conductivity in the late winter which allows them to start transporting water earlier in the spring than deciduous trees, as they experience higher loss of conductivity and thus leaf out later. The majority of the competition for the hydric sites in costal B.C. comes from coniferous trees, possibly

creating a further depleted water source for the costal white birch. White birch does exhibit indeterminate growth, which means it can develop fewer leaves in early spring and continue to add leaf area through summer when water becomes available (Wang et al. 1992), however, the amount of rainfall decreases towards the summer in the costal sites creating another issue for leaf production.

Figure 1.2 shows that the entire west coast of B.C. experiences higher amounts of average annual rainfall than anywhere else in the country. While this was a small sample size, future studies should examine different areas of western coastal sites with white birch populations to see if this trend continues along a coastal gradient as well as to examine the hydraulic architecture of these sites and compare them to the results in the rest of the country to see if they differ as greatly as presented in this thesis.

It would be interesting to extend common garden and genetic testing to coastal sites and see if it is phenotypic plasticity that caused such difference in xylem and foliar features, or if the extremely different climate regime caused an ecotypic differentiation.

4.5 CONCLUSION

I failed to reject the key hypotheses in this study, as the mesic and xeric sites vessel diameter increased across rain regimes and vessel frequency decreased and it was also shown that leaf area increased as sapwood increased. A connection between xylem and foliar structures was observed as total leaf area increased as vessel diameter increased, and these increases were differentiated across moisture regimes.

In conclusion, I recommend further sampling of white birch from areas of the natural distribution that were not sampled (i.e. Alaska, east coast, Quebec) to further explore its' hydraulic architecture. Also I recommend common garden tests and DNA testing to deduce whether the difference across moisture regimes is an ecotypic response to physical environments or a phenotypic response.

The hydric sites showed contradicting results and I showed that the climate cycles in these sites are different from the rest of the country. Therefore, I also propose a study of white birch in coastal sites to explore the hydraulic architecture of white birch in these sites and to examine if they follow the results presented in this study.

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APPENDICIES

APPENDIX I: SAMPLE VESSEL IMAGES FROM ALL SITES
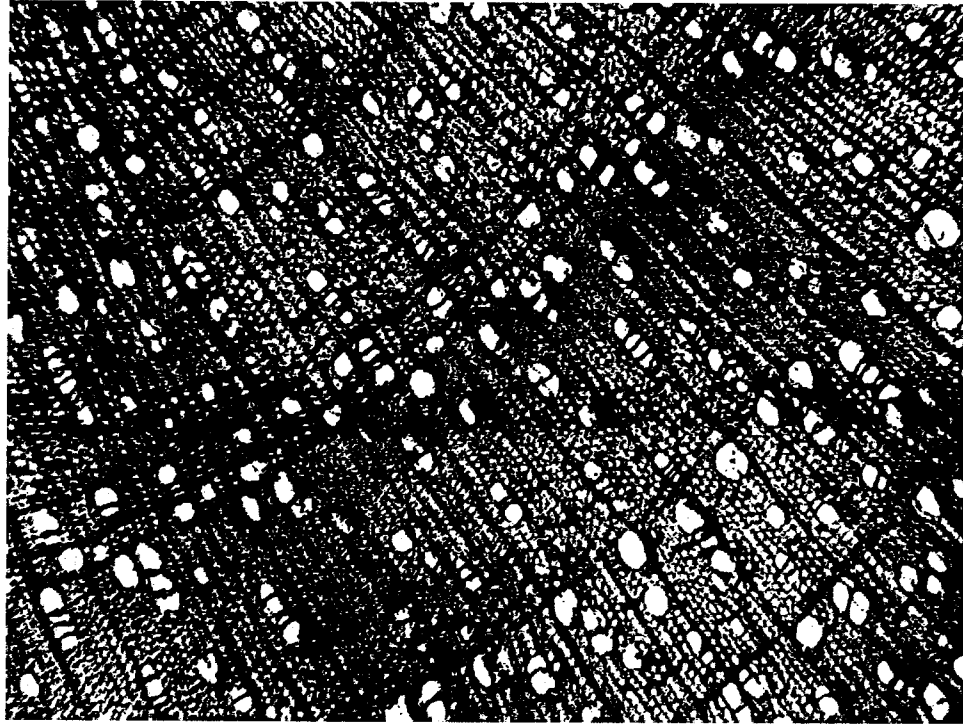
Figure A1. Sample vessel image from LA1.
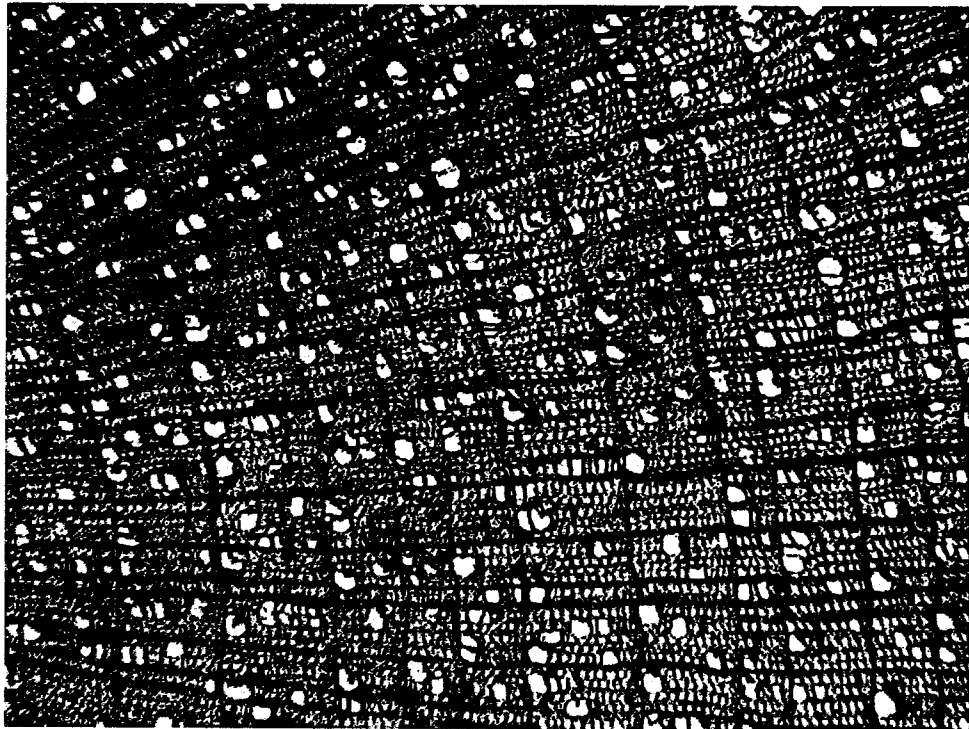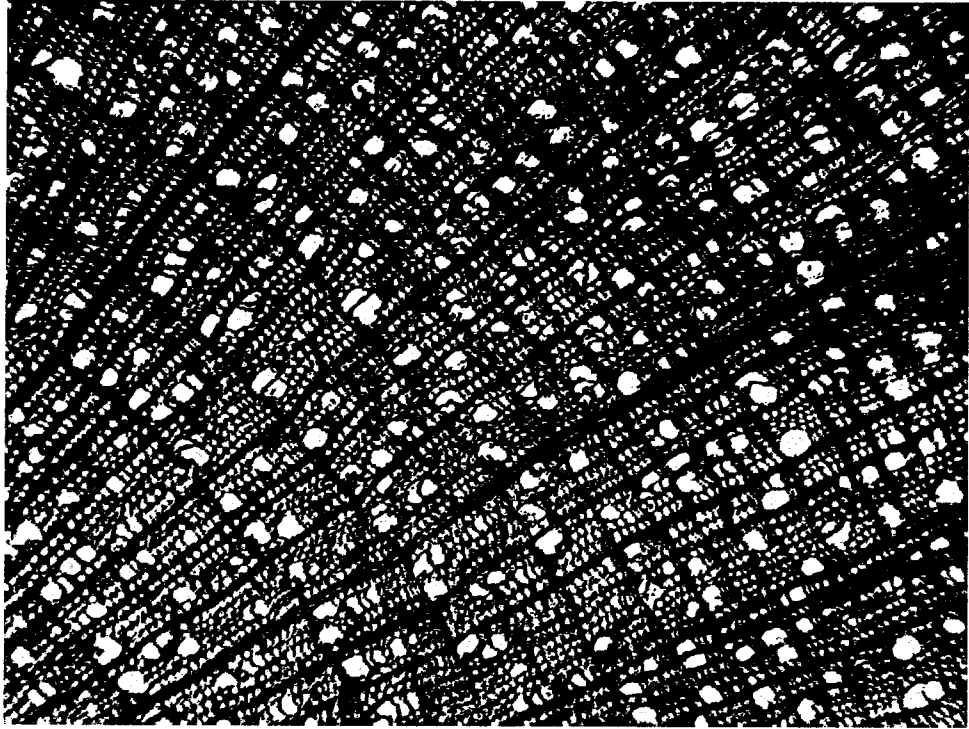

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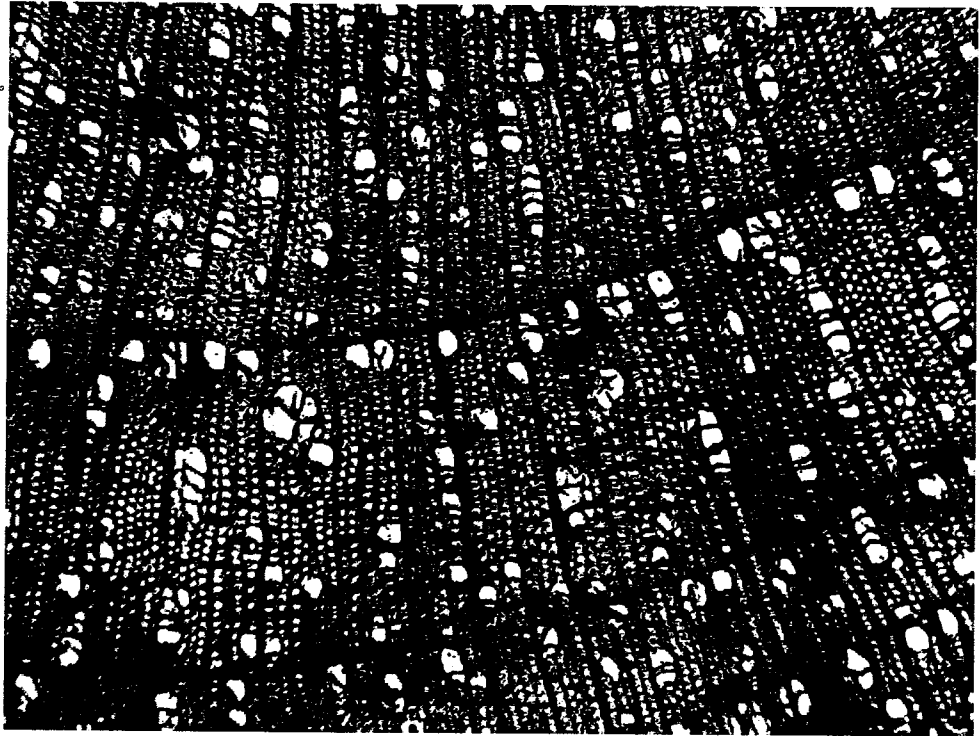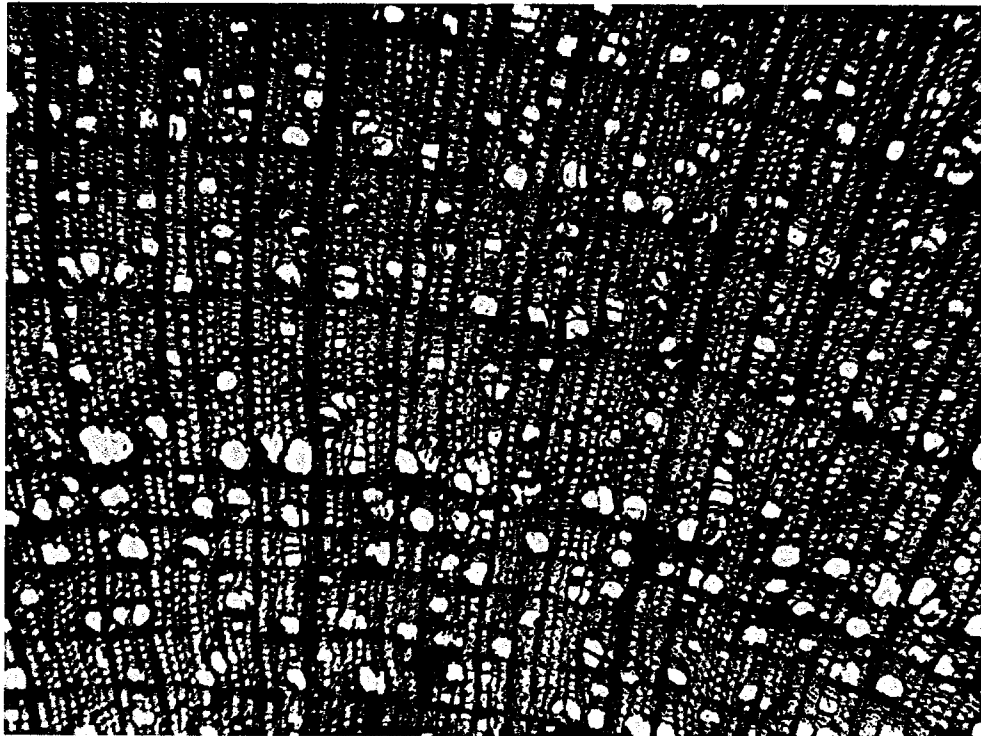
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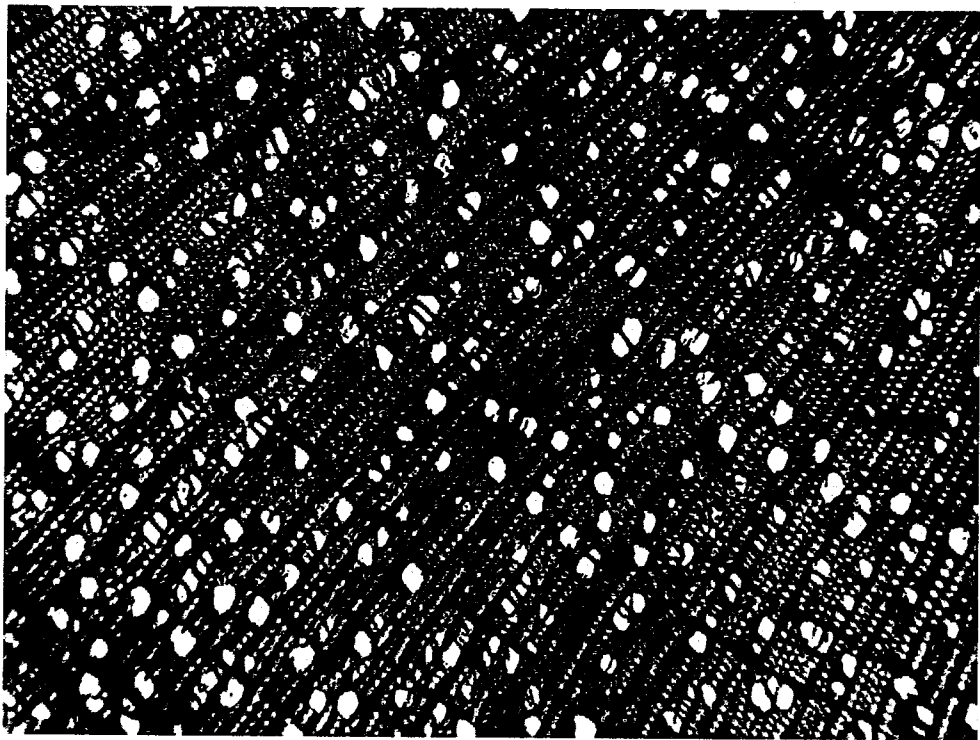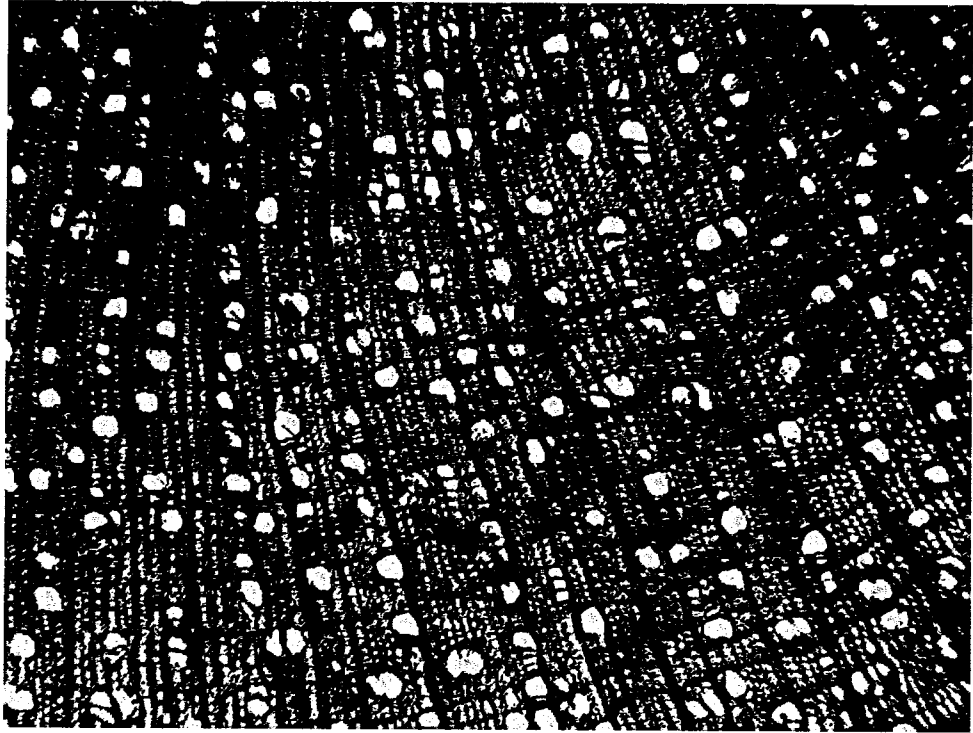

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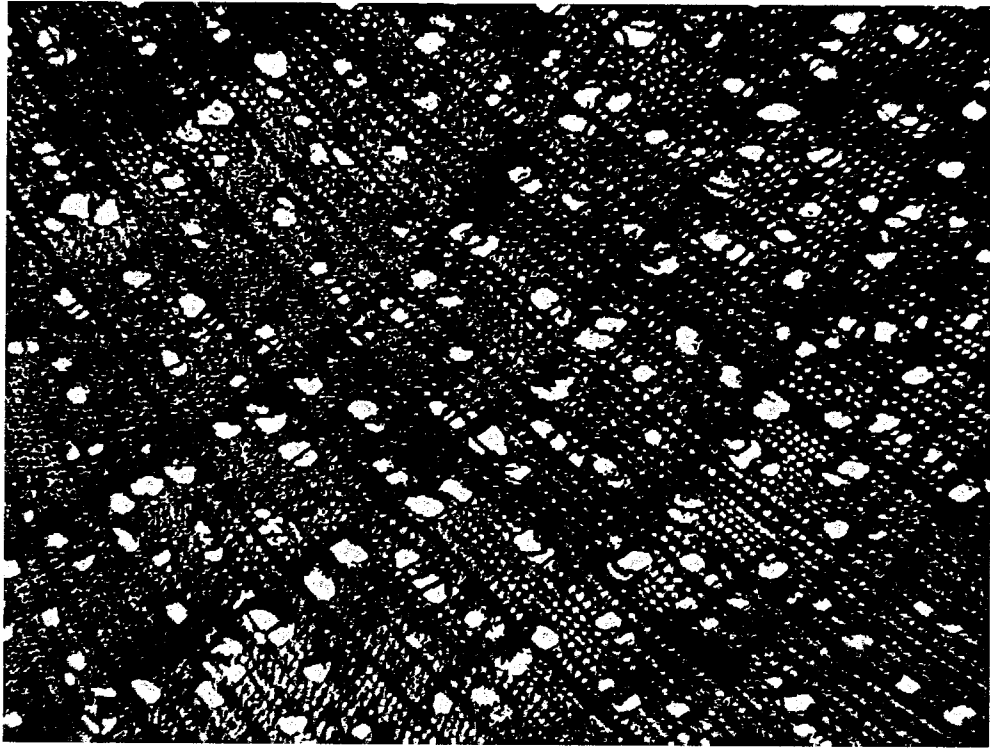
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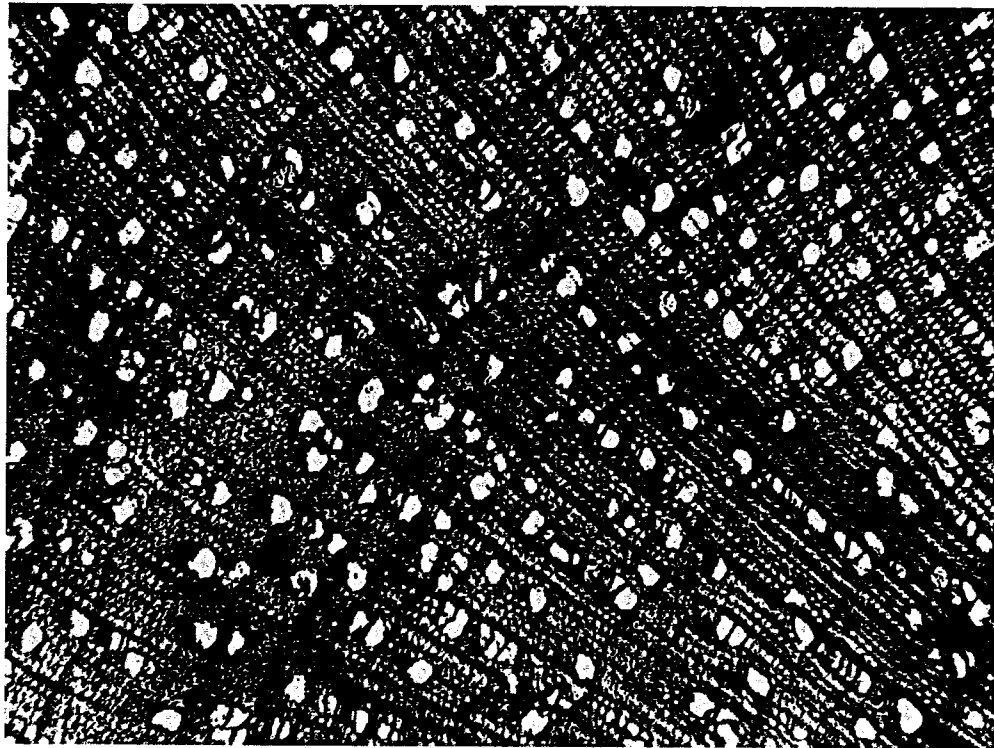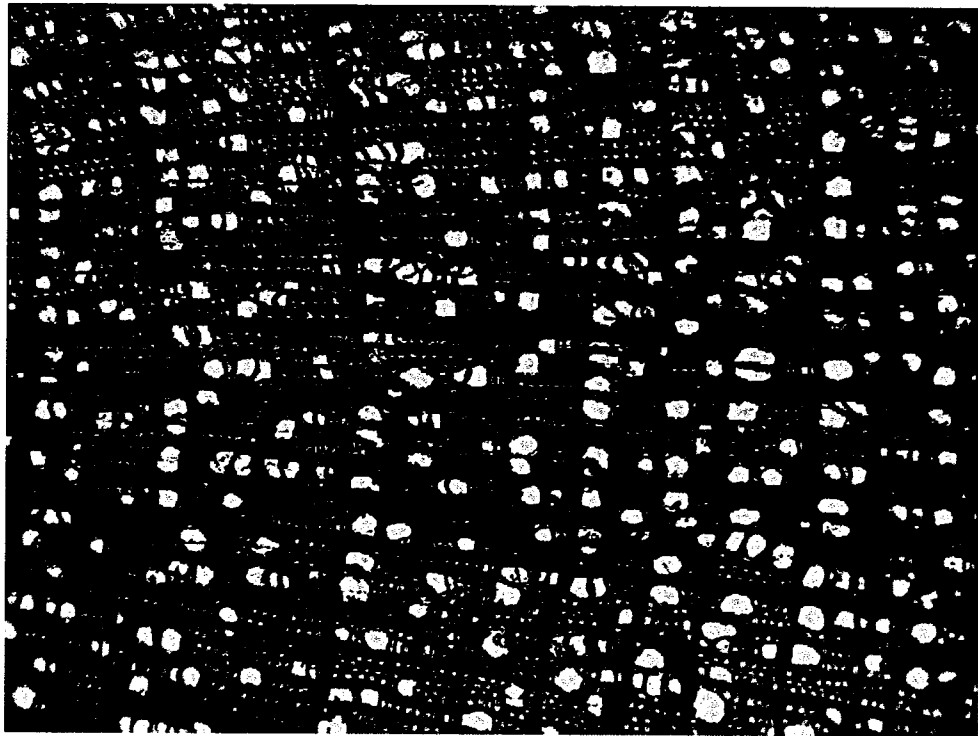

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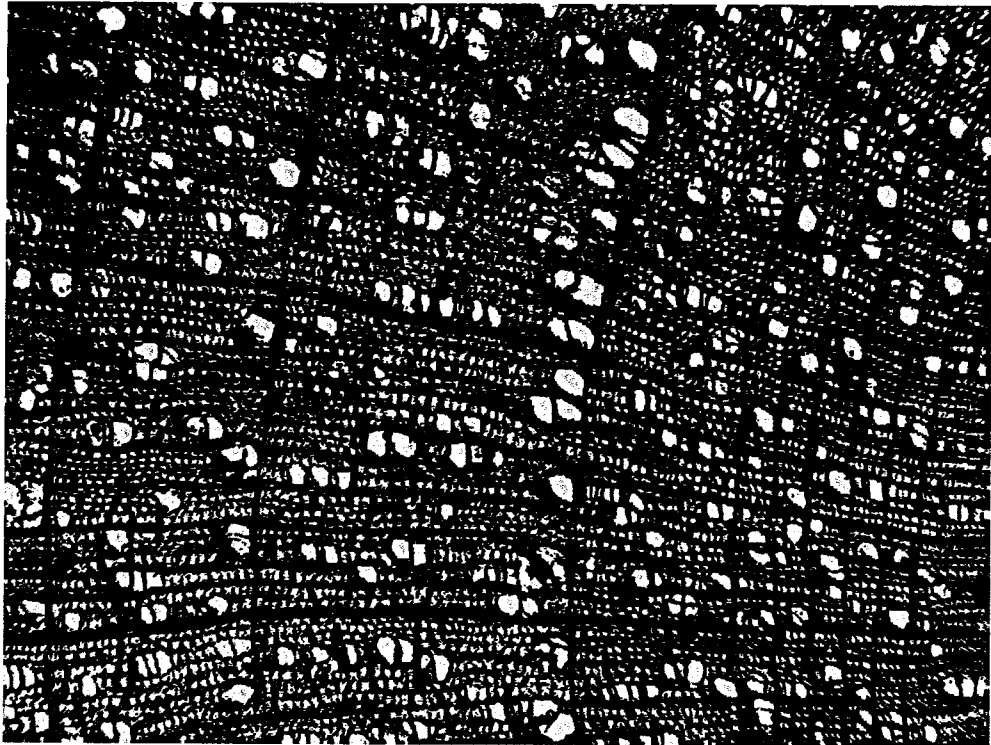
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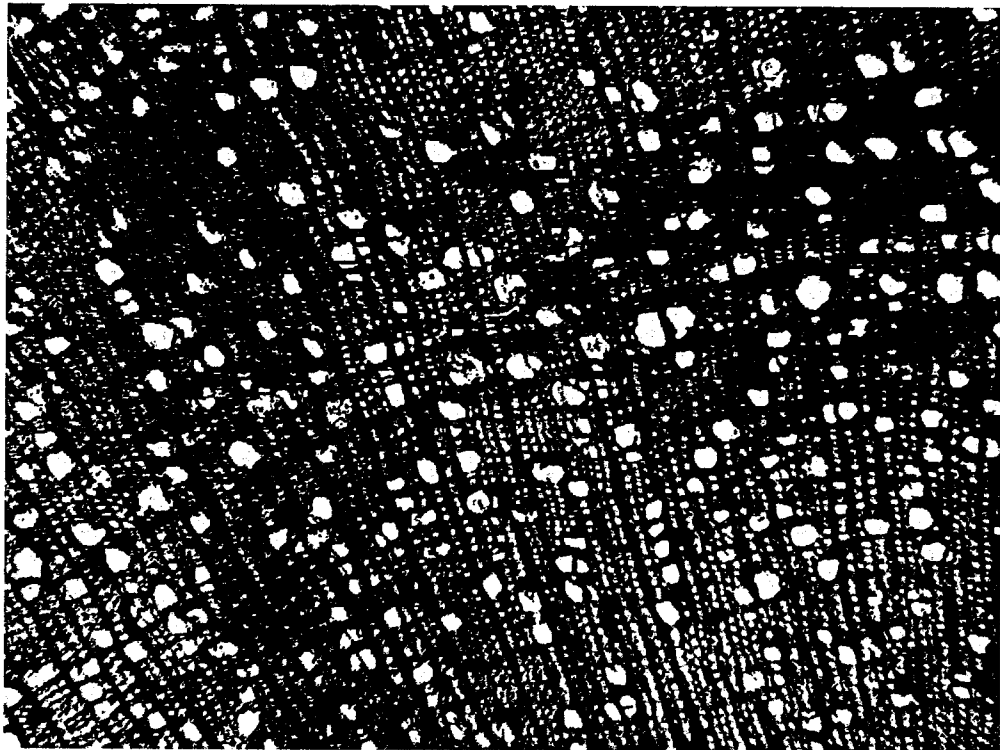
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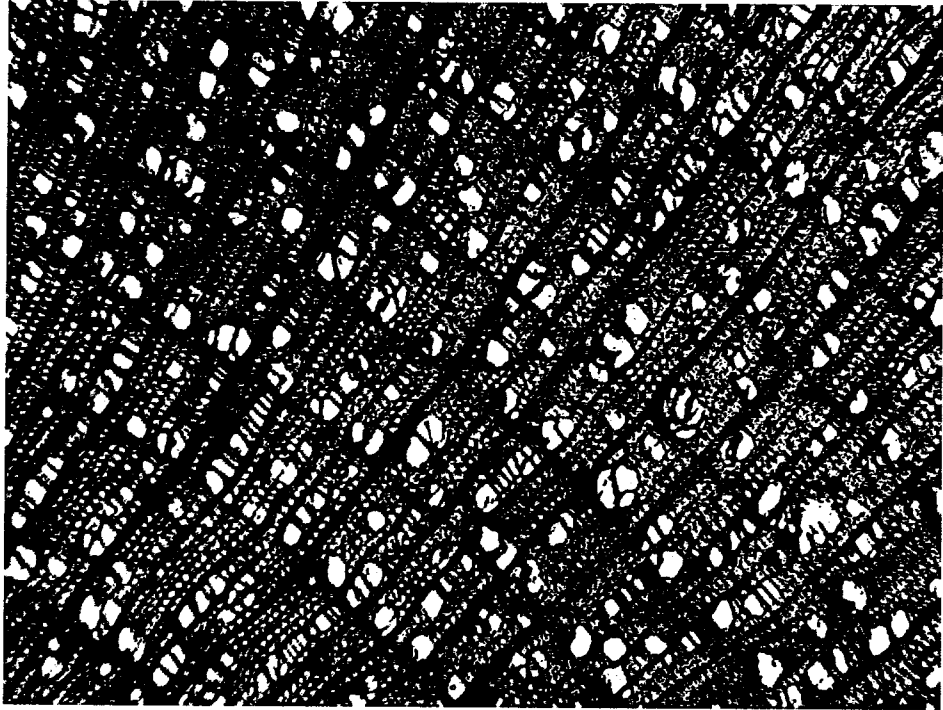
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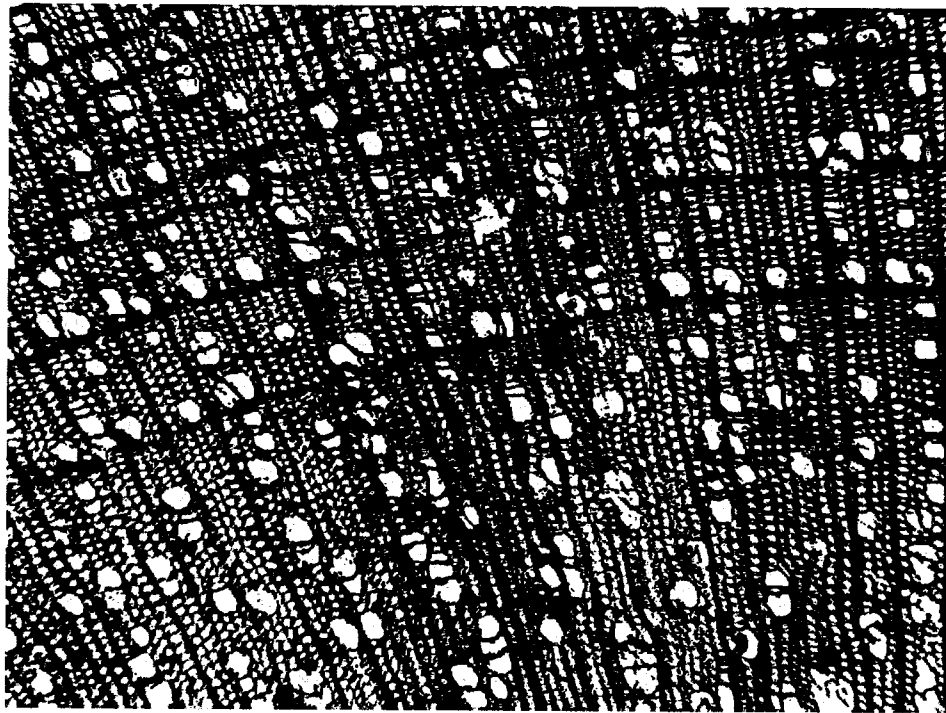
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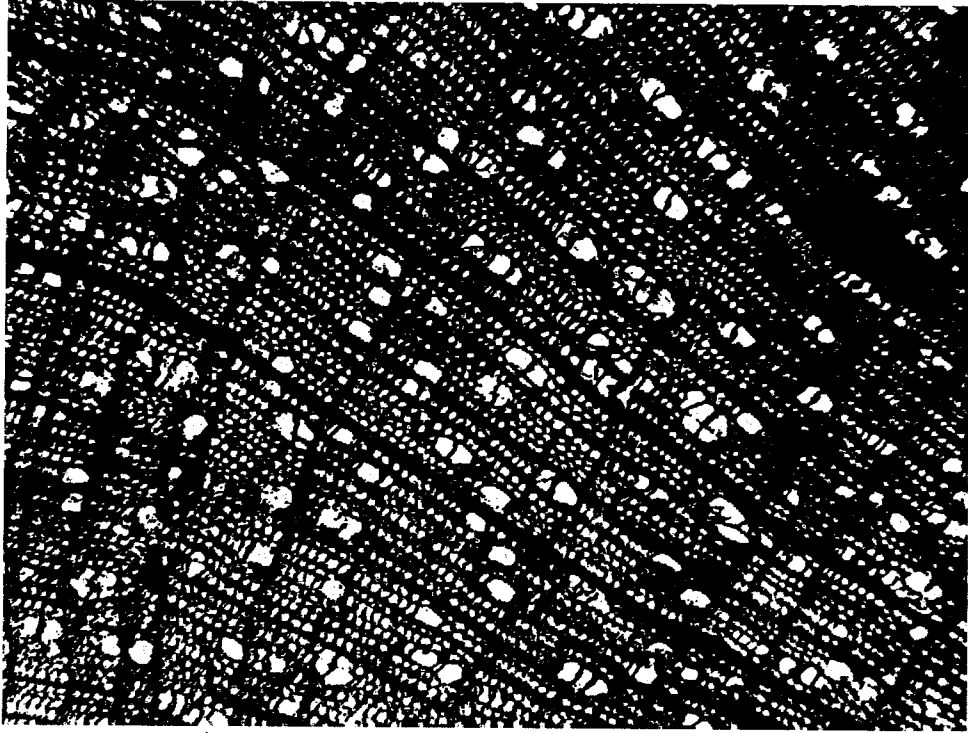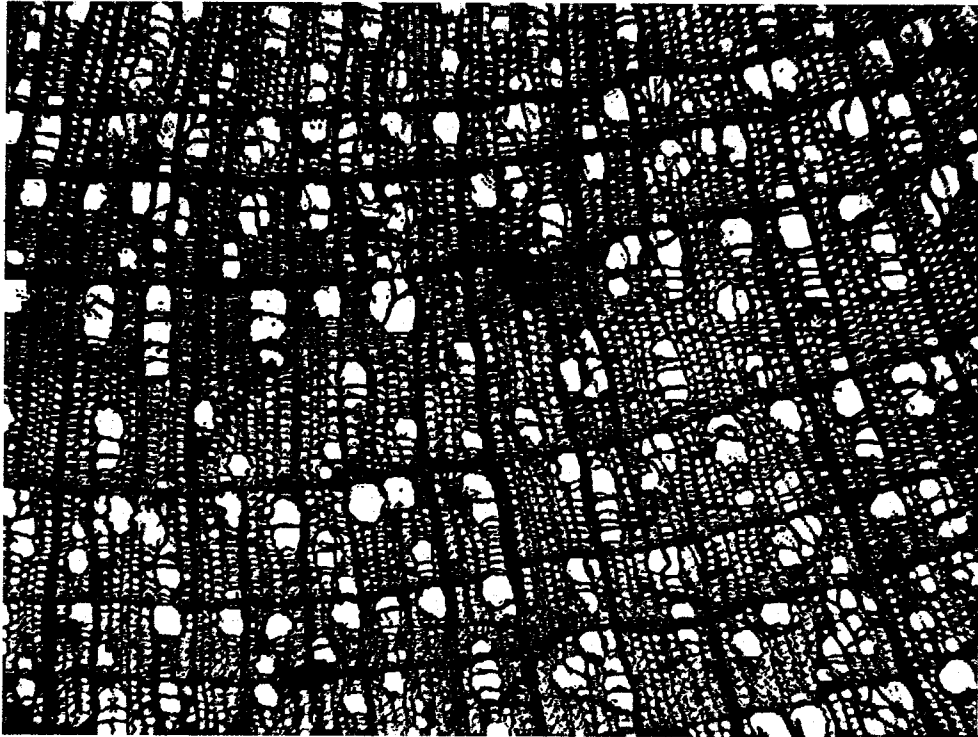
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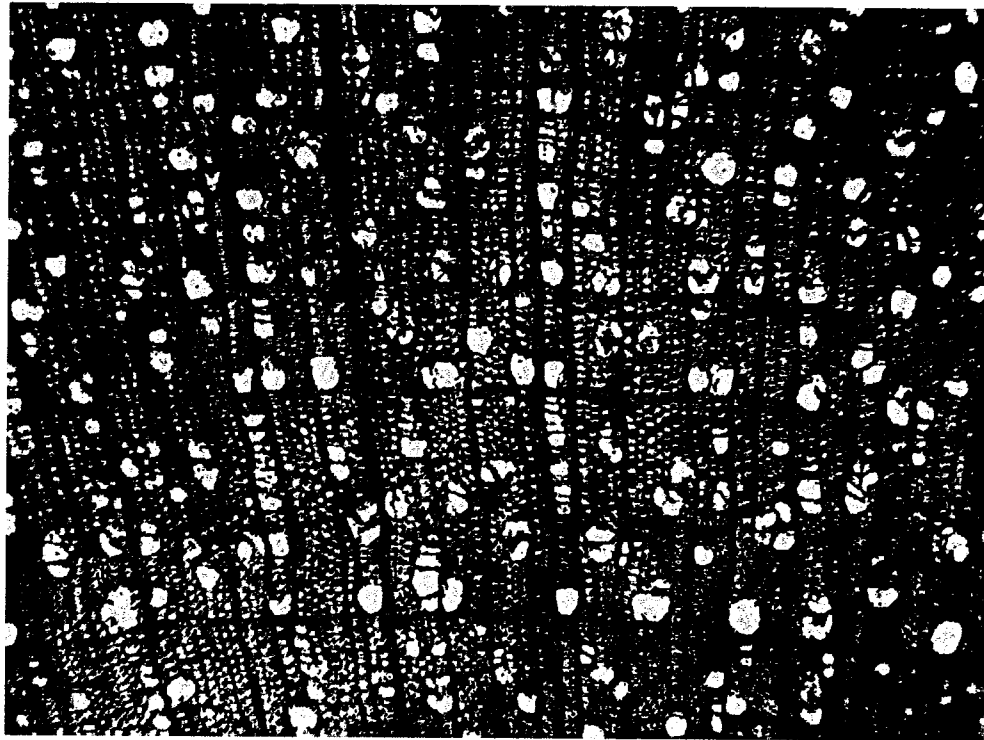
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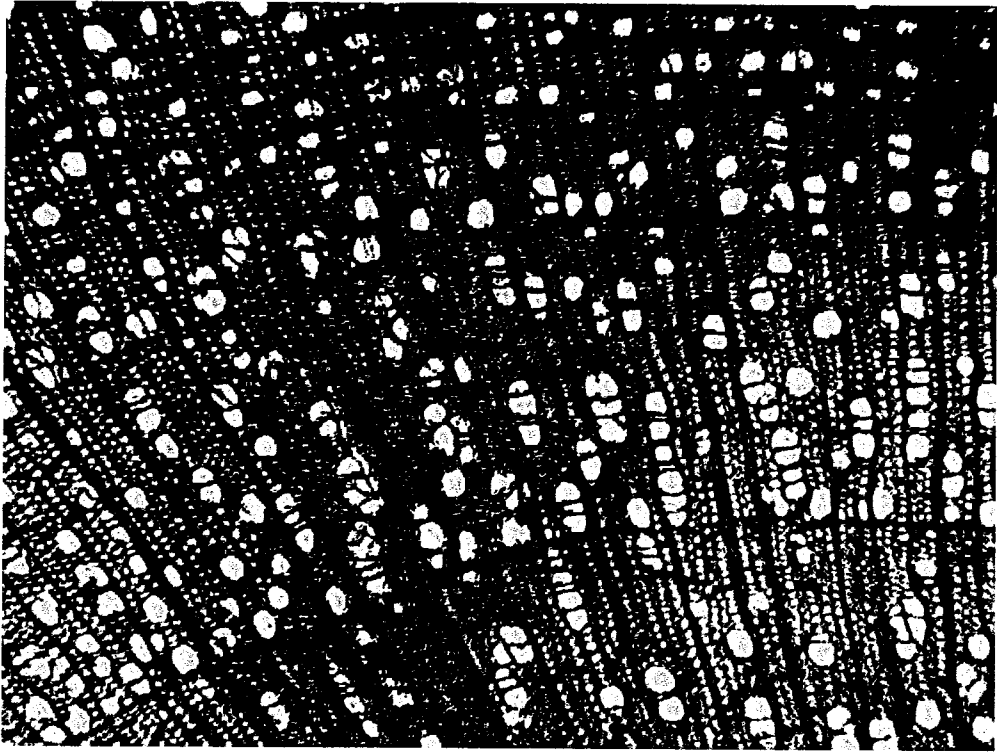
Figure A13. Sample vessel image from LB9.
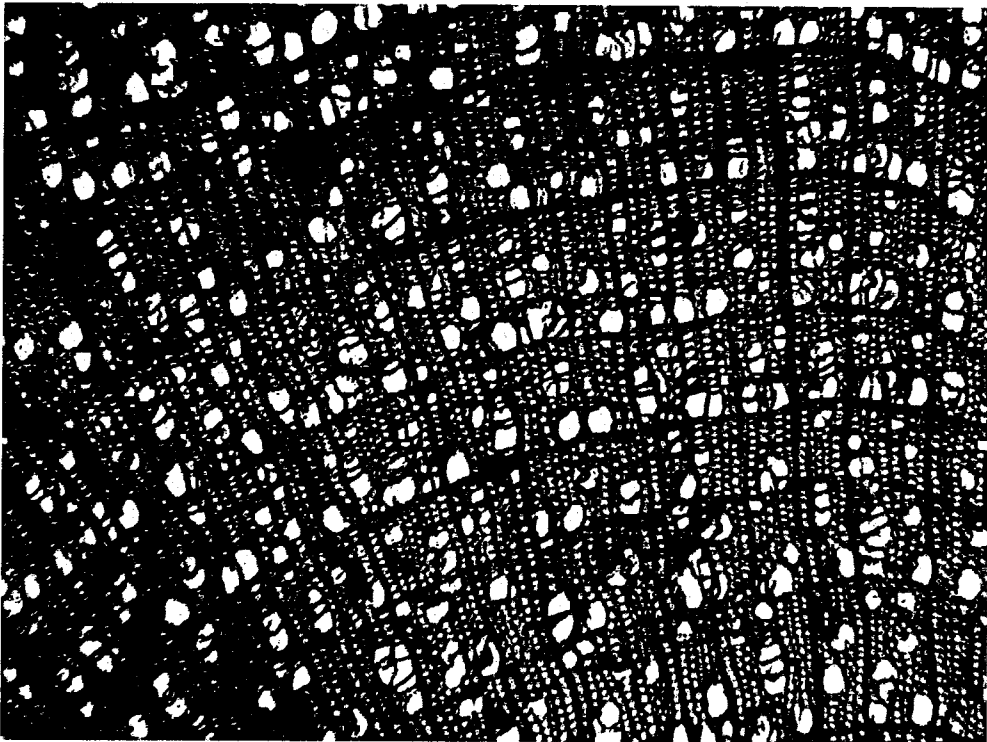
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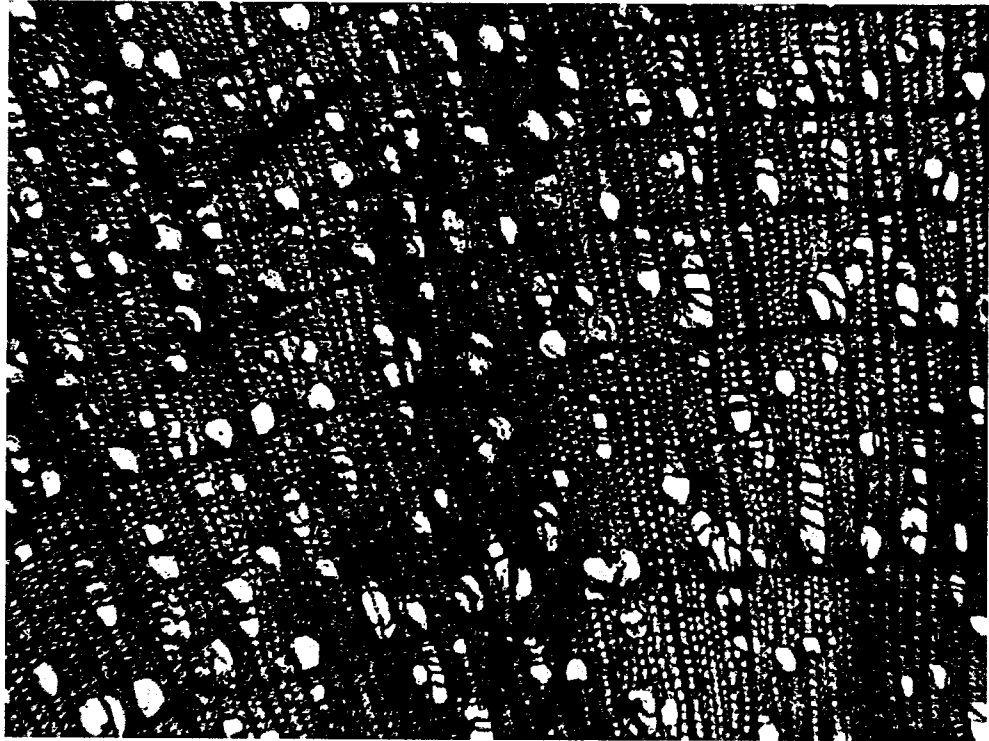
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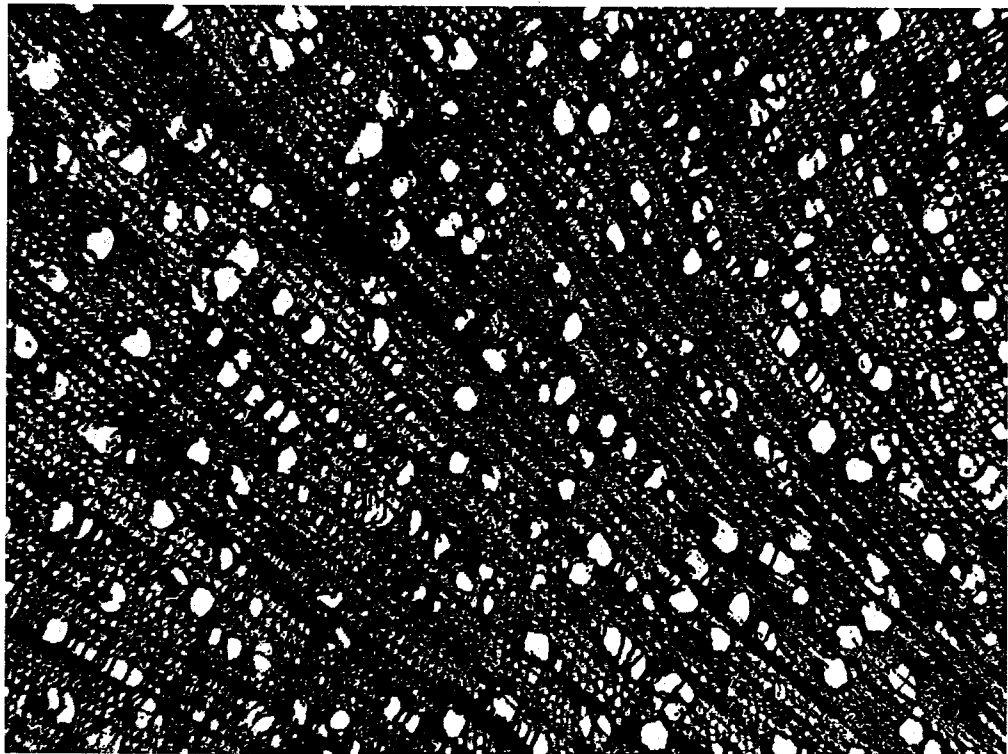
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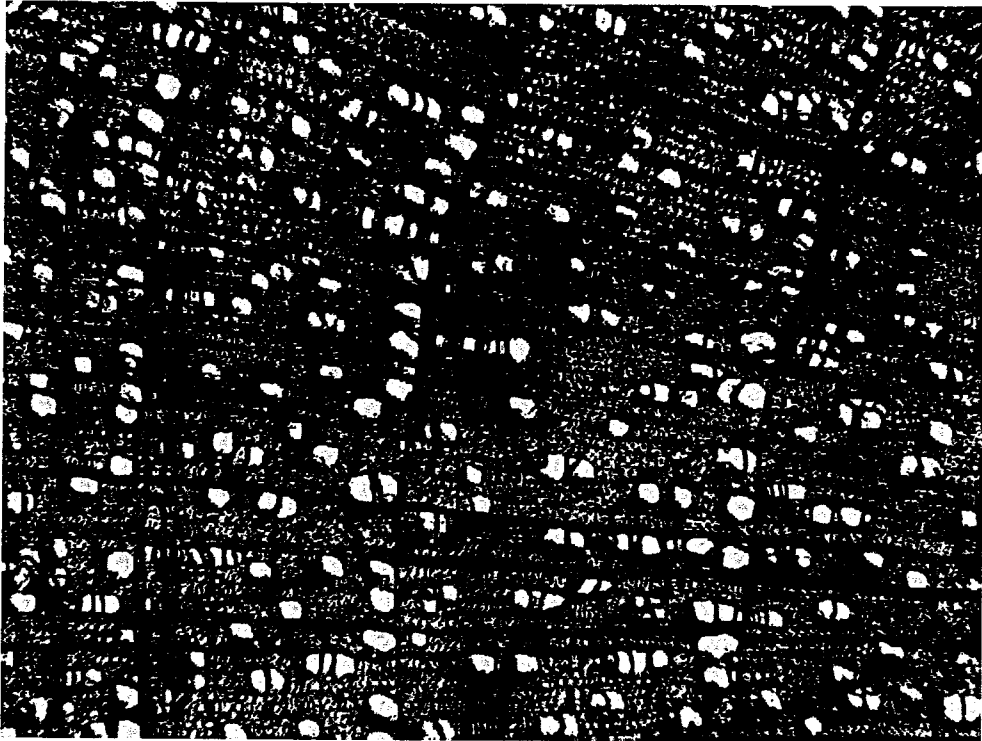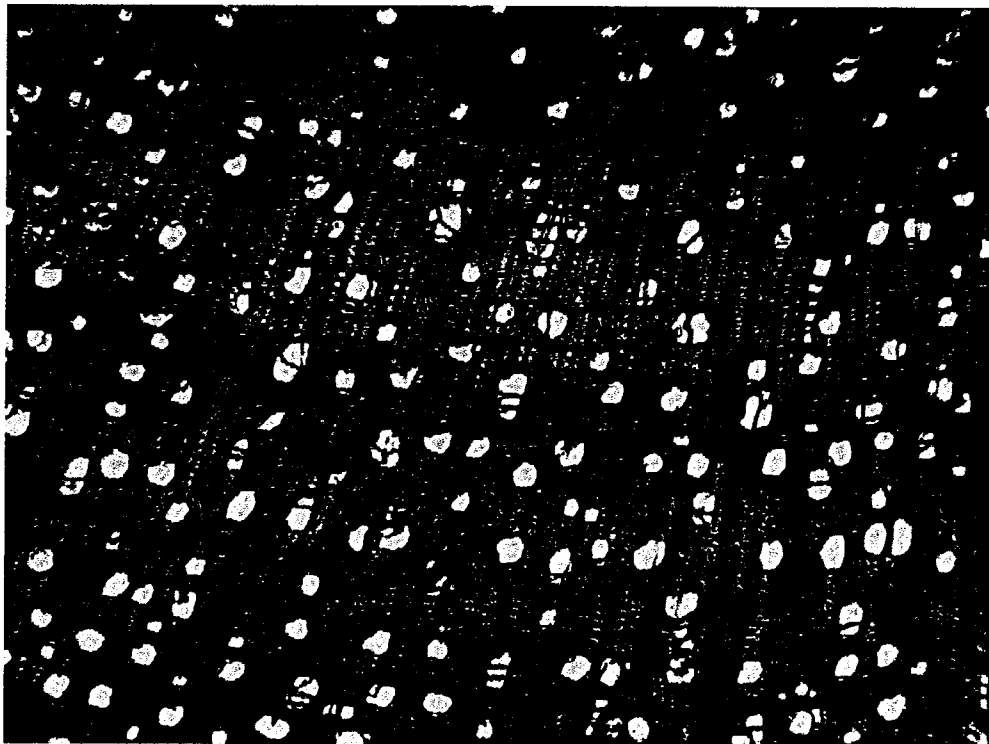
Figure A17. Sample vessel image from LO1.
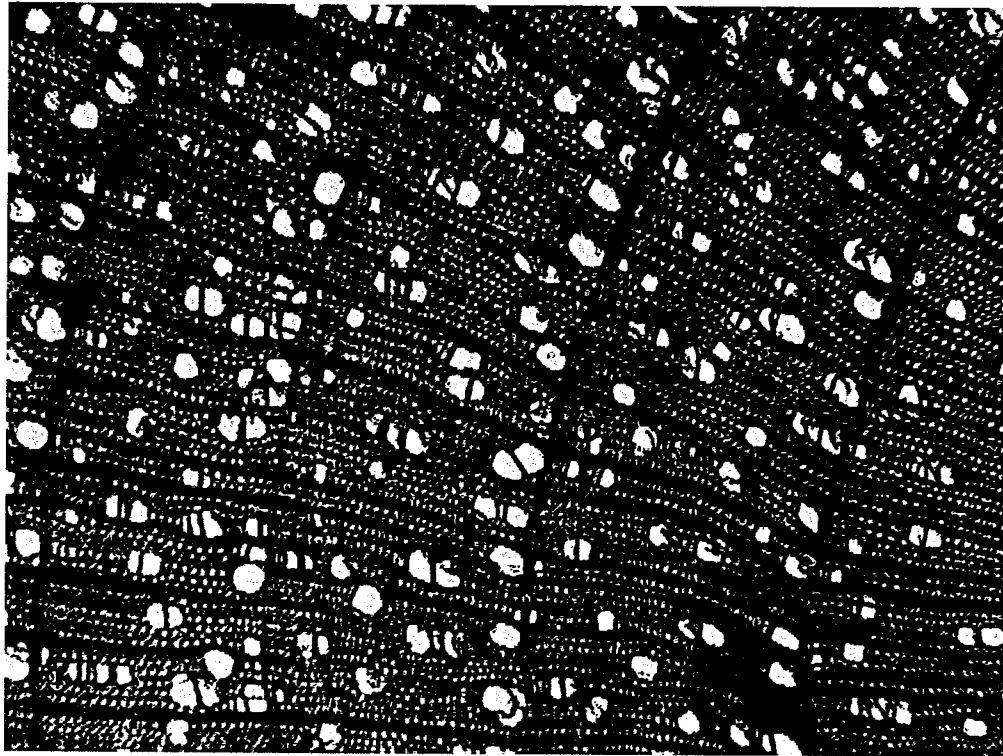
Figure A18. Sample vessel image from LO2.
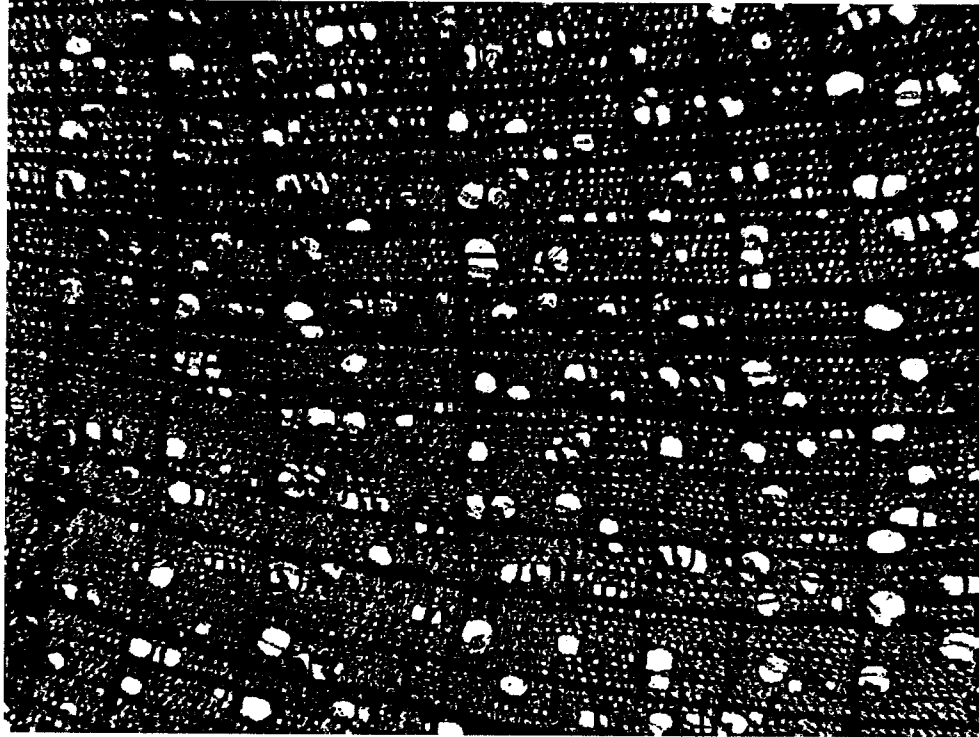
Figure A19. Sample vessel image from LO3.
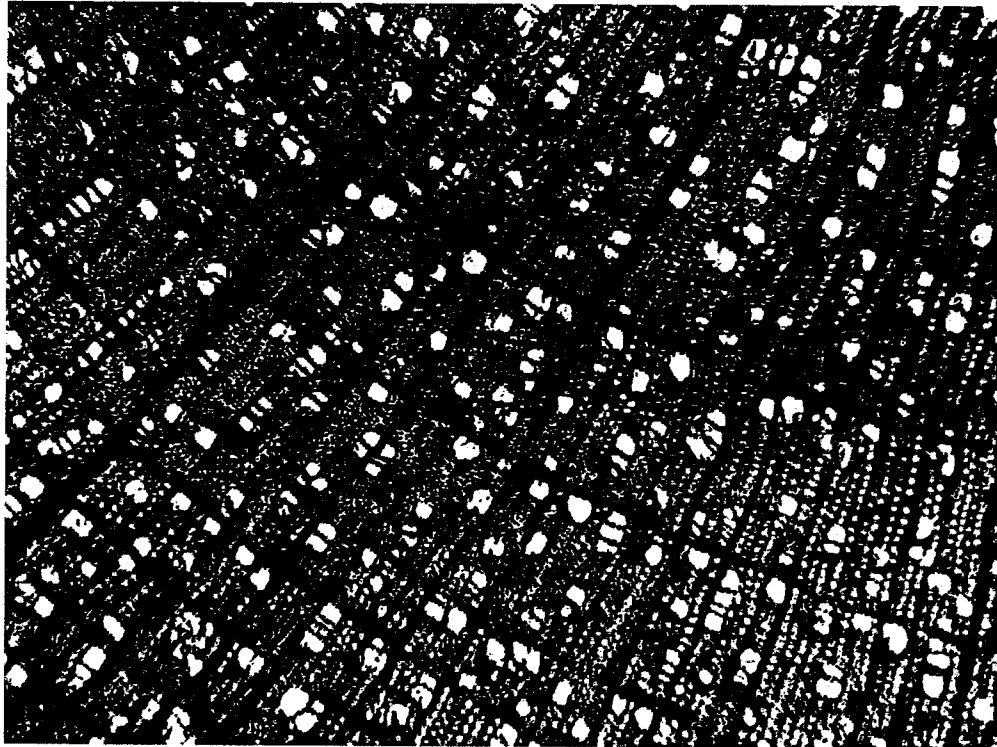
Figure A20. Sample vessel image from LO4.
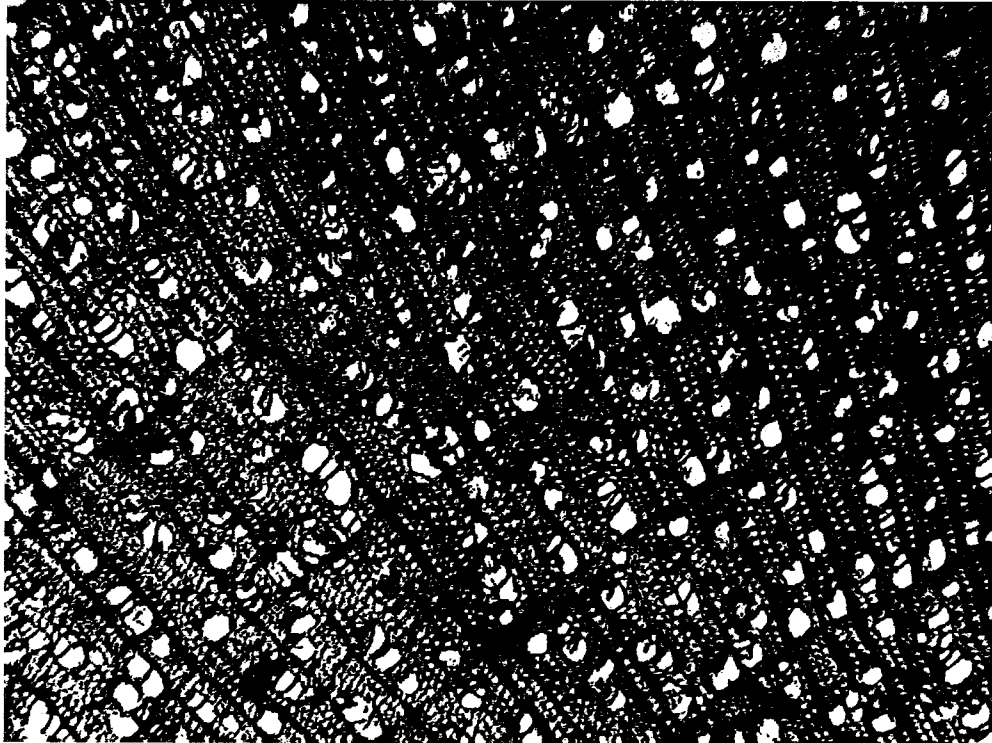
Figure A21. Sample vessel image from LO5.
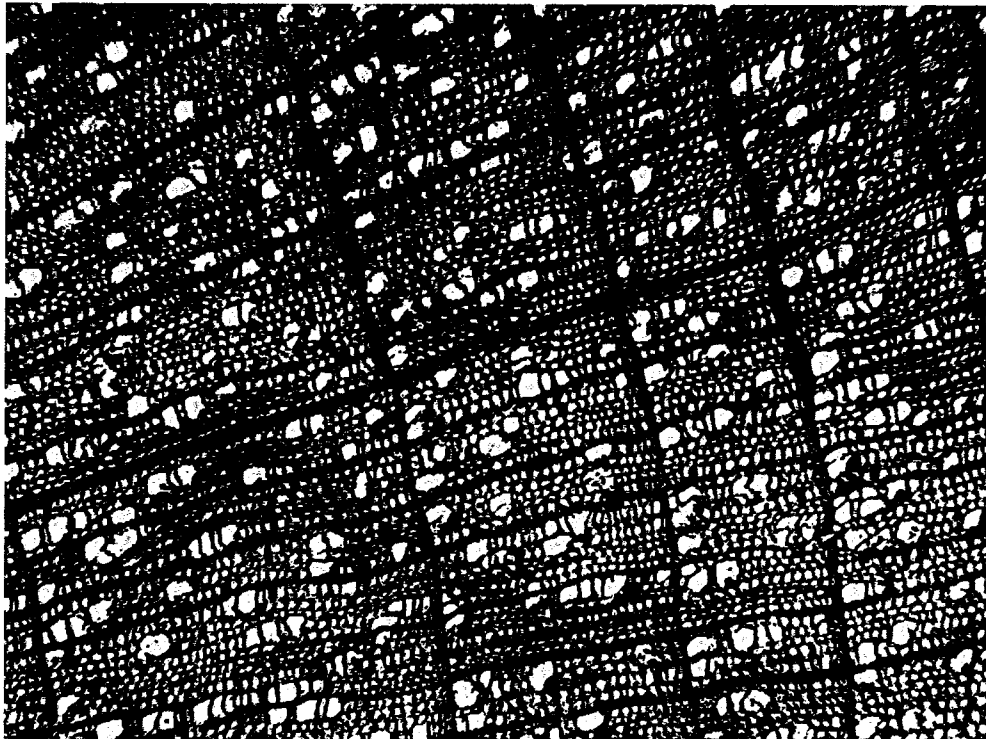
Figure A22. Sample vessel image from LO6.

Figure A23. Sample vessel image from LO7.

Figure A24. Sample vessel image from LO8.

Figure A25. Sample vessel image from LO9.

Figure A26. Sample vessel image from LO10.

Figure A27. Sample vessel image from LO11.

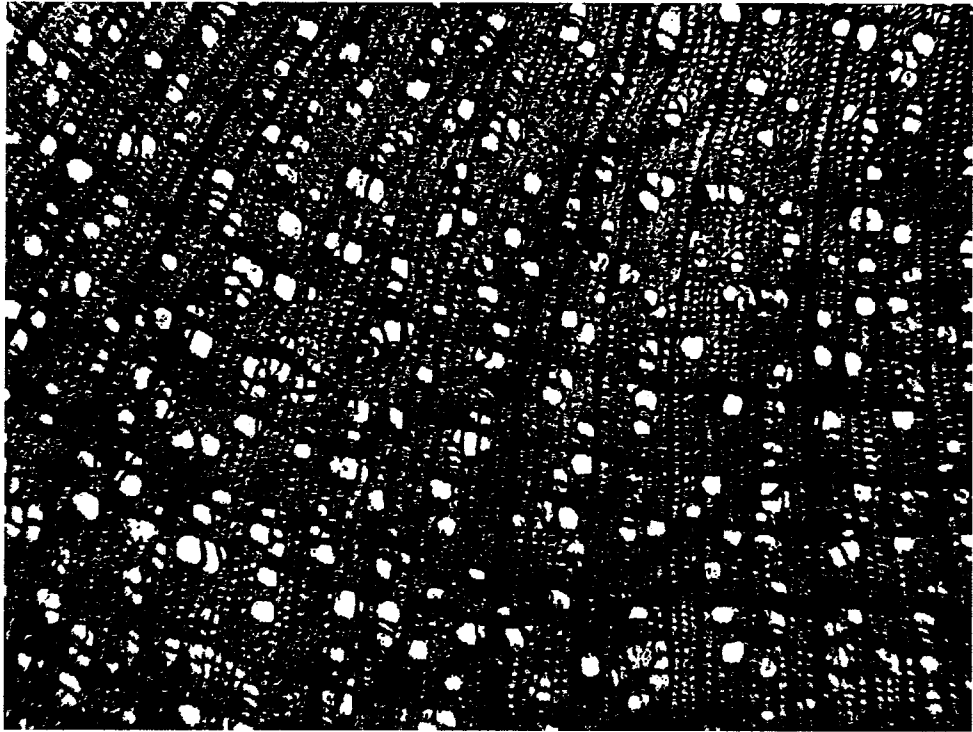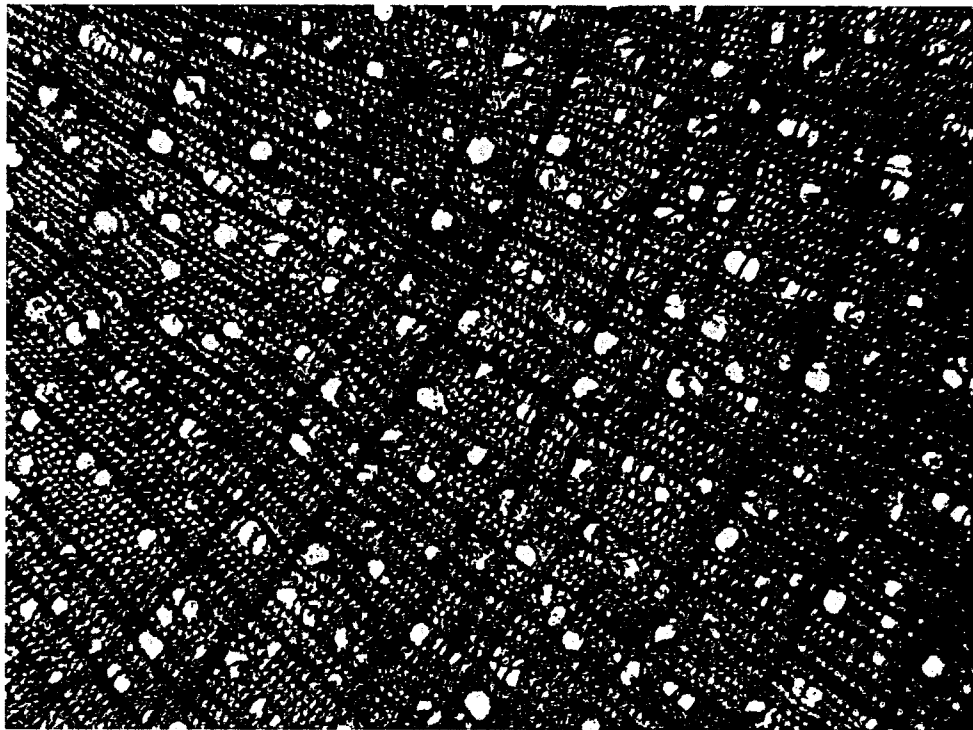Figure A28. Sample vessel image from LO12.

Figure A29. Sample vessel image from LS1.

Figure A30. Sample vessel image from LS2.