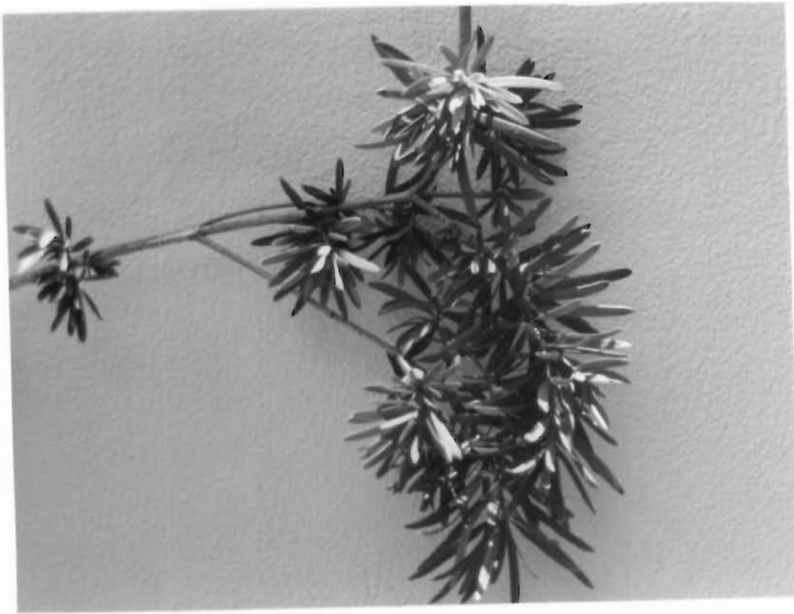# THE INTER-RELATIONS AMONG XYLEM ANATOMY, HYDRAULIC CONDUCTIVITY AND LEAF WATER STATUS IN FIVE SUB-TROPICAL TREE SPECIES.

BY

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Submitted in partial fulfilment of the requirements

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Podocarpus latifolius

Tecomaria capensis

Cinnamomum camphora

Trichilia dregeana

Barringtonia racemosa

"Trees and stones will teach you that
which you can never learn
from Masters."
St. Bernard of Clairvaux

"For nature is pleased with Simplicity,
and affects not the
pomp of superfluous causes."
Isaac Newton

PREFACE

The experimental work described in this thesis was carried out in the Department of Biology, University of Natal, Durban, from January 1990 to November 1991, under the supervision of Professor Norman W. Pammenter.

These studies represent original work by the author and have not been submitted in any form to another University. Where use was made of the work of others it has been duly acknowledged in the text.

H.W. Sherwin

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ABSTRACT

The wood anatomy, hydraulic properties and leaf water status of five sub-tropical plant species were studied. The specimens studied were growing in a private, irrigated garden. Consequently, any differences in xylem anatomy would be a result of phylogenetic and not environmental factors.

Podocarpus latifolius, being a gymnosperm, had only narrow, short tracheids as the conducting conduits. The size of the vessels of the four angiosperms increased in the following order: Tecomaria capensis, followed by Cinnamomum camphora, Trichilia dregeana and finally Barringtonia racemosa had the widest vessels. T. capensis and T. dregeana had the shortest vessel lengths. Those of C. camphora were slightly longer and the vessels of B. racemosa were the longest.

Measurements of hydraulic conductance (K_h), twig specific conductivity (TSC) and xylem specific conductivity (XSC) followed similar trends to those of conduit diameters. The measurements of leaf specific conductivity (LSC), however, did not follow these trends. T. dregeana, which had a far higher K_h than P. latifolius, did not have a significantly different LSC. This is because the twigs of T. dregeana supported a far greater leaf area than did the twigs of P. latifolius. There was also no significant difference in LSC among T. capensis, C. camphora and B. racemosa,

although their LSC's were all significantly higher than those of P. latifolius and T. dregeana. The consequence of efficient xylem anatomy thus seems to be, not only a greater supply of water to the leaf but also, and perhaps more importantly, it allows a greater leaf area to be produced.

The length of the vessels was also shown to have a large effect on the hydraulic conductivity of the twigs. The K_h values measured on excised twigs were found to range between 40% and 87% of the K_h calculated using the Hagen-Poiseuille equation. Conduit size distributions were also found to be important in calculating the K_h.

The more efficent xylem anatomy of B. racemosa resulted in little decrease in plant water potential even with large increases in transpiration. P. latifolius on the other hand showed a considerable decrease in leaf water potential with just a slight increase in transpiration. The other three species showed decreases in leaf water potential inter-mediate to these two extremes. The inferred root-to-leaf condutivity, shown by the inverse of the slopes of the water potential versus transpiration curves, were lower than the LSC measurements taken on excised twigs in the laboratory. The difference between the inferred and the measured LSC's could give an indication of resistances such as those within the root and at the soil-root interface.

CONTENTS

CHAPTER 1: INTRODUCTION

GENERAL INTRODUCTION

Background

Weatherley (1976) stated that the development of the tracheid (an inert, empty conduit allowing relatively unimpeded mass flow) was the greatest single evolutionary step in the colonization of the land by plants. Since the first plants with their primitive conducting systems colonized land, a great deal has changed. There now exist two distinct types of xylem conducting conduits: tracheids (possessed by the gymnosperms and thought to be primitive), and vessels (the more recently evolved conducting elements of most angiosperms). While angiosperms also have tracheids, they do not appear to play a major role in water conduction in these plants. Not only do these two different types of conduits occur, but there has also been the evolution of a great variety in the size, length, densities and sculpturing of these conduits. The evolutionary trends of these features have been discussed in detail by Carlquist (1975).

Land plants must not only provide their leaves with sufficient water and nutrients, they must also provide them with mechanical support (Ewers, 1985). Trees produce xylem which serves these dual roles (Gartner, Bullock, Mooney, Brown & Whitbeck, 1990). These two vital

functions, however, can lead to conflicting demands on wood structure for physiological fitness (Baas, 1983). Photosynthetic products must be used to produce not only conducting elements, such as tracheids and vessels, but also parenchyma and strengthening elements, such as fibres. This resource allocation between conducting and strengthening tissue will vary from species to species and habitat to habitat. This particular study, however, will deal primarily with the conductive properties of wood.

Water transport in plants

The cohesion theory of Dixon (1914 loc. cit. Zimmermann, 1983) states, in summary, that water flows down gradients of decreasing hydrostatic pressures through the xylem. The rate of water movement is determined by the steepness of these gradients in water potential and the resistance to flow (van den Honert, 1948 loc. cit. Nobel & Jordan, 1983). Based on van den Honert's description of the soil-plant-atmosphere-continuum, Elfving, Kaufmann and Hall (1972) described leaf water potential (Ψ_{leaf}), measured in MPa, as being dependent on three elements: soil water potential (Ψ_{soil}), also measured in MPa, flux of water through the system (J), measured in $kg\ m^{-2}s^{-1}$, and resistance between the soil and the leaf ($R_{soil-leaf}$), measured in $MPa\ m^2s\ kg^{-1}$:

$$\Psi_{leaf} = \Psi_{soil} - J \cdot R_{soil-leaf} \quad \cdots\cdots\cdots\cdots\cdots 1.1$$

Ever since the introduction of the cohesion theory of sap ascent in plants (Dixon, 1914) it has been recognized that water in the conduits (vessels and tracheids) of xylem can be under considerable negative pressure, or more correctly tension. Xylem has been termed the "vulnerable pipeline" (Tyree & Dixon, 1986; Tyree, Fiscus, Wullschleger & Dixon, 1986) because liquid water in the xylem is in a metastable state. The moment the metastable state is disrupted, the xylem water undergoes an explosive phase change, called a cavitation event, and the xylem conduit is left with a near vacuum filled only with water vapour. The cavitated conduit soon becomes embolized, that is, fills with air that comes out of solution from surrounding water (Tyree et al., 1986).

This instability of xylem poses a direct threat to the photosynthetic productivity and even survival of plants (Tyree & Dixon, 1986). Embolisms decrease water conduction and thereby increase water stress. Water stress is a major factor limiting terrestrial plant productivity on a worldwide basis (Boyer, 1982). Productivity is limited because a wide variety of growth-related processes are affected by water deficits, with cell expansion being one of the most sensitive (Tyree & Jarvis, 1982). Woody plants appear to use three strategies that constrain the threat to water flow: 1) they possess conducting systems that are resistant to cavitation; 2) they have well developed mechanisms for isolating individual cavitation events, so that only a small fraction of the conducting system is

affected and 3) plants with secondary growth can produce new xylem, replacing losses to cavitation. (Field & Holbrook, 1989). It has also been suggested by Sperry, Holbrook, Zimmermann & Tyree (1987) and Zimmermann (1983) that cavitated xylem can be refilled when positive pressures inside the xylem elements causes the air to dissolve. These refilled xylem elements could thus become functional again. Root pressures have been thought by Sperry et al. (1987) to play a role in the creation of these positive pressures in the xylem.

Hydraulic conductance of the xylem is an important physical characteristic in determining the rate of water movement in plants (Zimmerman, 1983; Calkin, Gibson & Nobel, 1986). A number of characteristics influence hydraulic conductance. These include xylem conduit diameters, lengths, and densities (i.e. number of conduits per unit xylem cross-sectional area); type and orientation of perforation plates between xylem elements; the degree of sculpting on the inside of conduit walls; and characteristics of the pores between conduits. However, in the simplest cases hydraulic conductance should be positively correlated with vessel diameter (Gartner et al., 1990). This is because flow through xylem is thought to obey Poiseuille's Law which relates hydraulic conductance (K_h), measured in $m^4MPa^{-1}s^{-1}$, to the number and the diameter of the conduits. The Hagen-Poiseuille equation is as follows:

$$K_h = \pi \; \Sigma d^4_i \; / \; 128 \; \eta \; \dots\dots\dots\dots\dots\dots\dots\dots\dots 1.2$$

where d is equal to the diameter of all the conducting elements for the ith capillary (in meters) and n is the dynamic viscosity of the fluid in MPa seconds (Ewers, Fisher & Chiu, 1989).

Measurements of hydraulic conductance can be made on excised twigs by measuring the rate of water flow through the twig while a pressure gradient is applied across it (Zimmermann & Brown, 1971). Many workers (Calkin et al., 1986; Ellmore & Ewers, 1985; Ewers, 1985; Ewers & Zimmermann, 1984a; 1984b; Ewers et al., 1989; Gartner et al., 1990; Ginter-Whitehouse, Hinckley & Pallardy, 1983; Petty, 1978; Schulte & Gibson, 1988; Sperry, Donnelly & Tyree, 1988; Sperry, Tyree & Donnelly, 1988b; Tyree, Caldwell & Dainty, 1975; Zimmermann, 1978) have measured hydraulic conductance on excised twigs. Other workers (Camacho-B, Hall & Kaufmann, 1974a; Camacho-B, Kaufmann & Hall, 1974b; Küppers, 1984; Meinzer & Grantz, 1990; Meinzer, Sharifi, Nilsen & Rundel, 1988; Nobel & Jordan, 1983; Reich & Hinckley, 1989; Sanchez-Diaz & Mooney, 1979) have calculated or inferred hydraulic conductance from measurements of leaf or canopy transpiration and leaf water potential based on equation 1.1.

Many workers have also compared the measured hydraulic conductance of the vessels of hardwoods with the theoretical conductivity of cylindrical capillaries of the same diameter (Ellmore & Ewers, 1985; Ewers & Fisher, 1989; Ewers et al., 1989; Petty, 1978; Schulte & Gibson,

1988; Zimmermann & Brown, 1971). These measured values have ranged from about 10 to 100% of the theoretical values derived using the Hagen-Poiseuille equation, equation 1.2, (Petty, 1978; Zimmermann, 1982).

Zimmermann and Brown (1971) have suggested that the discrepancy between theoretical and measured conductivities arises from the limited length of conduits in many species and the presence of perforation plates at the ends of conduit elements. Conduits also end blindly and are interconnected in networks. None of these features, which are generally considered safety mechanisms (Baas, Werker & Fahn, 1983; Zimmermann & Brown, 1971), are taken into account in the Hagen-Poiseuille equation. In calculating the K_h, the contribution of every conduit is taken into account. However, some conduits may not be active due to the presence of embolisms. If the workers referred to in Petty (1978) and Zimmermann (1982) had not flushed the twigs they took their measurements on, they would have got measurements on twigs which could have contained embolized conduits. This may also explain some of the discrepancies between the K_h they measured and the K_h they calculated.

Variability in wood anatomy

Xylem anatomy is often described in terms of safety versus efficiency. A xylem anatomy which is efficient at water conduction is also thought to be more susceptible to

embolism formation. Conversely, a xylem anatomy that has safety features is also thought to be inefficient at conducting water (Baas, 1983; Zimmermann, 1983). It is not surprising to find a large variety in wood anatomical features, as different balances between safety and efficiency evolved in response to different environmental constraints.

Woods that have small, short vessels or tracheids have lower conductances but are higher in conductive safety. As conductance is related to the fourth power of the diameter of the conduit, the wider the conduit the more efficient it will be at conducting water (Baas, 1983; Zimmermann, 1983). Longer total conduit lengths are also thought to infer more efficient conducting systems (Zimmermann, 1983). However, these features are also thought to be dangerous as wider and longer conduits would incapacitate a greater proportion of the xylem conducting pathway if cavitation was to occur (Zimmermann, 1982; Zimmermann, 1983). Wider conduits are also thought to cavitate more readily than narrower conduits (Zimmermann, 1983). Carlquist (1989) said that the wood of each species could be regarded as an intricate series of adaptations for both efficiency and safety.

Many studies (Baas, 1976; Baas et al., 1983; Carlquist, 1975; den Outer & van Veenendaal, 1976; Patterson & Tanowitz, 1989) have revealed both strong and weak correlations between various wood anatomical

characteristics and ecological factors such as water
availability, temperature, and seasonality. Guthrie (1989)
related xylem anatomy to ecological dominance.
Functionally adaptive interpretations of these ecological
trends, however, remain highly speculative and have
sometimes given rise to controversy, because the precise
functional significance of variation in most wood
anatomical traits has never been experimentally
established (Baas, 1983).

Liquid phase resistance

It was previously assumed that the main resistance to
liquid water flow resides in the non-vascular tissue,
i.e., in the cell walls or membranes (Passioura, 1982;
Weatherley, 1976). Many workers have since shown that
xylem represents a substantial part of the total
resistance to water flow through the soil-plant-atmosphere
continuum (Calkin et al., 1986; Ewers, 1985; Tyree, et
al., 1975; Tyree, 1988). It is suggested Weatherley (1976)
and more recently by Meinzer, et al. (1988) that while
stomatal aperture necessarily represents the major
physical resistance controlling transpiration, plant
hydraulic resistance, can under certain conditions,
represent the functional resistance through its effects on
stomatal aperture.

Restriction of liquid phase conductance within the plant,
without concurrent restriction of stomatal conductance,

would cause leaf desiccation. Thus regulation of
transpiration by plants must not only occur in the vapour
phase, but stomatal conductance should remain in balance
with the capacity of the leaves to acquire water. This
would avoid leaf desiccation at one extreme, and
unnecessary restriction of CO_2 uptake at the other, both
of which inhibit photosynthetic carbon acquisition
(Meinzer & Grantz, 1990).

Leaf water status

To determine how effective a stem is at supplying its
leaves, one needs to consider not only measured K_h, but
also the leaf area that the stem segment supplies i.e.
leaf specific conductivity (LSC) and the transpiration of
the leaves (Ewers, et al., 1989). In well watered soil the
efficiency of water transport to leaves may be elucidated
by measuring the response of Ψ_{leaf} to different steady
state transpiration rates attained by changing the
evaporative demand of the atmosphere. Small decreases in
Ψ_{leaf} resulting from large increases in flux would
indicate a low $R_{soil-leaf}$ and an efficient water transport
system.

Many studies have been conducted measuring changes in
Ψ_{leaf} with changes in transpiration. Aston and Lawlor
(1979) found little change in leaf water potential under a
wide range of atmospheric conditions and rates of water
flux. These results agreed with those obtained by Stoker

and Weatherley (1971) who found that leaf water potential
was constant over a wide range of transpiration rates.
This work was, however, carried out on herbaceous species,
which have efficent water transport systems. Camacho-B et
al. (1974a; 1974b) and Meinzer et al. (1988), while
finding that herbaceous species presented no measurable
response of leaf water potential to transpiration changes,
also found that leaf water potential decreased with
increasing transpiration in woody plants.

Differences in water transport efficiency may also operate
in parallel with differences in stomatal regulation of
water loss from plants. Many workers have found positive
correlations of stomatal conductance with the apparent
hydraulic conductance of the soil/root/shoot pathway in a
number of species (Küppers, 1984; Meinzer et al., 1988;
Sanchez-Diaz & Mooney, 1979). Teskey, Hinckley and Grier
(1983) found that stomatal closure could be rapidly
induced with a change in the flux of water through the
soil-plant-atmosphere continuum. Changes in stomatal
conductance do not necessarily have to be in response to
changes in the bulk leaf water status. Stomata have been
reported to be able to respond directly to changes in the
air humidity without changes in bulk leaf water status
(Küppers, 1984; Teskey et al., 1983).

Conclusion

There appear to be two physiological characteristics

important to plant adaptation with respect to water relations: the efficiency of the water transport system and the regulatory mechanisms for water loss. The combination of these characteristics provides species with different capabilities for responding to the environment. The responses observed have been placed by Camacho-B et al. (1974a; 1974b) into three categories: (a) species that combine strong regulation of water loss by stomata with low efficiency of their water transport system and which are unable to prevent depression of their Ψ_{leaf} as transpiration increases; (b) species that strongly regulate water loss by stomata but have a more efficient water transport system than the previous case; (c) species with little stomatal regulation of transpiration and a highly efficient water transport system.

THIS STUDY

AIM → pg 40

The aim of this study was to determine what effect, if any, xylem anatomy had on the hydraulic conductance and hydraulic conductivity of woody species and if this had any influence at the leaf level. There were two possible approaches to this study. One was to study a single species with a wide distribution, having a range of different ecologically determined xylem anatomies. The second approach, the one that was adopted for this study, was to study a number of species with different xylem anatomies that were growing under the same environmental conditions. This approach was chosen because the travelling costs of the first approach would have been prohibitive and there exists in this sub-tropical climate, an abundance of very different species found growing under the same conditions.

Differences in the xylem anatomy of these species found growing together should be phylogenetically determined and not environmentally determined, as the environment in which they are all growing would be very similar. No matter what the xylem anatomies of these species are, the plants must all photosynthesize and grow. The water relations of species found growing together, is therefore, of particular interest, as water is a common limiting feature to growth (Ginter-Whitehouse et al., 1983).

This study was carried out in a domestic garden in which

was found a number of plant species. The garden was
irrigated daily and the soil was thus thought to have a
high water potential. The garden is situated in Durban,
which is a coastal city on the east coast of South Africa
(approximately 30°S and 31°E). The climate is sub-tropical
with an average rainfall of 1018mm per annum. The average
summer minimum and maximum temperatures are 19°C and 26°C
respectively and the average winter minimum is 12°C and
the winter maximum is 23°C (Michelin, 1990). The study was
carried out over the late spring and summer months, when
rainfall was high. The average rainfall over the summer
and spring months is   100 - 200mm per month (Michelin,
1990).

After an initial survey of the wood anatomy of a number of
species, five species were chosen. These five species had
very different wood anatomies and were all flourishing on
this site. The five species chosen included one gymnosperm
and four angiosperms.

The gymnosperm chosen was <u>Podocapus</u> <u>latifolius</u> (real
yellowwood). These trees are large and slow growing,
occurring in evergreen forests. They can also withstand
several degrees of frost (Coates Palgrave, 1984). The four
angiosperms selected were: <u>Tecomaria</u> <u>capensis</u> (Cape
honeysuckle), an evergreen shrub, which occurs naturally
at the margins of evergreen forests, bush, scrub and along
stream banks and rocky outcrops (Coates Palgrave, 1984);
<u>Cinnamomum</u> <u>camphora</u> (Camphor tree), a very large,

evergreen tree common in warm-temperate and subtropical areas, originally imported into South Africa from Australia (Immelman, Wicht & Ackerman, 1973); <u>Trichilia dregeana</u> (Forest Natal mahogany), a very large, slow growing tree, naturally occurring in evergreen forests (Coates Palgrave, 1984); <u>Barringtonia</u> <u>racemosa</u> (Powder-puff tree), usually a small tree naturally occurring near water, along the banks of rivers and fresh water swamps. It is a fast-growing tree which cannot withstand frost (Coates Palgrave, 1984).

This study has been divided into three main areas: wood anatomy, hydraulic properties and leaf water relations. Each of these three areas will be discussed in detail in separate chapters. The final chapter will attempt to tie these three areas together in a general discussion. Although only one plant of each of the five species was studied they are referred to, in terms of this study, by their genus and species names. Conclusions from this study do not infer that the particular plant species, as a whole, has the same features and operates the way the individual plant appears to do in this study. While phylogenetic factors do certainly play a role and will affect all the plants of the same species, the conclusions drawn from this study apply only to the individual plants used in this study.

CHAPTER 2: WOOD ANATOMY

INTRODUCTION

Wood or secondary xylem provides a woody plant with a complex tissue for sap transport, for mechanical strength and for metabolic processes such as storage and mobilization of reserve carbohydrates and lipids (Baas, 1983). For the investigation into the hydraulic properties of wood, only those features involved in water transport were studied, but it is important to note that wood does more than just transport water. Features important to other functions of wood may even be at the expense of efficient water transport, for example, less total xylem area to allow for more strengthening tissue.

Xylem anatomy has been reported to change from environment to environment within a species (Baas, 1983). To try and remove this source of variability from this study, five different species were chosen which were all growing under the same conditions. Differences in xylem anatomy should thus be viewed as phylogenetic differences and not related to different environmental constraints.

The most important features with regard xylem anatomy and water transport include conduit diameters, conduit densities and vessel lengths. Although other features such as helical thickenings and perforation plate presence and type are also thought to play a role in water transport

(Baas, 1976; 1983; Baas et al., 1983; Carlquist, 1989), their role is thought to be minor in comparison with conduit size and density. Slight increases in the diameters of xylem conduits would lead to large increases in hydraulic conductance as hydraulic conductance is proportional to the fourth power of the radius according to Poiseuille's Law (Zimmermann, 1983). Conduit density is important as the conductances of individual conduits are additive. However, the effect of increased density is not nearly the same as increasing conduit diameters. The wider the conduits, the fewer the number that can fit into a specified area, so often narrow conduits go together with high conduit densities (Carlquist, 1989).

Conduit size distribution would play an important role in hydraulic conductance because it is not the mean conduit diameter that is important in calculating hydraulic conductance but the diameters of all the conduits. Wider conduits would have a larger role to play in hydraulic conductance as hydraulic conductance is dependent on the fourth power of the radius/diameter of the conduit.

Angiosperm vessels are made up of a series of vessel elements placed end to end. In terms of function, the total vessel length is thought to be a more important characteristic than vessel element length as it is in the movement of water from one vessel to another that a large resistance to flow, in the form of pit membranes, is encountered (Baas, 1983). Vessel length distribution is

said by Zimmermann and Jeje (1981) to be a fundamental

parameter in the hydraulic construction of long distance

transport channels of plants, with important implications

for physiology, pathology and other disciplines. It is for

this reason that vessel length distributions are also

taken into account in this study.

The xylem anatomy of the five species studied was not

viewed from the classical, descriptive wood anatomical

approach. Rather it was viewed as an adaptive feature

enabling a plant, or species, to cope successfully with

its environment. While very detailed anatomical work is

possible, this investigation looked only at a general

qualitative examination of the five species. However,

hydraulically important parameters such as xylem conduit

diameters and densities and distributions as well as

vessel length distributions (in the angiosperms) were

quantified.

MATERIALS AND METHOD

Wood anatomy

Cross sections of all five species were taken from fresh
twigs (all about 1 to 2 years old) using a sliding
microtome (a sledge microtome would have been preferrable
but was not available). The sectioning was carried out to
get a clean cut on a small stub of twig, not to use the
sectioned pieces. The twig stubs were then sputter coated
and viewed with a Jeol 520 scanning electron microscope.
Micrographs were taken.

The measurements of mean xylem conduit diameters, conduit
densities and conduit diameter distributions were done on
a single micrograph from each of 20 different twigs for
all five species. Means and standard deviations were
calculated for all values. A completely randomised ANOVA
and a Duncan's Multiple Range Test were performed to test
for significant differences between mean xylem conduit
diameters and conduit densities.

Vessel length distributions

The following procedures were only carried out on the four
angiosperm species as P. latifolius, being a gymnosperm,
has no vessels only tracheids. An attempt was made to
measure the tracheid lengths using the same procedure. It
was observed, however, that the tracheids were less than

1cm in length, thus this procedure was not suitable for measuring tracheid length distributions.

The method used for vessel length distribution was modified from Zimmermann and Jeje (1981). An inert, carmine pigment manufacured by Hoechst (brand-name Colanyl) was used instead of latex paint. The particles were filtered with Whatman no. 6 filter paper to remove particles larger than 3μm. A portion of this sample was then filtered through a Whatman GF-F glass fiber filter to collect the particles greater than 0.75μm. It was found that no particles passed through the GF-F filters and therefore the particles after filtration with Whatman no. 6 papers were all between 0.75μm and 3μm. These particles were small enough to enter the cut end of the xylem vessels but too large to pass through the bordered pits separating one vessel from another. Siau (1984) reported that the pores in pit membranes of dicotyledons range from about 0.005 to 0.17 μm in diameter depending on the species.

The twigs of T. capensis, C. camphora, T. dreqeana and B. racemosa were all cut early in the morning on cool, overcast days so that the plant would be under little water stress and this would reduce the formation of embolisms. The twigs were cut at their branch junctions so as to use their full lengths. The twigs were then flushed with degassed, de-ionised water at 200kPa for ten minutes. The technique of flushing, or the forcing of water through

the twig under high pressure, was developed by Sperry et al. (1988a) to remove any embolisms which may have formed naturally or when the twig was cut and transported.

After the removal of embolisms by flushing, the pigment suspension was allowed to flow through the twigs until flow stopped. A pressure head of 2m was used and the solution was fed to the twigs using thick-walled PVC tubing. This allowed the vessels to become packed with these coloured particles. This took up to 5 days in the case of B. racemosa. Figure 2.1 illustrates the apparatus designed to carry out this procedure. The paint filled twigs were then cut into 1cm portions and the excess paint was blotted away with filter paper. The number of paint filled vessels in each section was counted at 40 times magnification using a Zeiss dissecting microscope.

The vessel length distribution was calculated according to Zimmermann and Jeje's (1981) adaptation of the work done by Skene and Balodis (1968). The complete derivation of this formula is shown in Zimmermann and Jeje (1981). The number of paint-containing vessels was given the designation m, with the length of the stem at which they were counted as the subscript. For example, m_5 which would represent the number of paint-containing vessels at 5cm. The contribution of vessels to the cumulative total at a particular length class is calculated using the formula:

$$[(m_{x+2} - m_{x+1}) - (m_{x+1} - m_x)] * \text{no. of steps to zero} \quad \ldots \ldots \text{2.1.}$$

The number obtained from this formula is equal to the percentage of vessels that fall within the length class $\underline{x}$.

This method for calculating the vessel length distribution makes the assumption that vessels belonging to different length classes are randomly arranged in the stem. Thus where vessels belong to a particular length class a positive number would be obtained from the formula (2.1). Where there are no vessels belonging to a particular length class a zero should be obtained. If negative values are obtained it indicates that the vessels belonging to the different length classes are

 not randomly arranged in the stem.

Negative values were obtained for vessel length classes in this study. The negative values were subtracted from the exaggerated positive values of the preceding vessel length class to give a net value for the two classes. Six replications for each species were carried out and the mean and standard deviation was calculated for each length class.
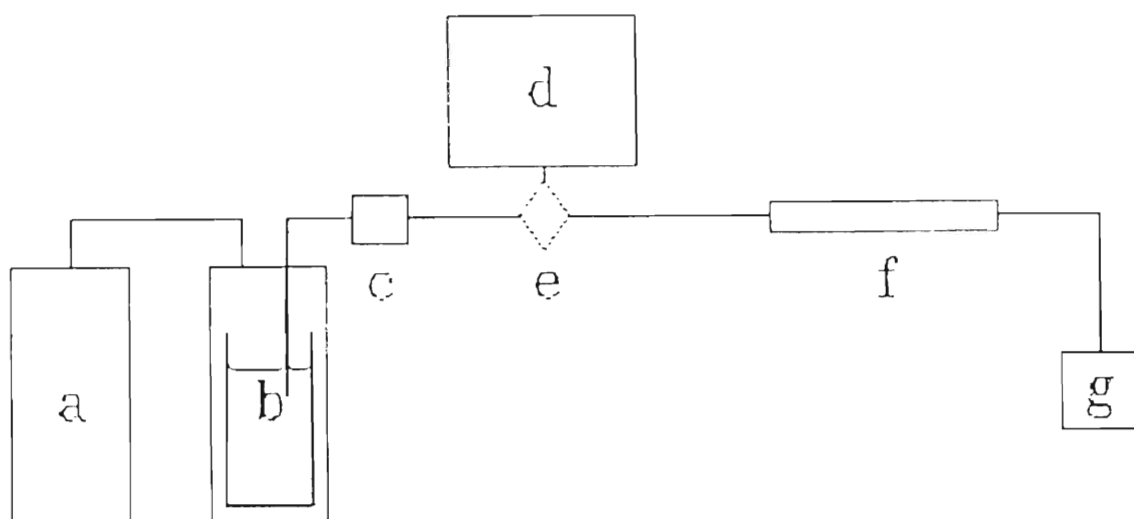
Figure 2.1: A diagramatic representation of the apparatus
used to measure vessel length distributions.
a = cylinder of compressed air used to "flush"
water through the twig; b = reservoir of de-
gassed de-ionised water; c = membrane filter
holder and membrane filter (0.22μm) used to
prevent micro-organisms or small particles
being flushed into the twig; d = reservoir of
pigment suspension; e = two-way stopcock;
f = twig; g = beaker to collect water dripping
out of the twig

RESULTS

Wood anatomy

Figures 2.2 - 2.6 show scanning electron micrographs of cross sections of the five species. The gymnosperm P. latifolius (Fig. 2.2) possesses only tracheids while the four angiosperms species (Figs. 2.3 - 2.6) possess vessels as well as tracheids. The xylem anatomy of the four angiosperm species can be described as being diffuse porous. The differences in sizes of the xylem conduits as well as in densities are visible from these micrographs.

Table 2.1: Mean xylem conduit diameters and conduit densities are presented in this table. Standard deviations are given in parentheses and n = 20 for all the means. The letters in superscript indicate values which are significantly different (Duncan's Multiple Range Test P $\leq$ 0.05).

Species	Mean Conduit Diameter (μm)	Density (conduits mm^{-2})
P. latifolius	7.32 (1.16) [a]	9087.4 (2060) [a]
T. capensis	12.66 (1.48) [b]	915.6 (176.3) [b]
C. camphora	19 47 (2.17) [c]	270.9 (68.78) [c]
T. dregeana	27.8 (3.13) [d]	160.4 (42.8) [c]
B. racemosa	30.13 (2.72) [e]	268.6 (75.7) [c]

Mean conduit diameters and densities, for all five species, are given in Table 2.1. P. latifolius, having only tracheids, has the narrowest conduits. Mean conduit

diameter then increases from the rocky, scrub species
T. capensis to C. camphora, the forest species, followed
by T. dregeana, the coastal forest species, and finally,
B. racemosa, the swamp forest species. These mean conduit
diameters were all significantly different from each other
at $P \leq 0.05$.

As conduit diameters increased, conduit densities
decreased. This is what would be expected as wider
conduits take up more space than their narrower
counterparts. However the relationship is not linear.
There was no significant difference in the vessel
densities of C. camphora, T. dregeana and B. racemosa even
though there was a significant difference in their conduit
sizes.

The conduit diameter distributions of the four angiosperm
species are given in Figure 2.7. The range of conduit
diameters for P. latifolius was very small, thus a plot of
its conduit diameter distribution was not carried out. The
distribution for C. camphora appeared to be normal with
that of T. capensis skewed slightly to the right. The
distribution of T. dregeana was skewed to the left, with
that of B. racemosa skewed to the right. There was quite a
large degree of variability in these results as shown by
the high standard deviations.

Vessel length distributions

Figure 2.8 shows the vessel length distributions for the four angiosperm species. There was considerable variability in the vessel length distributions shown by the relatively high standard deviations.

The majority of the vessels of T. capensis (69%) belonged to the shortest vessel class of 0 - 5cm. The longest vessel class was only 10 - 15cm. The vessel length distribution of T. capensis appeared to be exponential. C. camphora appeared to have four distinct vessel length classes possibly in a bimodal distribution (16% of the vessels belonged to the 0 - 5cm class; 39% to the 5 - 10cm class; 23% to the 10 - 15cm class and 18% to the 20 - 25cm class). A small percentage of vessels appeared to belong to the 15 - 20cm and 25 - 35cm classes.

T. dregeana had 45% of its vessels in the 0 - 5cm class and 22% in the 5 - 10cm class. Both the 10 - 15cm class and the 15 - 20cm class had over 10% of the vessels. A few vessels had lengths between 20cm and 30cm. As was the case with T. capensis the vessel length distribution appeared to be exponential. B. racemosa had the longest vessels with approximately 25% of its vessels between 30cm and 45cm long. The 0 - 5cm class contained only 16% of the vessels while 31% were between 10cm and 15cm and 29% were between 20cm and 25cm. There was also an absence of vessels in certain vessel length classes in B. racemosa.

The vessel length distribution of B. racemosa appeared to be irregular.

A number of negative values were obtained from the calculations using equation 2.1 with all four species. This indicated that the vessel length classes in all the four species were not randomly arranged throughout the stem.
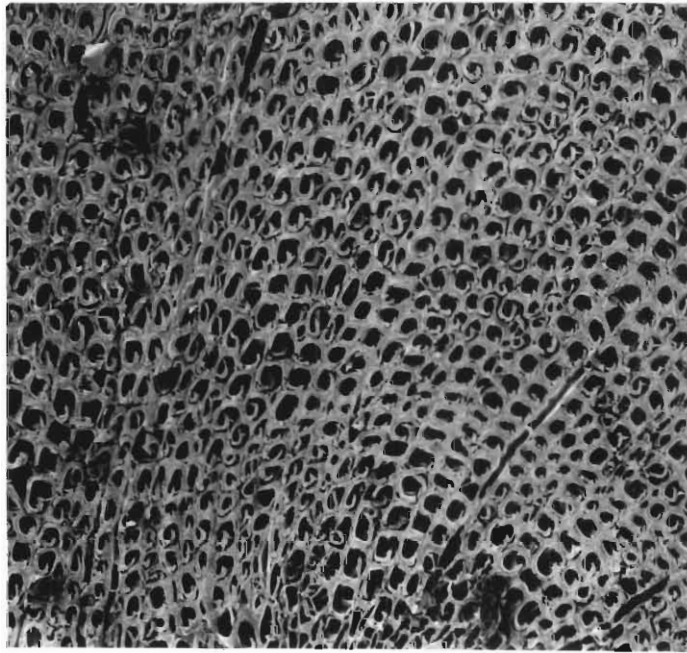
Figure 2.2: A micrograph of a cross-section of <u>Podocarpus</u>
    <u>latifolius</u>. There are no vessels present only
    tracheids (t). Mag. x 350
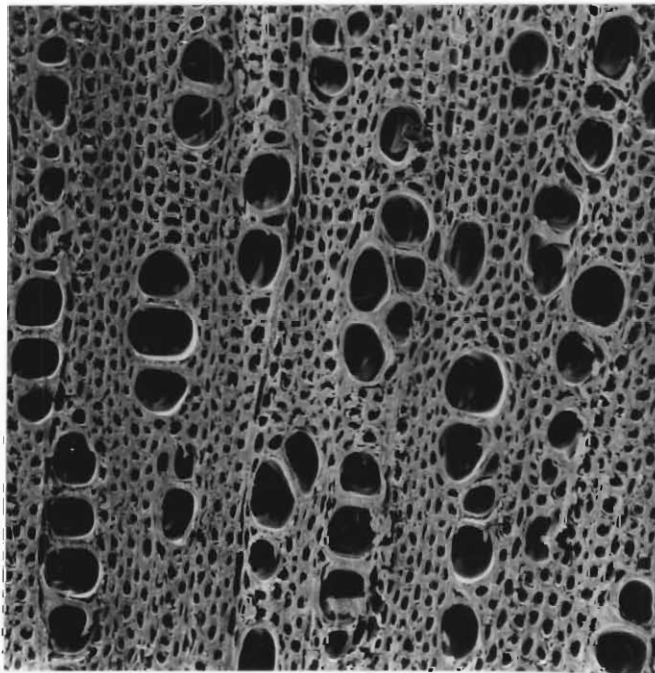
Figure 2.3: A micrograph of a cross-section of <u>Tecomaria</u>
    <u>capensis</u>. Vessels (v) are in a diffuse porous
    arrangement and are clustered in groups of 2
    or more. Mag x 350.
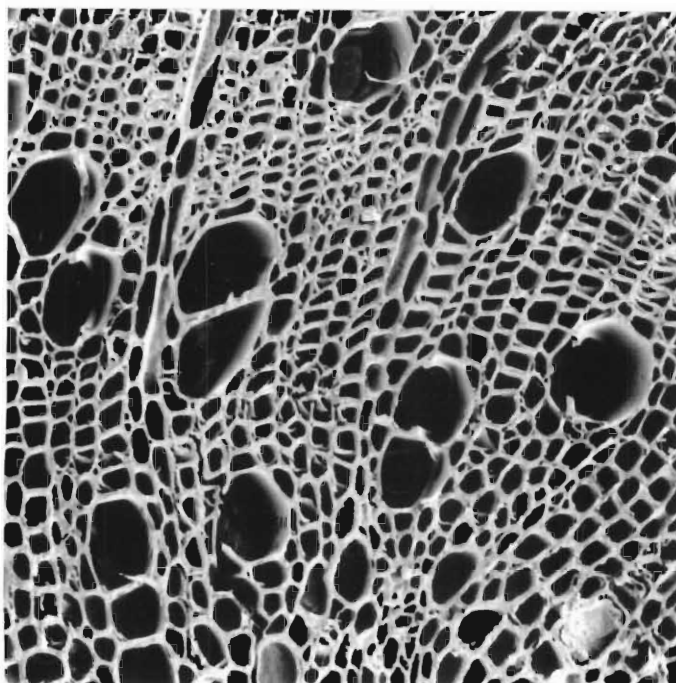
Figure 2.4: A micrograph of a cross-section of Cinnamomum camphora. The vessels (v) are solitary or clustered in twos or threes and have a diffuse porous arrangement. Mag x 350.
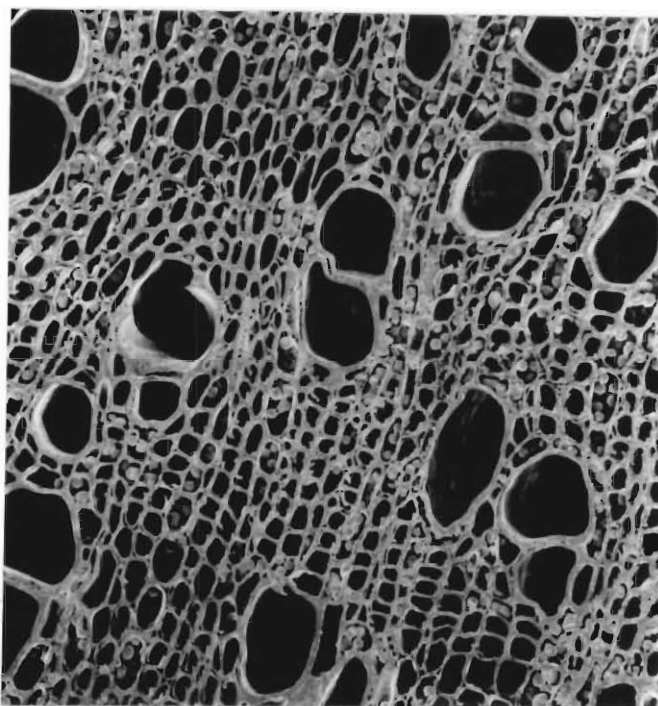
Figure 2.5: A micrograph of a cross-section of Trichilia dregeana. Vessels (v) are solitary or clustered in twos or threes and have a diffuse porous arrangement. Mag x 350.
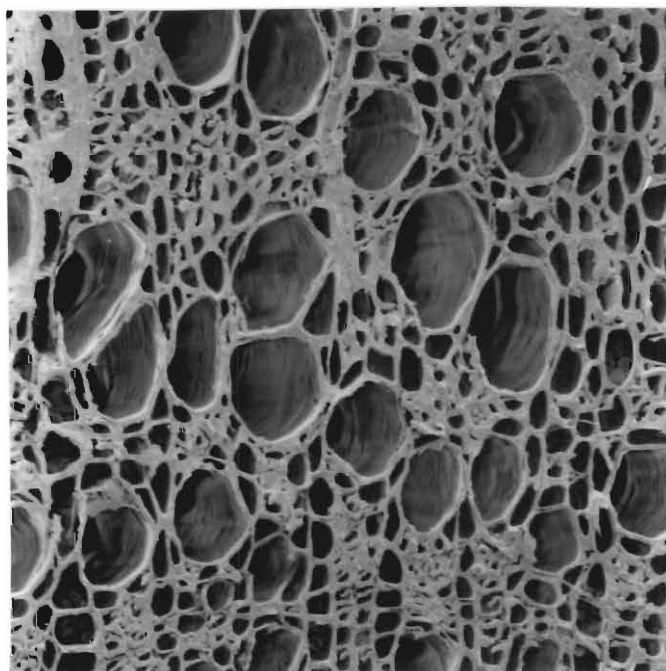
Figure 2.6: A micrograph of a cross-section of

Barringtonia racemosa. Vessels (v) are large

and densely packed. The vessel arrangement is

said to be diffuse porous. Mag x 350.

Tecomaria capensis

Cinnamomum camphora

Trichilia dregeana

Barringtonia racemosa
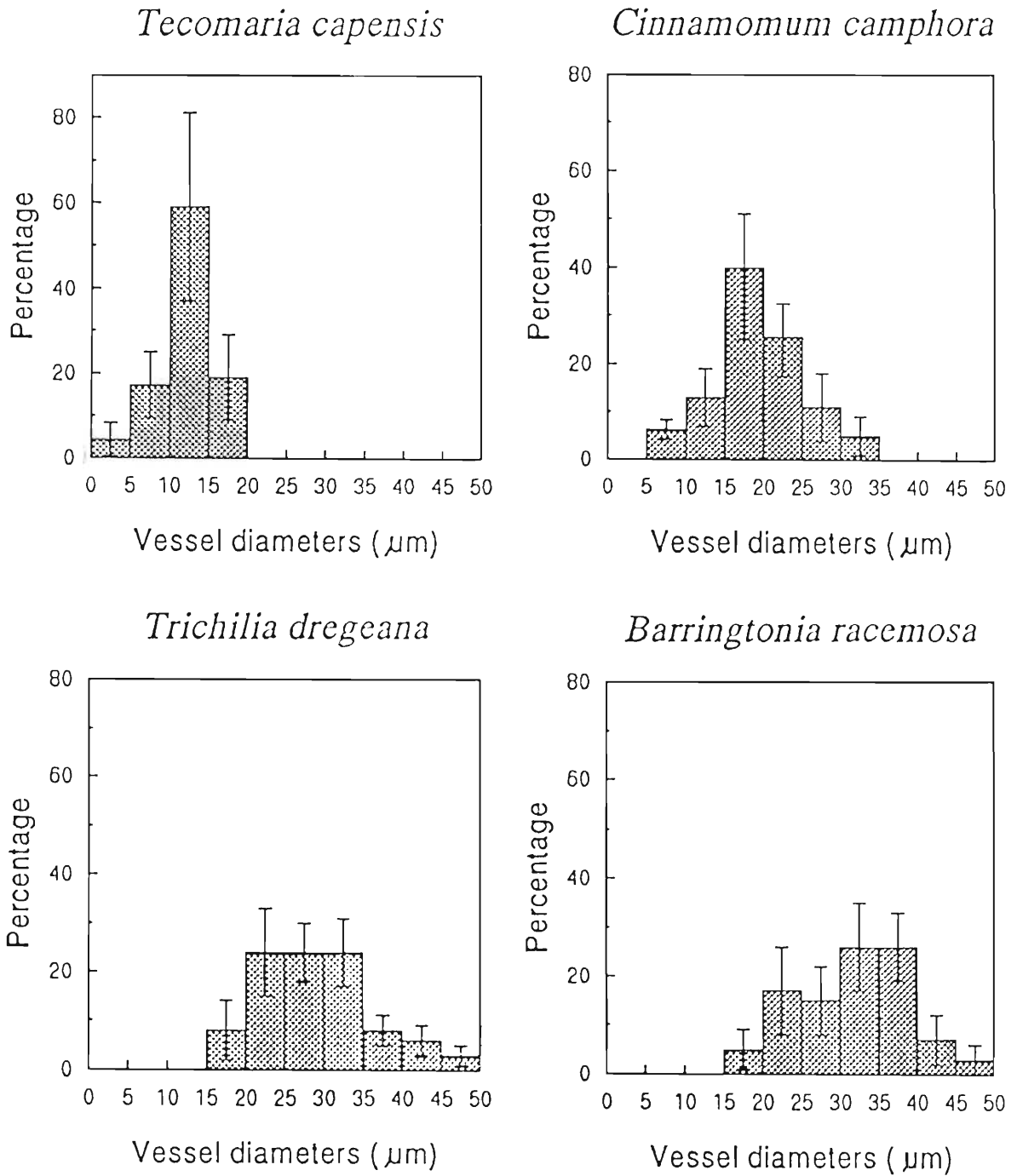
Figure 2.7: The distribution of vessel diameters in twigs of the four angiosperm species: T. capensis; C. camphora; T. dregeana and B. racemosa. The vertical lines indicate standard deviations, n = 10 for all four species.
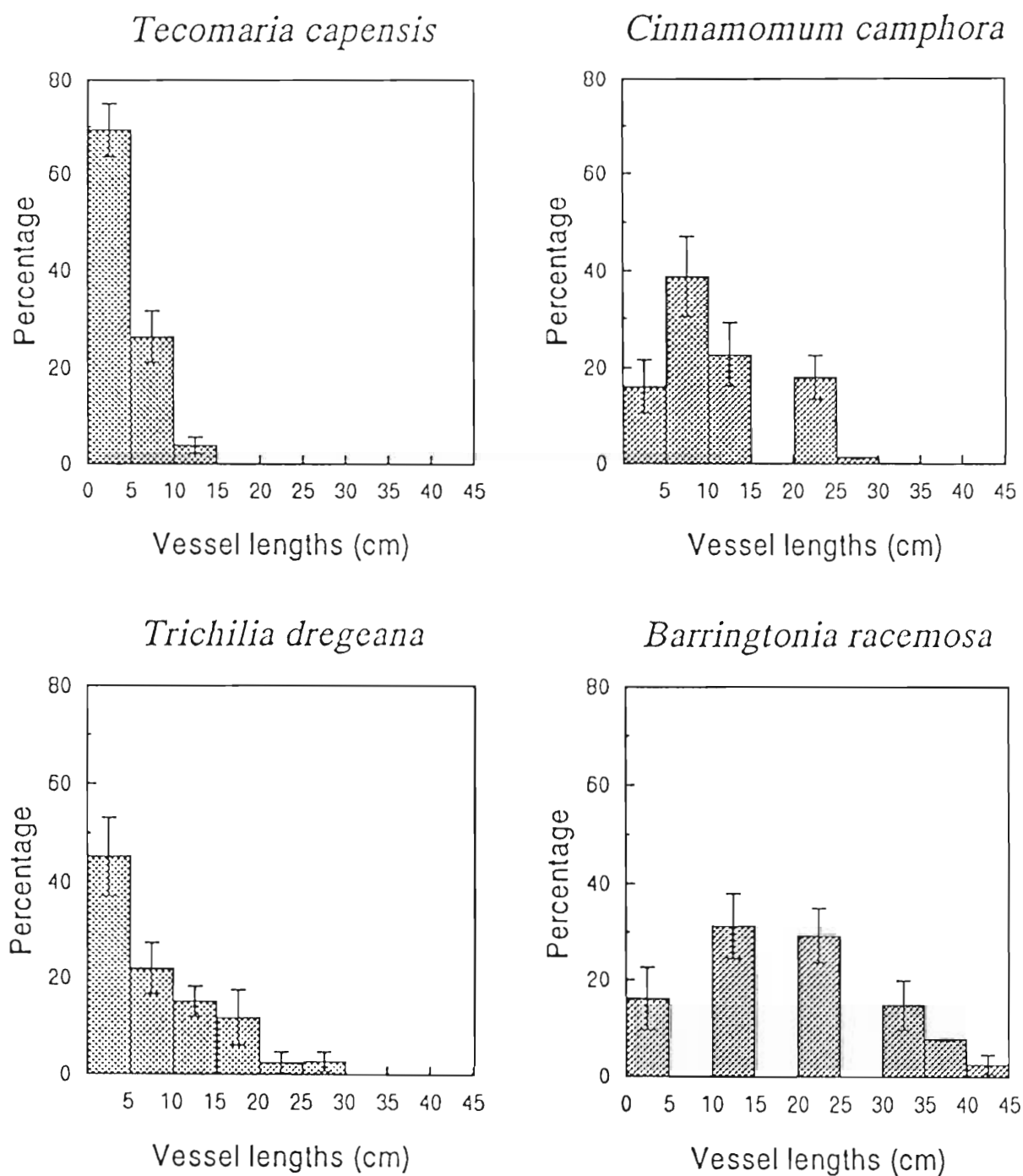
Figure 2.8: The distribution of vessel lengths in twigs of
the four angiosperm species: T. capensis;
C. camphora; T. dreaqeana and B. racemosa. The
vertical lines indicate standard deviations,
n = 6 for all four species.

DISCUSSION

P. latifolius, being a gymnosperm, has no vessels, only
tracheids. The tracheids of P. latifolius are narrower than
the vessels of the four angiosperms but their densities are
very high. This forest species is relatively slow growing
compared to species like B. racemosa. The xylem anatomy of
P. latifolius has, what is traditionally thought to be, a very
"safe" design having many narrow conducting elements. The
design, however, is not thought to be that efficient due to
the narrow diameters of the tracheids. Tyree and Dixon (1986)
however, have found that under water stress, vessel bearing
wood retained water far better than tracheid bearing wood, so
the tracheids may not be safer than vessels even though they
are much narrower.

The bush, T. capensis, possesses vessels, but the diameter of
these vessels are less than twice the diameter of the
tracheids of P. latifolius. The conduit density of
T. capensis, however, is not as high as that of P. latifolius
but is significantly higher than that of the other three
angiosperms (Table 2.1). Zimmerman (1982) suggests that high
vessel density confers safety by virtue of redundancy. The
natural habitat of T. capensis is rocky outcrops or scrub.
This could perhaps explain why it has a large number of narrow
vessels, a xylem anatomy often characterising plants of drier
habitats (Baas, 1983; Baas et al., 1983).

C. camphora has narrower vessels than T. dregeana and

B. racemosa. There is no significant difference in the vessel densities among these three species. T. dregeana, a slow growing coastal forest species, has relatively wide vessel diameters but a low vessel density. The swamp forest species B. racemosa has the widest vessels of the four angiosperm species and a relatively high vessel density. This xylem anatomy should lead to efficient water conduction probably at the expense of safety. However, this probably would not be important for B. racemosa, as water supply is unlikely to be limiting in its natural habitat of swamp forests and stream beds.

The tracheid diameters of P. latifolius compared favourably with other gymnosperm species reported in the literature (Ewers, 1985; Ewers & Zimmermann, 1984a; 1984b; Schulte & Gibson, 1988). None of these workers, however, reported on tracheid densities. The tracheid density for P. latifolius was very high relative to the angiosperms, particularly to T. capensis where the conduit diameters were not very different. It is possible, however, that there could be a great deal of redundancy in these tracheids and thus not all of them would be used for water transport. This redundancy will also result in increased safety for the plant.

In comparing the vessel diameters and densities of the four angiosperm species to those reported by other workers (Baas, 1983; Carlquist, 1989; Gartner et al., 1990; van Wyk, Robbertse & Kok, 1983) it was found that the conduit diameters were quite narrow and the densities very high. Carlquist

(1989) reported that the mean vessel diameter for dicotyledons as a whole is 94μm and the mean vessel density is 31 vessels per mm^2. The conduit diameters of the four species in this study ranged between 12μm and 30μm and densities from 160 conduits mm^{-2} to 915 conduits mm^{-2}. It is known, however, that conduit diameter decreases from the centre and the top of the tree to the side branches (Ewers & Zimmermann, 1984a; 1984b). As these measurements were taken on side branch twigs, this may explain this discrepancy. The high densities were possible because of the narrowness of the vessels. Vessels from the early wood of ring-porous species are also known to be wider than those of diffuse porous species (Zimmermann & Brown, 1971). As the four species used in this study were diffuse porous it is not surprising to find that their vessel diameters were narrower than those of many angiosperms.

The conduit diameter distributions shown in this study were not as irregular as those reported by Ewers and Fisher (1989). However, there were not nearly as many vessel diameter classes present in the four species used in this study as there were in Ewers and Fisher's (1989) study. This may be due to the fact that T. capensis, C. camphora, T. dregeana and B. racemosa are diffuse porous species and therefore do not have the large range of vessel diameters found in the early and late-wood of ring-porous species.

The results obtained for vessel length distribution compared favourably with those obtained by Baas (1983); Ewers and Fisher (1989); Zimmermann (1983) and Zimmermann and Jeje

(1981) who also found that a large portion of the vessels were less than 10cm long in a range of species. Other species, such as <u>Quercus</u> <u>robur</u> however, have earlywood vessels greater than 1m in length (Zimmermann, 1983).

<u>B.</u> <u>racemosa</u>, as well as having the largest vessels, also has the longest vessels. This relationship between the largest and longest vessels has been reported in Baas (1983). The longer the vessels are, the less resistance presumably is imposed on water flow by vessel-to-vessel connections (Baas, 1983; Zimmermann & Jeje, 1981). Longer vessels are also thought to make the plant more vulnerable to catastrophic embolisms. If an embolism develops in a long vessel it will affect a larger portion of the xylem pathway than if it was contained in a short vessel (Baas <u>et</u> <u>al.</u>, 1983; Ewers & Fisher, 1989; Zimmermann & Jeje, 1981).

<u>B.</u> <u>racemosa</u> then appears to be ideally adapted to its swamp forest and stream bed habitat as it has a very efficient xylem anatomy (numerous large, long vessels) but little with respect to safety features. It would not need these safety features due to its wet habitat. Safety features would possibly impede the ability of <u>B.</u> <u>racemosa</u> to conduct water and thus impair its competitive ability in its natural environment.

<u>T.</u> <u>dregeana</u>, while having relatively wide vessels does not have very long vessels. This would impart a degree of safety to it in its coastal forest environment which can be subject to dry periods. <u>C.</u> <u>camphora</u>, on the other hand, has narrower

vessels but they are longer than those of T. dregeana. The
narrower vessels may provide a limited degree of safety during
dryer periods.

T. capensis has almost the opposite xylem anatomy to
B. racemosa. T. capensis has a very high density of narrow
vessels. This xylem anatomy would impart a high degree of
safety to the plant but would be far less efficient in
conducting water than is the case with B. racemosa. The
natural habitat of T. capensis, rocky outcrops and scrub,
would require it to have a high degree of safety as it would
be subject to dry, harsh conditions.

The differences in xylem anatomy have been discussed in
respect to the plant's natural habitat. However, these five
plant species were all growing under the same conditions where
water supply was not limiting. Thus the differences are likely
to be due to phylogenetic differences and not environmental
differences. It is not known what differences, if any, would
occur in the xylem anatomy of these five species in their
natural environment. While many of the diagnostic features of
xylem anatomy are thought to be species specific, features
such as conduit diameters and densities are known to change
under different environmental conditions (Baas, 1983). The
xylem anatomies of the five species discussed here are very
different even though they are growing under the same
conditions. There thus appears to be a high degree of
phylogenetic control over the xylem anatomy of the five plant
species discussed.

CHAPTER 3: HYDRAULIC PROPERTIES

INTRODUCTION

The hydraulic conductance of the xylem is an important physical characteristic in determining the rate of water movement in plants (Zimmermann, 1983; Calkin, Gibson & Nobel, 1986). Hydraulic conductance (measured in this study as kg m $MPa^{-1}s^{-1}$) is typically measured on excised twigs or branches which are attached to a hydraulic system. The mass flow of water through the twig is measured while a pressure gradient is applied across it (Sperry et al., 1988a). The initial segment cut from the plant must be long enough so that few, if any, conduits at the cut end extend through to the other cut end as this will decrease the resistance to flow and give a falsely high reading (Zimmermann, 1978; Ewers, 1985).

It is probable that the excised twigs contain embolisms and the values obtained for the measurement of hydraulic conductivity depend on the degree of embolism. Sperry et al. (1988a) devised a method for removing embolisms from excised twigs. This technique involved forcing water, which was under pressure, through the twig to remove the embolisms. This was referred to as "flushing". One can acquire information on the degree of embolism in a twig by comparing the measurements of hydraulic conductance before and after flushing.

Hydraulic conductivity ($kg\ m^{-1}MPa^{-1}s^{-1}$) is a measure of the hydraulic conductance per unit area. The area could be the twig cross-sectional area or the cross-sectional xylem area in the twig used for the measurements. These measurements would be referred to as the twig specific conductivity (TSC) and xylem specific conductivity (XSC). Hydraulic conductivity can also be measured in terms of leaf area supplied by the twig to give leaf specific conductivity (LSC). LSC is the most meaningful measure of hydraulic conductivity with respect to leaf physiology as it gives an indication of the potential for water supply per unit area of leaf.

Hydraulic conductance (K_h) can also be predicted by measuring the size of all the conduits and using the Hagen-Poiseuille equation (equation 1.2) which relates the number of conduits as well as their diameters to hydraulic conductance (Zimmermann, 1983; Ewers et al., 1989). It is of interest to compare how close the measured value for hydraulic conductance is to the predicted, calculated value. The calculated K_h does not take into account vessel endings and other resistances caused by perforation plates and wall thickenings (Zimmermann & Brown, 1971). It treats the xylem conduits as ideal capillaries, which they are not. Other workers have found that the measured values range from about 10 to 100% of the theoretical values derived using the Poiseuille equation (Ellmore & Ewers, 1985; Ewers & Fisher, 1989; Ewers et al., 1989; Petty, 1978; Schulte & Gibson, 1988; Zimmermann & Brown, 1971).

Petty (1978) used the mean minimum and maximum conduit diameters to predict K_h according to equation 1.2. It is not clear, from the literature, whether some of the workers cited in Petty (1978) and Zimmermann and Brown (1971) used the conduit diameter distributions or just the mean conduit diameters to calculate K_h. Workers such as Ellmore and Ewers (1985); Ewers and Fisher (1989); Ewers et al., (1989) and Schulte and Gibson (1988) used conduit diameter distributions in their calculations. As conductance is related to the fourth power of the conduit diameter, conduit diameter distributions are important as a single wide conduit will influence K_h far more than a few narrow conduits. A modelling exercise was performed to ascertain the importance of conduit diameter distributions in calculations of conductance.

A resistance to liquid flow is caused by vessel endings as the water has to cross the narrow pit membranes (Zimmermann, 1983). The hydraulic conductance can be measured on excised twigs of varying length in an attempt to assess how much this resistance affects the hydraulic conductance. No reports of such measurements have been found in the literature. These measures should correlate with the measures of vessel length distribution (refer Chap. 2).

Huber (1928 loc. cit. Ewers & Zimmermann, 1984) devised a ratio (the Huber value) which is the xylem transverse

sectional area divided by the weight of leaves supported. In this study the leaf area supported by the xylem was used, not the leaf weight. Leaf areas were chosen for the measurement of the Huber value as well as the LSC, because they were thought to be a more meaningful measurement, as far as water transport is concerned, than leaf weights (Ewers & Zimmermann, 1984a; 1984b). Huber values reflect not only the mechanical properties of the stem but also the resource allocation by the plant, i.e. how much wood is produced per unit leaf area supplied (Ewers, 1985). The Huber value is closely related to the leaf specific conductivity (LSC).

By definition:

LSC = Huber value x specific conductivity 3.1

(Ewers & Zimmermann, 1984a; 1984b). The specific conductivity referred to in this case is xylem specific conductivity. Leaf weights, not areas, were used by Ewers and Zimmermann (1984a; 1984b) in their studies.

The aim of this part of the study was to examine the hydraulic properties of the five species and to relate these to the anatomical characteristics presented in Chapter 2.

AIM

MATERIALS AND METHOD

Hydraulic conductance measurements

The method used in this study for measuring hydraulic
conductance on excised twigs was modified from the method
of Sperry et al. (1988a). The apparatus used was similar
to that shown in Fig. 2.1, except that a degassed, de-
ionised, 0.05% formaldehyde solution replaced the colanyl
suspension and a reservoir of Safranin dye was added to
the system.

The water used for the measurement of hydraulic
conductance was degassed to prevent the formation of air
bubbles and the possible reformation of embolisms after
flushing. Air bubbles could form becasue during flushing
the water is pressurised and when that pressure is
suddenly released as flushing stops, air bubbles are in
danger of being formed as the air comes out of solution.
The water used for flushing was passed through a membrane
filter (0.22μm) to prevent particulate matter being forced
into the open conduits and thus causing blockages.

A 0.05% solution of formaldehyde was used to prevent long
term decline in conductance. Sperry et al. (1988a) found
that perfusing the stems with a 0.05% formaldehyde
solution prevented long term decline in conductance by
arresting microbial development in the stem.

Water used to determine the rate of water flow through the twig was stored in the reservoir. The reservoir was of adjustable height. This allowed different pressure gradients to be applied to the twig. Lower pressure gradients were needed if the rate of flow was too fast to take accurate measurements. The water used to flush was placed in a beaker in a pressure bomb. The water from the reservoir and the pressure bomb was transported to the twig in PVC tubing. A reservoir of Safranin, used for staining the walls of the xylem conduits, was also connected to the twig with PVC tubing. Access of the water and Safranin from all these sources was controlled using screw clamps.

The twig was connected to the water supplies with thick walled, high density PVC or rubber tubing of varying diameters. It was important to ensure that no air was trapped in the tubing as it could be forced into the cut surface of the twig and result in an embolism. The far side of the twig was connected to a glass tube via pvc or rubber tubing. Water dripping from the glass tube was collected in a beaker which was placed on a balance.

Twigs were all cut on cool overcast days to prevent them being very water-stressed and thus more likely to have formed embolisms. The twigs were all cut longer than their longest vessel in the case of the angiosperms and about 15cm long in the case of the gymnosperm P. latifolius. The twigs were quickly placed in plastic bags to prevent the

loss of water from their leaves. They were then transferred to the laboratory and put in a bucket of water where both ends of the twig were re-cut under water. Before taking measurements on a twig, thin slivers of wood were sliced off the cut ends with a very sharp knife to remove any loose or damaged tissue which may block the open ends of the conduits.

The rate of water flow, under gravity, from the water reservoir was measured for 5 minutes. This was done by measuring the weight of water on the balance every 30 seconds. The twigs were then flushed, using a pressure of 200kPa, for 5 minutes to remove any embolisms. The rate of water flow from the reservoir was again measured. This procedure was repeated until the rate of water flow under gravity did not increase following pressure flushing. This was taken to be the maximum rate of water transport for that twig. Safranin was then passed through the twigs under the same pressure as the water during the conductance measurements. From this the area of active xylem could be determined. The length of the twig as well as the cross sectional area of the narrowest portion of the twig were also measured.

Hydraulic conductance K_h was calculated using the formula:

$$K_h = \frac{\text{rate of flow} * \text{twig length}}{\text{pressure head}} \quad \ldots\ldots\ldots\ldots\ldots\ldots 3.2$$

where the rate of flow is measured in kg s^{-1}; twig length in meters and the pressure head in MPa. K_h is thus

measured in the units of kg m $MPa^{-1}s^{-1}$

Hydraulic conductivity (units = kg $m^{-1}MPa^{-1}s^{-1}$) was calculated by dividing hydraulic conductance by the cross-sectional area of the twig, twig specific conductivity (TSC), or the area of stained xylem, xylem specific conductivity (XSC), or the leaf area supplied by the twig, leaf specific conductivity (LSC).

The measurements of hydraulic conductance, TSC, XSC and LSC were taken on a number of twigs for all five species. The data was analysed using an ANOVA and Duncan's multiple range test to determine significant differences between the species.

Huber values

The original Huber value was calculated by dividing the area of xylem tissue by the weight of leaves that xylem tissue supplied (Zimmermann, 1983). In this study the xylem area was divided by the leaf area. This was done because the measurements of LSC, which is closely related to the Huber value (refer to equation 3.1), were done using leaf areas and not leaf weights.

Hydraulic conductance versus twig length

To try to determine what effect vessel endings were having on the hydraulic conductance of the twig, twigs were cut

at their branch juncture. These twigs were then flushed to remove any embolisms. Hydraulic conductance was measured on these long twigs. The twigs were then cut back, from the distal end, by a few centimeters and hydraulic conductance measured again. This procedure was repeated until the twigs were only around 2cm long. This gave measures of hyraulic conductance and conductivity versus twig length. These data were compared to the vessel length distributions obtained during the anatomical studies.

Measured K_h versus calculated K_h

A small segment of each twig used to measure hydraulic conductance was sectioned and viewed with a Jeol 520 scanning electron microscope. Micrographs were taken and the conduit diameters, their distribution and their densities were measured on five different, representative portions of the twig. This was repeated on ten different twigs for each species. The conduit size distibutions were assumed to be the same throughout the twig and therefore the number of conduits of different sizes could be calculated.

From these anatomical measurements K_h was calculated using the Hagen-Poiseuille equation (equation 1.2). The units were converted from $m^4 MPa^{-1} s^{-1}$ to those which were used in the measurements on excised twigs (kg m $MPa^{-1} s^{-1}$) assuming the density of water to be 1000 kg m^{-3}. The value for the dynamic viscosity of water was taken as 0.001MPa s

(Machlup, 1988). The calculated conductances were then compared with the measured conductances taken on the same twigs from which the anatomical data were taken.

Conduit diameter distibution modelling

In an attempt to ascertain what effect conduit size distribution had on the determination of theoretical conductances, data sets were generated which fitted into a normal, exponential, uniform and left-skewed (gamma) distribution. All these data sets had a numerical mean of 20 and had 100 individual values. These data sets were generated using a computer program written by Murray (Dept. of Mathematical Statistics, University of Natal, Durban, 4001, South Africa).

Values for K_h were calculated using the Hagen-Poiseuille equation using the mean value (20) and the total number (100). Further values were calculated for K_h which took into account the individual values. This modelling exercise should show how different diameter distributions affected the calculated K_h. It would also show the error in using just the mean value, as one wide conduit would have a greater effect on hydraulic conductance than would a number of narrower conduits.

RESULTS

Hydraulic conductance measurements

Figure 3.1 shows the results of the hydraulic conductance
and hydraulic conductivity measurements taken on excised
twigs. Figure 3.1(a) shows that B. racemosa has the
highest hydraulic conductance (K_h) and P. latifolius the
lowest. Trends in K_h appear to be similar to the trends
observed in the measurements of conduit diameters as shown
in Table 2.1. This is not surprising as K_h is supposed to
be related to the fourth power of the conduit diameter.
Given this relationship, it is surprising to find that
C. camphora is not significantly different from
T. dregeana.

The different measures of conductivity, however, do not
follow such clear trends. When the conductance is divided
by twig area to give twig specific conductivity (TSC),
shown in Figure 3.1(b), the differences among the
angiosperm species are reduced. B. racemosa still had the
highest value and P. latifolius still has the lowest, but
there is no significant difference between T. dregeana and
B. racemosa as there was with the measurement of hydraulic
conductance. Differences in trends between TSC and XSC
would give an indication as to what proportion of the twig
cross-sectional area is occupied by functional xylem.

The results for xylem specific conductivity (XSC) shown in

Figure 3.1(c), show similar trends to those of twig specific conductivity. P. latifolius is statistically different from the four angiosperm species and T. capensis and C. camphora are not significantly different from each other but are significantly different from T. dregeana and B. racemosa which are similar.

The results for leaf specific conductivity (LSC), shown in Figure 3.1(d), are very interesting. T. dregeana and P. latifolius are not significantly different from each other, but are significantly different from T. capensis, C. camphora and B. racemosa which are similar. The trends shown in K_h (Fig. 3.1(a)), TSC (Fig. 3.1(b)) and XSC (Fig. 3.1(c)) are not evident in Figure 3.1(d) at all. While there was a large difference in K_h between P. latifolius and T. dregeana, the twigs of T. dregeana supplied a far greater leaf area than those of P. latifolius. The twigs of B. racemosa also supplied far greater leaf areas than did those of T. capensis and C. camphora.

Table 3.1 shows how flushing affected the measured K_h. Flushing is thought to remove any embolisms in the conduits and thus after flushing the measured K_h of the five species increased. The difference between the initial measure of K_h and the maximum K_h is an indication of the degree to which the twigs were embolised. While care was taken to prevent embolism formation in the cutting and transfer of the twigs to the laboratory some embolism formation is inevitable, thus this is not an accurate

measure of the degree of embolism formation.

Table 3.1: Differences in hydraulic conductance (K_h),
measured in kg m MPa^{-1}s^{-1}, before and after
flushing for a twig of each of the five
species. The maximum K_h was obtained by
flushing the twigs for periods of 5 minutes
until a consistant K_h was obtained. These twigs
were all cut on the same day within minutes of
each other.

Species	Initial K_h	Maximum K_h
P. latifolius	1.16E-06	1.56E-06
T. capensis	1.23E-05	2.2E-05
C. camphora	8.45E-06	2.31E-05
T. dregeana	2.67E-05	3.5E-05
B. racemosa	2.37E-05	4.3E-05

As can be seen from Table 3.1, there appears to be a great
deal of embolism formation in C. camphora, T. capensis and
B. racemosa. This is indicated by the fact that the
maximum K_h values are substantially higher than the
initial values for K_h. The degree of embolism formation is
less in P. latifolius and T. dregeana.

Huber values

The results displayed in Figure 3.2 show the xylem areas
per unit leaf area. This is an indication of the Huber
value, which was originally calculated using leaf weight
not area. The Huber value is an indication of how much
xylem a plant has per unit area or mass of leaf it

supports. P. latifolius the gymnosperm is significantly different from the four angiosperm species. From Figure 3.2 it can be seen that a larger amount of xylem is needed to support the leaf area of P. latifolius than that of the angiosperms. B. racemosa and C. camphora have the lowest xylem area per unit leaf area, this indicates a large leaf area supported by the xylem. T. capensis and T. dregeana, on the other hand, produce more wood per leaf supplied than the other two angiosperms.

Hydraulic conductance versus twig length

Figure 3.3 shows how hydraulic conductivity changes with the length of the twig for the four angiosperm species. The measure of conductivity used in these graphs is XSC. XSC was used as it was felt that this was the most relevant measure of hydraulic conductivity when xylem characteristics are being studied. There was considerable variation in the absolute values of XSC so the data were normalised to the value obtained for the longest twig to reduce this variation.

There appears to be little change of XSC over a wide range of twig lengths, until a certain point is reached where there is a sudden sharp increase in XSC. It is thought that this point would correspond with the point at which all or most of the vessels are open at both ends. There should be a correlation between this point and the vessel length distributions.

Table 3.2 shows a comparison of the twig length at which relative XSC increases sharply and the mode value of the vessel length distributions for the four angiosperm species. There appears to be a good correlation between these two values for all four species.

Table 3.2: A comparison of twig length at which relative XSC increases and the mode of the vessel length distributions obtained in Chapter 2.

Species	Twig length at which relative XSC increases	Mode of vessel length distribtuion
T. capensis	6 cm	< 5 cm
C. camphora	10 cm	5 - 10 cm
T. dregeana	10 cm	< 5 cm
B. racemosa	14 cm	10 - 15 cm

Measured K_h versus calculated K_h

Table 3.3 shows a comparison between values of K_h measured on excised twigs and values of K_h which were calculated using the conduit diameters and their distributions according to the Hagen-Poiseuille equation (2.2). There was a great deal of variation of these measurements within a species. The average values are indicated in Table 3.3. Measured K_h values ranged between 40% to 87% of the calculated K_h values for the five species.

Table 3.3: Comparisons between the calculated hydraulic conductance (K_h) using the Hagen-Poiseuille equation and the K_h measured on excised twigs in the laboratory. The percentage given is the average of 10 different measurements. It indicates how close the measured hydraulic conductance was to the predicted conductance.

Species	Measured K_h as a percentage of the calculated K_h
P. latifolius	40%
T. capensis	87%
C. camphora	43%
T. dregeana	73%
B. racemosa	64%

The measured hydraulic conductance for T. capensis was the closest to the predicted hydraulic conductance.

T. dregeana and B. racemosa also showed fairly high correlation between their calculated and measured K_h values. P. latifolius and C. camphora showed the greatest difference between their calculated and measured values.

Conduit diameter distibution modelling

Figure 3.4 shows the distributions of the four data sets that were used: a) normal; b) exponential; c) gamma (skewed to the left) and d) uniform. Table 3.4 shows the theoretical values which were obtained for K_h using the mean value for conduit size as well as the value for K_h obtained using the conduit size distribution which takes the size of every single conduit into account.

Table 3.4: The comparison of the theoretical hydraulic conductances (K_h), measured in kg m MPa^{-1}s^{-1}, calculated using just the density and the mean values and using the distribution, i.e. taking into account the size of every single conduit. The ratio of the K_h calculated using the mean (M) and the K_h calculated using the distribution (D) is also shown.

Type dist.	K_h using mean (M)	K_h using dist. (D)	Ratio M:D
Normal	3.93 E-16	4.18 E-16	0.94
Exponential	3.93 E-16	8.68 E-15	0.04
Gamma	3.93 E-16	1.38 E-15	0.28
Uniform	3.93 E-16	3.34 E-16	1.17

For the exponential, gamma and normal distribution the theoretical K_h was lower if one calculated it using the mean value as opposed to taking every single value into account, while in the case of the uniform distribution the K_h obtained using the mean value was higher than the K_h obtained when using all the values. The greatest difference between the two values was found with an exponential distribution, followed by the gamma distribution. The conductance of the normal distribution was the closest to the conductance calculated when using the mean.
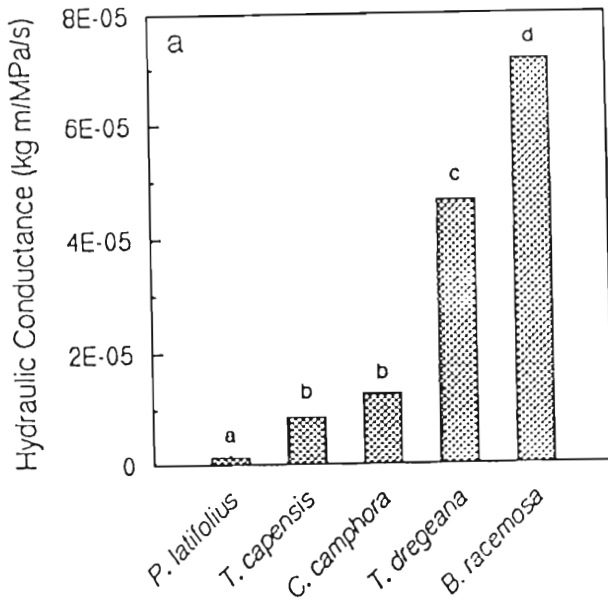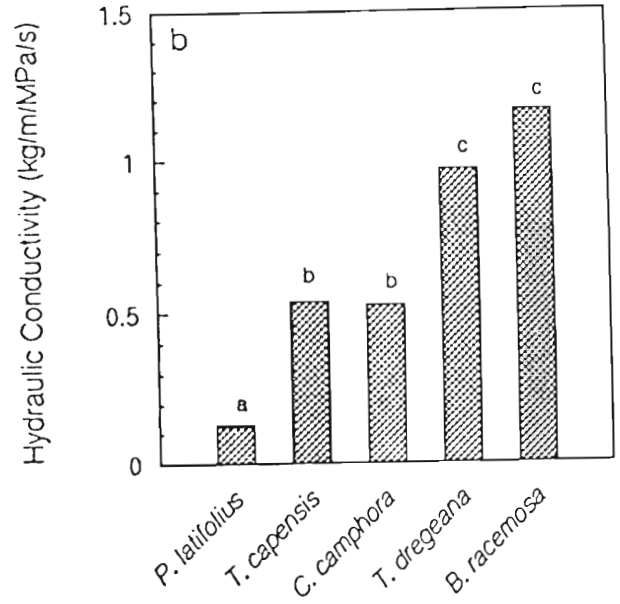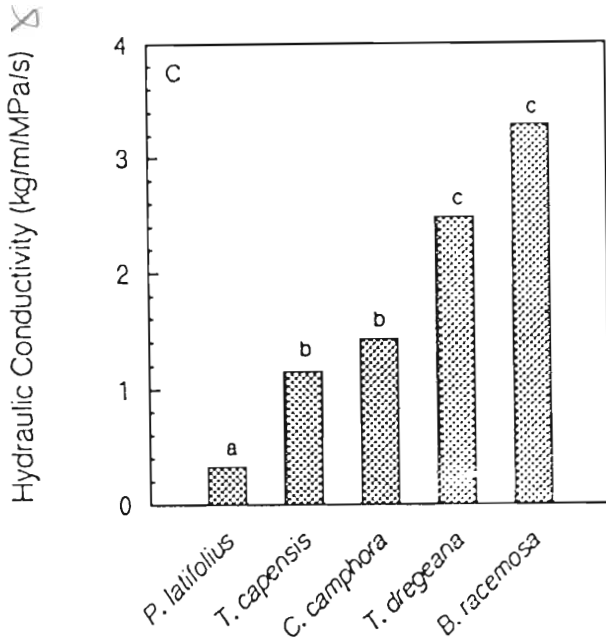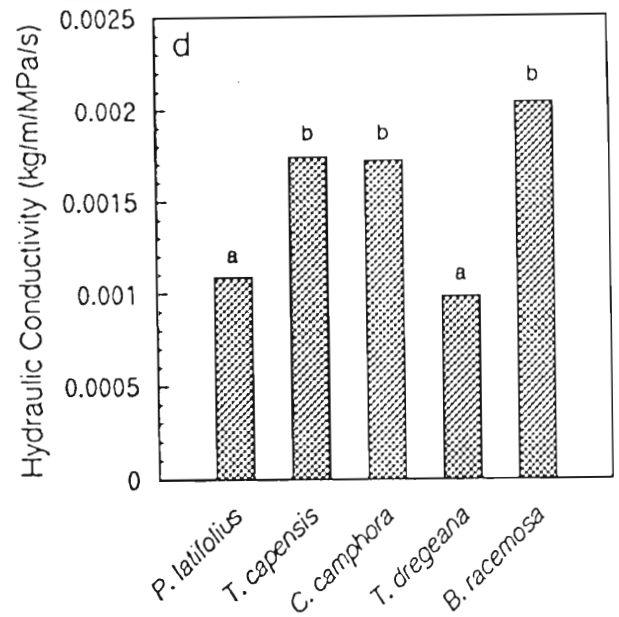
Figure 3.1: The hydraulic properties for the five species studied: a) Hydraulic conductance; b) twig specific conductivity; c) xylem specific conductivity and d) leaf specific conductivity. Values with different letters above the bars are significantly different (Duncan's multiple range test, P ≤ 0.05), n = 10 for all species.
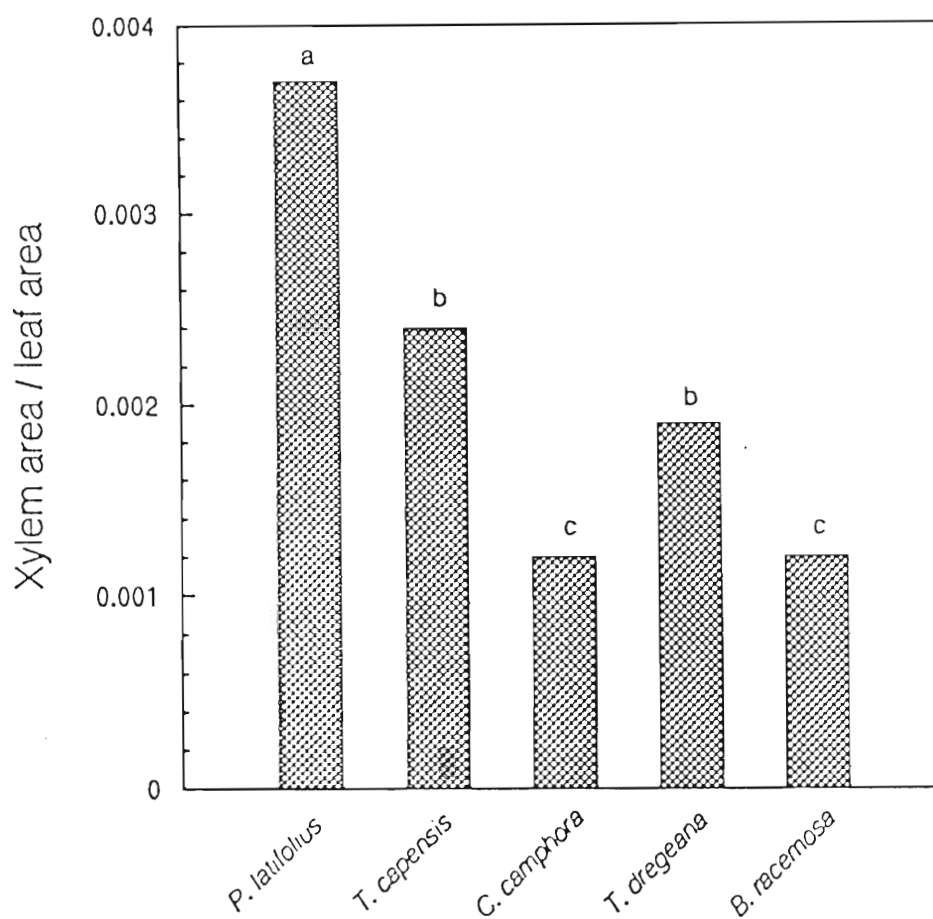
Figure 3.2: The ratio of xylem area to leaf area for the
five species studied. This value is an
indication of the Huber value. Values with
different letters above the bars are
significantly different (Duncan's multiple
range test, $P \leq 0.05$), n = 20 for all five
species.

Tecomaria capensis

Cinnamomum camphora

Trichilia dregeana

Barringtonia racemosa
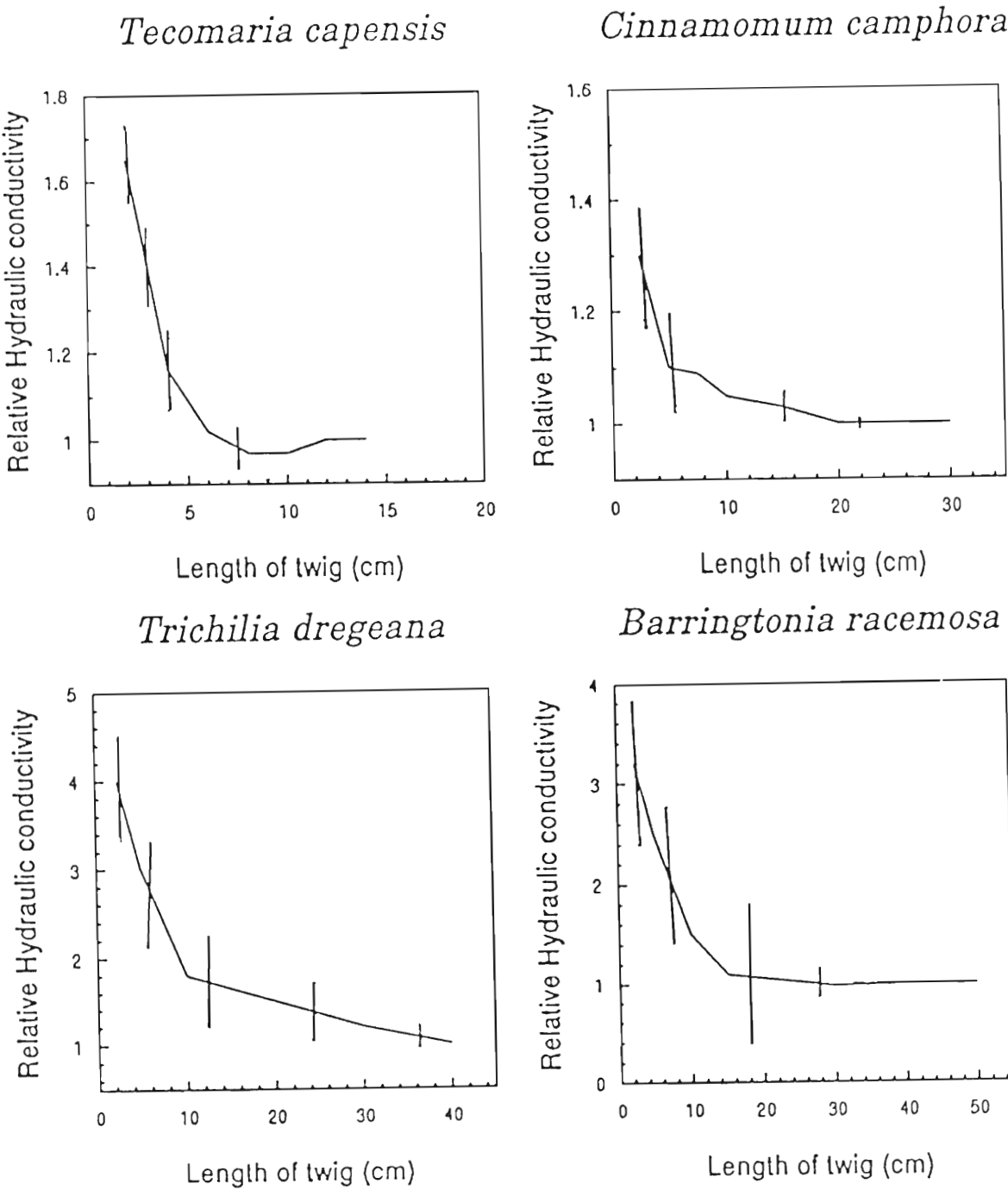
Figure 3.3: Relative xylem specific conductivity with decreasing twig length. Because of considerable twig to twig variation in absolute values, the data have been normalised to the value at maximum twig length. The vertical bars indicate standard deviations around the mean of five replicates for each species.

Normal Distribution
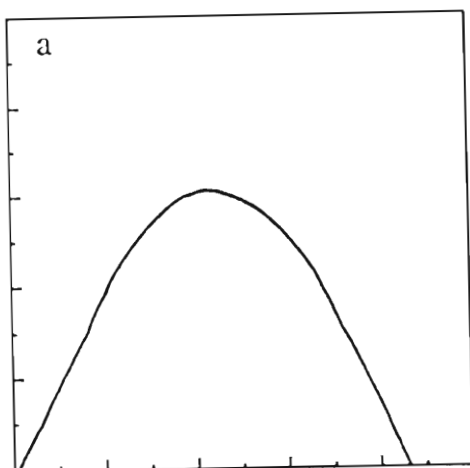
Exponential Distribution
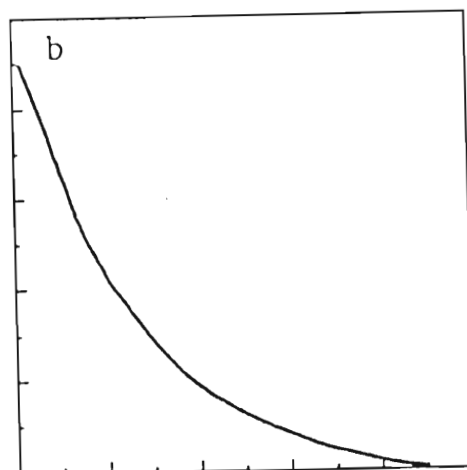
Gamma Distribution
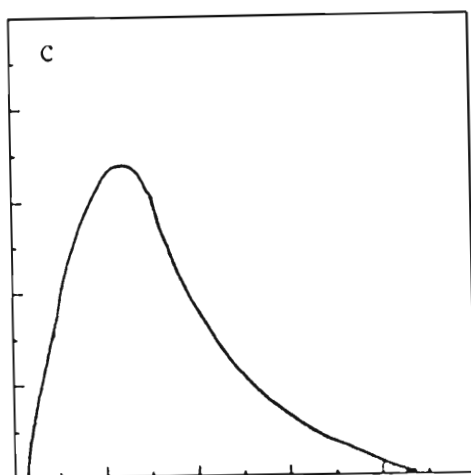
Uniform Distribution
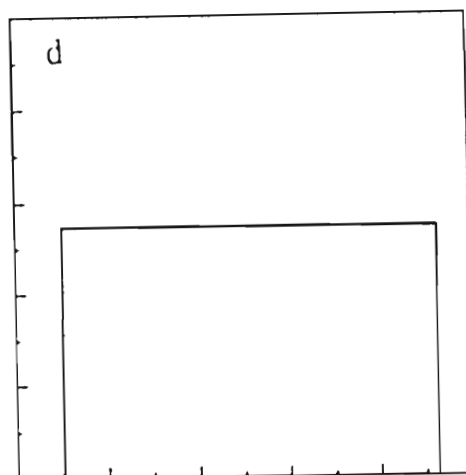
Figure 3.4: The distributions of the data sets used to compare calculated K_h, using the mean value and the number of data points and using each datum point. The distibutions used were: a) normal; b) exponential; c) gamma (skewed to the left) and d) uniform.

DISCUSSION

Hydraulic conductance measurements

In looking at Figure 3.1a and Table 2.1 it appears that
trends in hydraulic conductance (K_h) closely follow trends
in the mean conduit sizes. Why the K_h of C. camphora is
not significantly different from that of T. capensis is
not known, as the conduits of C. camphora are
significantly wider than those of T. capensis. It may be
due to the low density of conduits in C. camphora.

In looking at the measures of hydraulic conductivity the
trends between conduit diameter and the hydraulic
properties are not as clear. The differences among the
species of their TSC (Fig. 3.1(b)) and XSC (Fig. 3.1(c))
values are similar to those of K_h, but the large
differences among the species noted in K_h measurements,
are narrowed. This indicates that, while a species like
B. racemosa has a relatively high K_h it also has a wide
twig and a large xylem area which, to a certain extent,
are responsible for the high K_h.

With LSC (Fig. 3.1(d)), on the other hand, an interesting
trend emerges. There is no significant difference between
T. capensis, C. camphora and B. racemosa even though there
were significant differences in the measures of K_h, TSC
and XSC. This can be explained by the fact that a twig of
B. racemosa produces a far greater leaf area compared with

a twig of T. capensis or C. camphora. So while the K_h of a twig of B. racemosa is a lot higher than that of T. capensis and C. camphora, it is supporting a far greater leaf area and thus each of these species can potentially supply their leaves with the same amount of water per unit leaf area.

There is also no significant difference between the LSC's of P. latifolius and T. dregeana although their LSC values are significantly lower than those of the other three species. This is surprising as there are very large differences between P. latifolius and T. dregeana as far as K_h, TSC and XSC are concerned. T. dregeana produces a very large compound leaf, so the amount of leaf area supplied by a twig would be much larger than for that of P. latifolius which produces relatively small elongated leaves.

The natural habitats of P. latifolius and T. dregeana may explain the similarities of their LSC's. They are both mature forest species. Neither of them is fast growing, possibly as a result of their low LSC's. The other three species all have very different habitats but they are all relatively fast growing. The different hydraulic conductances therefore appear not only to affect the amount of water each unit area of leaf receives, but in turn may influence the leaf area that a twig can support.

It was difficult to compare the values obtained for

hydraulic conductance and conductivity in this study to those obtained by other workers. This is due to the variety of different ways these features have been measured and the different units that have been used. After converting the units used by Schulte & Gibson (1987), it was found that the measurements taken in this study for P. latifolius were far higher than those obtained by these two workers in their study of a number of temperate gymnosperms. It is not clear whether these workers flushed the stems they worked on as was done in this study. If they did not this could result in their lower measurements.

Gartner et al. (1990) measured the TSC of a number of vine and tree species. They found that the TSC of trees ranged from 0.8 to 5.1 kg $m^{-1}MPa^{-1}s^{-1}$. These are similar but somewhat higher than the values obtained in this study. Measurements in this study ranged from 0.15 kg $m^{-1}MPa^{-1}s^{-1}$ for P. latifolius to 1.18 kg $m^{-1}MPa^{-1}s^{-1}$ for B. racemosa.

Huber values

The Huber values, shown in Figure 3.2, give an indication of the resource allocation of the plant. P. latifolius produces more wood per unit leaf area than do all the angiosperm species. This is most probably due to its inefficient xylem. The hydraulic conductance of P. latifolius is low and it would need a lot of xylem to keep a few leaves well supplied with water so that they

could continue to photosynthesize. Inefficient xylem transport of water could lead to low leaf water potentials which could possibly result in a stomatal limitation to photosynthesis.

As far as the four angiosperm species are concerned B. racemosa and C. camphora produce less wood per unit leaf area than do T. capensis and to a lesser extent T. dregeana. It is surprising that the Huber value of C. camphora was lower than that of T. dregeana as T. dregeana appears to have a more efficient xylem anatomy (wider vessels, Chap. 2). However, the vessel densities are higher and the vessel lengths longer in C. camphora than in T. dregeana. These features may make the xylem anatomy of C. camphora more efficient than that of T. dregeana. According to the results obtained in the hydraulic conductance versus twig length section, it does appear that vessel endings have a marked effect on the resistance to water flow (Fig. 2.3).

Hydraulic conductance versus twig length

It appears, from Figure 3.3, that twig length, as a result of xylem vessel lengths, has a large impact on hydraulic conductance and conductivity. If the limited length of vessels was having no impact on the hydraulic properties of the stem then the relative XSC should not have changed as the twig was cut shorter. This was the case over a fairly large range of twig lengths for all four angiosperm

species. However, once the twig was reduced to a certain
length the relative XSC increased dramatically. In the
case of T. dregeana relative XSC more than doubled and in
B. racemosa relative XSC tripled.

It is assumed that the relative XSC started increasing
sharply once most of the vessels were cut open at each
end. The resistance posed by the vessel endings must,
therefore, be fairly substantial to result in such large
increases in relative XSC once this resistance was
removed. It is not surprising that there was a strong
correlation between the mode value of the vessel length
distribution and the length of twig at which the relative
XSC increases (Table 3.2).

Measured K_h versus calculated K_h

In the calculation of K_h using the Hagen-Poiseuille
equation, the xylem conduits are assumed to be ideal
capillaries (Zimmermann, 1983), thus the only resistance
to flow would be presented by the size of the conduits and
any frictional resistance between water molecules and the
smooth sides of the conduits. Xylem conduits are however
not ideal capillaries. They have finite lengths, their
internal walls are also not smooth, they are often pitted
and may have thickening tissue in steps or spirals. As
water crosses from one conduit to the other it also meets
with resistance in the form of bordered pits. In some
cases perforation plates existing between individual

vessel elements may also add to the resistance to water transport. It is not, therefore, surprising that the measured hydraulic conductance is lower than the calculated conductance.

The measured K_h of P. latifolius was only 40% of the calculated K_h. In viewing the xylem anatomy of P. latifolius (Chap. 2) it is not surprising that there is this large difference. The conduits are very short in length (less than 1cm). This would lead to a great deal of resistance as water passes from one conduit to another. Due to the narrowness of the conduits it is also very easy for them to become blocked by obstructions.

The vessel lengths of T. capensis were short and one would have expected this to pose considerable resistance to water flow. However, the measured K_h was 87% of the calculated K_h. The limited vessel length could explain the difference but it is surprising that the other angiosperms with longer vessels, especially B. racemosa, had measured K_h values which were further away from the calculated K_h than that of T. capensis. It is not known why the measured K_h was so much lower than the calculated K_h for T. dregeana, B. racemosa and in particular C. camphora.

It would have been thought that perhaps B. racemosa would have had the closest correlation between the two values as it has the longest vessels. This, however, was not the case. Why there should be such a low correlation for

C. camphora is also not understood. These results could, however, be due to experimental error. It was a difficult and tedious task measuring the size of a representative portion of conduits from a micrograph. Other workers (Ewers & Fisher, 1989; Ewers et al., 1989) had projected slides of their micrographs onto a wall and measured them from the projected images to get a greater degree of accuracy. This was not done in this study and would have perhaps yielded better results had it been done.

Even though the measurements of K_h were taken on twigs that had been flushed, some conduits may still have been blocked or obstructed or even embolized. It is a feature of xylem anatomy that there are more conducting conduits than are neccessary. This redundancy infers a certain degree of safety to the system by permitting conduction despite de-activation of part of the tissue (Zimmermann, 1983). Some of the conduits in the twigs on which measurements were made may have become permanently de-activated in some way, thus lowering the measured K_h below theoretical.

Conduit diameter distibution modelling

Looking at the results shown in Table 3.4 it can be seen that it is important to take the vessel size distribution into account when calculating the K_h. While the mean conduit diameter is a useful anatomical measurement and it does give an indication of what the hydraulic conductance

could be, it is not very meaningful when looking at detailed hydraulic conductance.

Conclusion

Measurements of the hydraulic properties of the five species seemed to show some correlation with their xylem anatomies (Chap. 2). From the results of LSC's, though, it can be seen that a certain type of xylem anatomy does not guarantee that the leaves of that plant will receive a greater supply of water. From the results of this study it appears that a more efficient xylem anatomy would allow for a greater leaf area to be produced, perhaps more so than supplying a given leaf area with more water.

It has also been shown, through this work, that although Poiseuille's Law is useful in trying to estimate a potential hydraulic conductance, water flow through the xylem is not as simple as water flow though a narrow pipe. Many factors, particularly the resistance posed by the limited length of conduits need to be taken into account if hydraulic conductance is going to be modelled. The conduit diameter distribution is also an important feature in trying to estimate K_h.

CHAPTER 4: THE RELATIONSHIP BETWEEN TRANSPIRATION RATE AND LEAF WATER POTENTIAL

INTRODUCTION

The plant is a hydraulic system in which water moves down gradients of water potential along pathways which have a frictional resistance to flow (Sanchez-Diaz & Mooney, 1979). According to equation 1.1 derived from the van den Honert model (1948) by Elfving et al. (1972), the slope of the line drawn from measurements of transpiration versus water potential, would be equal to the soil-to-leaf resistance. In well watered soil, this would be similar to root surface to leaf resistance. Hydraulic conductance between the root and leaf would be similar to the inverse of this resistance.

There are, however, resistances other than those encountered in the xylem elements. The resistance encountered at the endodermis as the water has to cross membranes before entering the stele of the plant is an example of such a resistance (Passioura, 1982). It is also suggested by Passioura (1982) that there could still be a major resistance to water flow between the soil and the root even when the soil is very moist. Thus the inferred hydraulic conductance done by measuring the change in Ψ_{leaf} with increasing transpiration rate is not equivalent to the hydraulic conductance measured on excised twigs as it is also taking these resistances into account.

Many workers (Camacho-B, et al., 1974a; 1974b; Küppers, 1984; Meinzer, et al., 1938; Meinzer & Grantz, 1990; Nobel & Jordan, 1983; Reich & Hinckley, 1989; Sanchez-Diaz & Mooney, 1979) have used this equation and measurements of leaf or canopy transpiration and leaf water potential to estimate the soil-to-leaf hydraulic conductance. No reports in the literature have been found that included both the measurement of hydraulic conductance on excised twigs and measurements of the change in leaf water potential with transpiration and compared the two measurements.

There have also been a lot of conflicting results obtained from measurements of leaf water potential with increasing transpiration rates. Aston and Lawlor (1979) and Stoker and Weatherley (1971) found that there was very little change in leaf water potential with increasing transpiration rate. On the other hand, Camacho-B, et al. (1974a; 1974b) and Meinzer et al. (1988) found that leaf water potential decreased to various degrees with increasing transpiration. No, or very little, change in water potential with changing transpiration would imply a very low, internal resistance to water flow from the soil to the leaves. It is not surprising then, that most of the studies which found little or no change in water potential were done on herbaceous species (Aston & Lawlor, 1979; Camacho-B et al., 1974a).

The importance of maintaining a high leaf water potential lies in the effect leaf water potential has on stomatal conductances of both water vapour and CO_2. A very low leaf water potential, or more correctly a low turgor potential, will inevitably result in a closing of the stomata which would limit CO_2 uptake and thus decrease photosynthesis. The short-term productivity of a plant depends on maintaining its photosynthetic tissue at a high water status while its stomata remain open (Passioura, 1982). Stomata can, however, respond directly to the environment (Küppers, 1984; Teskey et al., 1983) and not just through a lowering of leaf water potential. Thus plants need to maintain a balance between water supply and water demand in order to avoid desiccation, on one hand, or the unnecessary restriction of CO_2 uptake, on the other hand (Meinzer & Grantz, 1990).

In an attempt to understand how plants operate as a complete unit, subject to a dynamic environment, it is of interest to compare hydraulic conductance inferred from measurements of transpiration (E) and Ψ_{leaf} taken in the field with direct measurements done on excised twigs made in the laboratory. The measurements of hydraulic conductance on excised twigs, as described in Chapter 3, are the measures of maximum hydraulic conductance. All embolisms are removed by flushing and are prevented from reforming using an abundant water supply and a constant pressure gradient. It is not, therefore, expected that the two measures will be equivalent as it is likely that

embolisms will be common under natural conditions, but the trends among the five species could be similar.

Differences between inferred and measured values of hydraulic conductance could also give information on resistances other than xylem frictional resistances. These resistances would include the resistance found at the endodermis of the root and resistances between the soil and the root. The difference between the inferred and measured value will also be affected by the root surface area to leaf surface area ratio, though this ration was not measured in this study.

MATERIALS AND METHOD

The following work was carried out in the field on three consecutive, hot, summer days. Transpiration rates were measured using an MCS 301 Null Balance Porometer for all five species from just after dawn until midday. Changes in water potential were measured with increasing tranpiration rate as opposed to a decreasing transpiration rate to avoid any possible hysteresis effects associated with stomatal closure. Water potential measurements were taken of the leaves (in the case of B. racemosa and T. dregeana) or twigs (the other three species) from which transpiration measurements were taken. The water potential was measured by obtaining the balance pressure with a pressure bomb according to methods described by Scholander, Hammel, Bradstreet, Hemmingsen (1965).

A regression analysis was carried out on the five sets of data and graphs were drawn of the resultant regression lines. A comparison of the slopes of the regression lines (Q test) was carried out according to Sokal and Rohlf (1981). The slopes (measured in mmol $m^{-2}MPa^{-1}s^{-1}$) would give an indication of the resistance of the conducting pathway between the soil and the leaves divided by the leaf area, as transpiration is calculated per unit area of leaf.

The inverse values of the slopes were then calculated to give an estimate of the conductivity of the pathway. The

measurement of mmol was changed to kg to give units of $kg\ m^{-2}MPa^{-1}s^{-1}$. These values had to be multiplied by the approximate length of the above ground conducting pathway to give the final units as $kg\ m^{-1}MPa^{-1}s^{-1}$ for the inverse slopes. These are the same units in which LSC was calculated in Chapter 3. The length of the total conducting pathway should have been used in the calculations but this was not possible, thus just the length of the above ground conducting pathway was used. These values allow an estimate of LSC from data collected in the field from an intact tree, as opposed to excised twigs in the laboratory. The values obtained from the field data will include soil-root interface and root endodermis resistances.

RESULTS

The results of the regression analysis of the water
potential versus transpiration data are shown in
Figure 4.1. Table 4.1 gives the statistics associated with
the regression analysis. T. capensis, C. camphora and
T. dregeana appear, from Figure 4.1, to operate similarly,
with their water potential gradually decreasing as
transpiration increases. B. racemosa, on the other hand,
shows little change of Ψ_{leaf} even though transpiration
increases substantially. P. latifolius on the other hand
shows a sharp decrease in water potential with only a
relatively slight increase in transpiration rate.

Table 4.1: The statistical data obtained from the regression
analyses of the water potential versus
transpiration plots. The standard error is shown
in brackets and n = 15 in all cases. Values with
different letters in superscript are significantly
different (Q test $P \leq 0.05$).

Species	Constant (MPa)	Slope (MPa m^2 s mmol^{-1})	R squared
P. latifolius	-0.51 (170)	-0.83 (114)[d]	0.82
T. capensis	-0.52 (79)	-0.18 (16)[b]	0.90
C. camphora	-0.56 (217)	-0.23 (39)[bc]	0.73
T. dregeana	-0.31 (107)	-0.26 (25)[c]	0.88
B. racemosa	-0.33 (67)	-0.035 (8.7)[a]	0.55

The slopes of the lines shown in Fig. 4.1 are an indication of the soil/root interface-to-leaf resistance, on a leaf area basis, in well watered soil. Although the slope of T. capensis is statistically different from the slope of T. dregeana they are both not significantly different from C. camphora. B. racemosa and P. latifolius are significantly different from each other as well as the other three species.

The inverse of this slope taking into account the length of the conducting pathway would be a measure of LSC. Table 4.2 shows these inferred values of LSC for the five species.

Table 4.2: The inverse values of the slopes from Table 4.1 with the units converted from mmol to kg and the slopes multiplied by the length of the conducting pathway to give an inferred leaf specific conductivity (LSC), measured in kg m^{-1}MPa^{-1}s^{-1}. The inferred LSC was compared to the values obtained for LSC before and after flushing (Chap. 3).

Species	Inferred LSC	Measured LSC before flushing	Measured LSC after flushing
P. latifolius	0.00015	0.00082	0.0011
T. capensis	0.00023	0.00095	0.0017
C. camphora	0.00069	0.00061	0.0017
T. dregeana	0.00046	0.00076	0.0010
B. racemosa	0.00308	0.00116	0.0021

From Table 4.2 one can see that there is a relatively large difference in the inferred LSC measured from the inverse of the slope of transpiration versus Ψ_{leaf} and the LSC obtained from measurements on excised twigs which have been flushed

(Chap. 3). The inferred LSC is closer to the LSC measured on excised twigs before flushing took place (B. racemosa does not appear to follow this trend as the inferred LSC is larger than both the LSC measured on excised twigs before flushing and the LSC measured after flushing). It is not surprising that the inferred LSC measurement is closer to the measurements done before the excised twigs were flushed as one would expect a certain degree of embolism to occur naturally. Flushing effectively removes all embolisms and the resultant LSC would be the maximum LSC for that twig.

The fact that the inferred LSC values are even lower than the measured values taken on unflushed twigs indicates that there are other resistances in the water conducting pathway not being accounted for in the laboratory measurements on excised twigs. It is not known why the inferred LSC for C. camphora is higher than the LSC measured on unflushed twigs. It could be due to the artificial creation of a large amount of embolisms when cutting and transferring the twig.

As shown in Figure 3.3 there is a great deal of resistance at vessel endings. One can assume a similar resistance to flow is also encountered at tracheid endings. The resistance caused by the vessel and tracheid endings may account for some of the difference between inferred LSC and measured LSC. The above ground conducting pathway of the plants ranged from about 2m in T. capensis to about 8m in C. camphora. There would thus be a great number of vessel and tracheid endings encountered by water as it flowed from the root to the

leaves. There may also be resistances other than those within the xylem of the plant. These resistances may be located at the soil-root interface or within the root itself.

The results obtained for B. racemosa do not appear to follow the trends shown in the other four species. It is possible that there is an error in the data collection for B. racemosa. The R squared value for B. racemosa is a lot lower than for the other four species indicating a lower confidence in the slope obtained from the regression analysis.
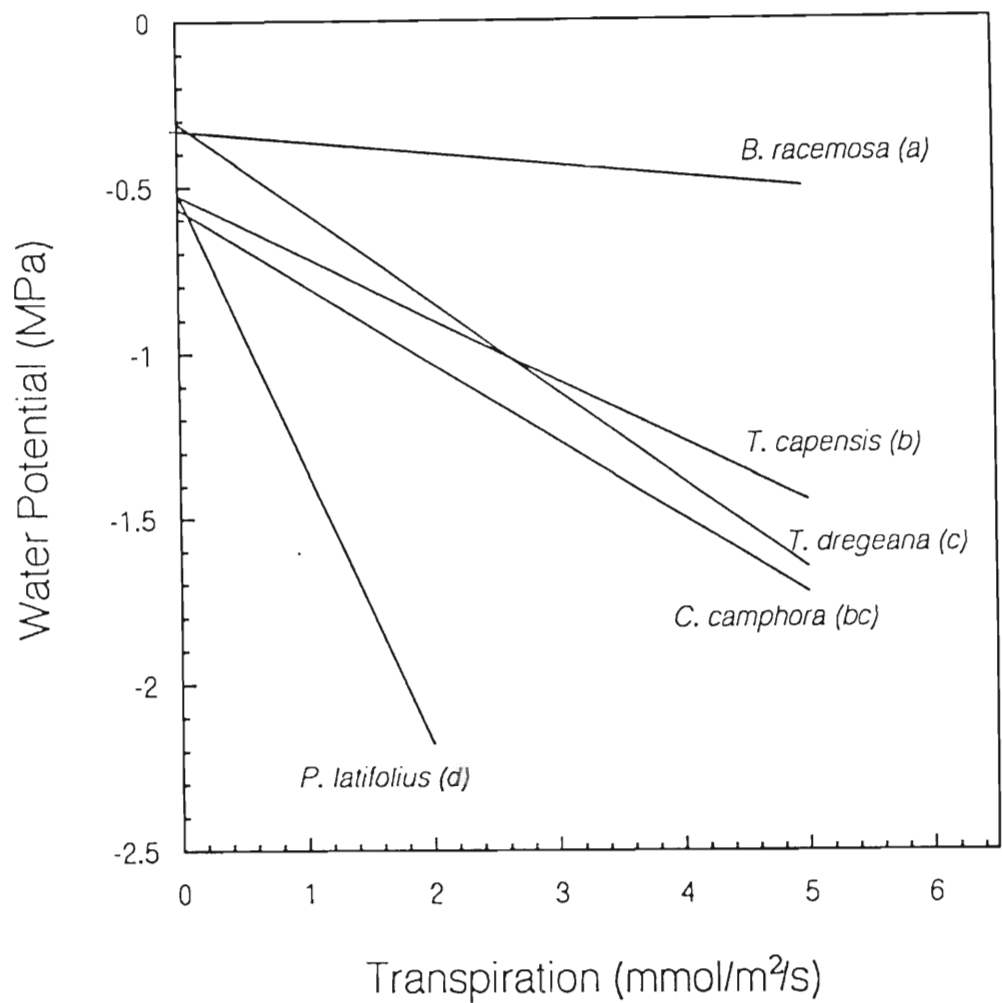
Figure 4.1: The change in leaf water potential with
increasing transpiration rate for the five
species. The lines represent the results of the
regression analysis, the details of which are
given in Table 4.1. The letters in parentheses
indicate slopes which are significantly different
(Q test P ≤ 0.05), n = 15 for all species.

DISCUSSION

Among the five species studied there appears to be varying degrees of decreasing water potential with increasing transpiration rate. The water potential of B. racemosa showed very little change even with large increases in transpiration. This suggests that there is little internal resistance to water flow. This could be a consequence of its xylem anatomy. Large, long vessels with a relatively high density of vessels results in a very efficient xylem conducting system.

P. latifolius, on the other hand, shows a sharp decrease in water potential even with a relatively minor increase in transpiration. This indicates a high internal resistance to water flow. This is probably due to the inefficient xylem anatomy of P. latifolius, i.e. narrow short tracheids. The other three species show intermediate responses of leaf water potential to increases in transpiration which ties in well with their intermediate xylem anatomy. If the slope, however, was dependent just on xylem anatomy one would expect that the slope of T. capensis to be steeper than that of T. dregeana, but the reverse is true. While the efficiency or safety of the wood anatomical features can explain a large portion of these results it is not sufficient to explain them fully.

It is thought that the inverse of the slope obtained from the type of measurements carried out in this chapter is similar to the root-to-leaf hydraulic conductance in well watered

soils. According to the terminology used in this thesis, the inverse of the slope would not be equivalent to hydraulic conductance but rather more closely related to the leaf specific conductivity (LSC) as transpiration is given per unit of leaf area. If the length of the path along which the water had to travel from the root to the twig on which the measurements were taken was also taken into account, then the inverse of the slope should give an indication of the LSC of the plant.

Table 4.2 compares the results obtained for LSC in Chapter 3 with the inferred LSC obtained in this part of the study. Differences between the inferred values and the measured values could be due to a number of factors. Under natural conditions there could be a number of cavitation events occurring, particularly when transpiration demand increased. This would have resulted in lower measurements in the field. Due to the inefficiency of the conducting system of P. latifolius large pressure gradients would develop between the roots and leaves and the xylem would be put under a great deal of tension. While the design of the xylem anatomy of P. latifolius is thought to be safe, cavitations could possibly occur more readily under natural conditions than with the other four species in which such large tensions would not develop due to the more efficient xylem anatomies.

It is known that plants produce more xylem conduits than are needed. This confers safety by virtue of redundancy (Zimmermann, 1983). Some conduits may have become permanently

dysfunctional due to blockage or embolism under natural conditions. This would have also resulted in a lower inferred LSC compared to the measured LSC.

The results of the s udy on hydraulic conductivity versus length, (Fig. 3.3) indicate that the length of the conducting pathway will have a substantial influence on the hydraulic conductivity possibly because of the resistance posed by conduit endings. Due to the length of the conducting pathways of the plants under natural conditions, it is probable that the conduit endings posed a substantial resistance to water flow thus lowering the inferred LSC. Only the approximate length of the above ground conducting pathway was ascertained for this work. It is not known how long the below ground pathway was and it can be assumed that had this also been taken into account it would have increased the values for the inferred LSC's.

As stated in Passioura (1982) there are also resistances besides those found within the xylem elements. There is thought to be a fairly substantial resistance to water flow posed by the endodermis as water needs to cross a membrane to enter the stele. Even though the soil was well watered there may have still been resistance to flow between the soil and the root (Passioura, 1982). The measurements taken on excised twigs in the laboratory, while very useful in trying to ascertain the hydraulic properties of a plant, are not reliable indicators of what the total soil-to-leaf hydraulic conductance and resistance is under natural conditions.

The difference between the inferred LSC and the measured LSC could be used to give an indication of how much of the total resistance to water flow lies within the xylem and how much is due to resistances in the root and at the soil-root interface. For this to be a meaningful measure, though, the resistance posed by the tracheid and vessel endings would need to be quantified. One would also need to be able to ensure that embolisms were not created artificially while cutting and transporting the twig for the laboratory measurements.

It is not clear why the inferred LSC for B. racemosa was higher than both the measured LSCs. It is possible that there was an error in the collection of the data for B. racemosa. It is possible that the measures of water potential for B. racemosa were in error. The balance pressure could have been read too early as phloem exudate was confused with water from the xylem. In order to get the leaves into the rubber bung one had to tear the base of the leaves. This may have in some way influenced the measuring of water potential. Alternatively there may be an error in the measurement of LSC on excised twigs in the laboratory.

Different maximum transpiration rates were also measured under the same environmental conditions for the different species. This may be accounted for by direct stomatal responses to changes in the humidity gradients between the air and the leaf. This has also been observed by Camacho-B

et al., (1974a) who noted this response in their studies of sunflower, pear, citrus, sesame and pepper plants. Species like T. capensis, C. camphora and T. dregeana could be using stomatal control to maintain relatively high leaf water potentials.

If the results presented here for B. racemosa are to be believed, then B. racemosa has a very efficient transport system which allows it to replace the water lost through transpiration very quickly. In the type of environment in which B. racemosa is found, where there is no shortage of water, stomata that do not close in dry air would not result in tremendous water deficits and growth would be favoured over water conservation. None of the other species occur naturally in such environments and they would therefore need to reduce excessive water loss by using stomatal control, particularly if their xylem anatomy was not efficient. It is possible that there is an error in the water potential readings reported for B. racemosa in this Chapter, but it is still possible that B. racemosa operates in a similar manner to that reported here. It is possible that the slope of the line in Figure 4.1 should be steeper but it is unlikely that it would ever be as steep as the slope of P. latifolius.

CHAPTER 5: GENERAL DISCUSSION

From the discussions of the previous four chapters, it can be seen that the study of the hydraulic properties of a plant in relation to its wood anatomy and its leaf water status is a complex one. Plants operate as dynamic, integrated wholes taking into account both internal and external factors. The success of a plant possibly depends on its ability to adapt to changing conditions. It is impossible in a study like this to take into account all the factors that affect the various parameters discussed here. It was also impossible to study the plants under a range of different conditions to try to determine how responses can change. It is hoped, however, that this study has, in some small way, contributed to a further understanding of whole plant water relations.

Chapters 2 and 3 indicate that the xylem anatomy of a plant does affect the hydraulic properties of that plant. The wood anatomy does not only affect the hydraulic properties, it can also affect the resource allocation of the plant. This is shown by the results of LSC shown in Figure 3.1(d). Features of the xylem anatomy which appear to be most important are the diameter of the conduits and their distribution and density and the total lengths of the conduits.

Features such as internal wall thickenings and presence or absence of perforation plates between vessel elements were

not considered in this study. Workers such as Baas (1983) and Baas et al. (1983) have studied these features and found that they do influence the hydraulic properties of the wood, but not to the same extent as the features that were measured in this work.

The different measures of the hydraulic properties, such as hydraulic conductance, TSC, XSC and LSC all give different information on the water conduction ability of the plant. They also, along with the Huber value (Fig. 3.2), give an indication of the resource allocation of the plant. A plant may have a high K_h, but this may be due to the fact that it just has a greater xylem cross-sectional area than a plant with a lower K_h. This was the case with B. racemosa and T. dregeana, their K_h was a lot higher than those of the other three species but this difference was decreased in the measures of TSC (Fig. 3.1(c)). A high K_h does not necessarily indicate that the leaves of that twig will receive a greater supply of water per unit area. In fact it appears more likely that the high K_h allows the plant to produce a greater leaf area.

The ability of plants to appropriately modify their pattern of development due to a change in their environment, is a major factor involved in their adaptation to specific habitats (Jones, 1983). It is possible that differences in xylem anatomy in different environments allow differences in leaf area production. In a water stressed environment xylem conduits tend to be

narrower and shorter than in non-stressed environments. Besides reducing the chances of embolism formation, this may result in less leaf area being produced, thus allowing the plant to concentrate its water supply to a few small leaves. Chaves (1991) claims that reduced growth and stress-induced senescence of leaves are of potential value for plant survival and adaptation to drought.

There may also be seasonal changes in xylem functioning, possibly due to embolism formation. The plant would have less operational xylem and thus a decreased water supply to its leaves. It would be advantageous for the plant to reduce its leaf area, thus allowing the remaining leaves to operate with a greater water supply than would be the case if the available water had to be spread over a greater leaf area.

These short term responses to environmental conditions are a measure of the phenotypic plasticity of the plant. In contrast to this short-term mechanism, genetic differentiation represents a more long-term mechanism to cope with the natural environment (Kuiper & Kuiper, 1988). It is these phylogenetic characteristics that are referred to in this study when viewing differences in the five species with respect to their natural habitat.

The ability of B. racemosa to maintain high leaf water potentials even with high transpiration rates could allow it to maintain open stomata longer than species with less

efficient xylem anatomies growing in the same environment. It has been established that the rate of CO_2 assimilation in the leaves is depressed at moderate leaf water deficits (Chaves, 1991). B. racemosa would have the ability, due to its efficient water transport, to maintain high levels of CO_2 assimilation, even under conditions of high evaporative demand, as long as water supply was sufficient. Under conditions of limited water supply there is a danger of a great deal of embolism formation as the tension in the xylem increases. This may be the reason that B. racemosa is not found growing naturally in anything except very well watered soils.

The gymnosperm P. latifolius, on the other hand, could develop a stomatal limitation to photosynthesis as evaporative demand increased. This would most likely be due to its relatively inefficient xylem anatomy. The inefficiency of its xylem anatomy would not allow it to compete very successfully with the angiosperms under natural conditions. This is perhaps why the gymnosperms appear to be less successful than the angiosperms, except under certain fairly stressful conditions.

The three strategies outlined by Camacho-B et al (1974a; 1974b), Chapter 1, concerning the possible relationships between hydraulic conductance and stomatal conductance appear to fit the five species in this study. While stomatal characteristics were not studied in great detail, it is still possible to hypothesis as to which class the

five species belong.

P. latifolius appears to fit into the first category of
species which combine strong regulation of water loss by
stomata with low efficiency of their water transport
system and which are unable to prevent depression of their
Ψ_{leaf} as transpiration increases. T. capensis, C. camphora
and T. dregeana, on the other hand could belong to the
second category of species which strongly regulate water
loss by stomata but have a more efficient water transport
system than plants in the first category. B. racemosa
possibly belongs to the third category of species which
have little stomatal regulation of transpiration and a
highly efficient water transport system.

Midgely (National Botanical Institute, Private Bag X16,
Rondebosch, 7700, South Africa) proposes that plants will
have different priorities when growing under different
conditions of water availability. If water availability is
high then their priority would be competitive usage of
resources. If water availability was moderate then growth
and reproduction would be a priority. If water
availability was low then dormancy and survival would be
priorities. It is possible that the priority of
B. racemosa in its natural habitat would be competitive
usage of resources. Its very efficient xylem anatomy could
allow this happen. The natural habitats of the other four
species are all of moderate water availability. It would
be of interest to try to relate Midgely's hypothesis to

differences in xylem anatomy that occur in these different environments.

There is a great potential for further studies similar to the ones conducted here. The same measurements could be taken on a species growing under a variety of different conditions. The same five species could also be studied in their natural environments and the results compared to those obtained in this study. Most of this work would be descriptive to start off with until enough is known to be able to manipulate changes in water relations in the laboratory. It would also be of interest to expand the idea of comparing the LSC measured in the laboratory to the inferred LSC measured in the field (Chap. 4) to try and learn more about what proportion different resistances play in the movement of water through the soil-plant-atmosphere-continuum.

Work, similar to that done in this study, also needs to be done in conjunction with plant growth analysis measurements. In particular measurements such as root area to leaf area ratios and the leaf area index, that is the functional size of the plant standing on a particular land area (Hunt, 1978). These measurements could help to shed further light on how water availability affects the resource allocation of the plant and what role xylem anatomy has in possibly controlling some of this resource allocation.

Generally more work needs to be done looking at whole plant water relations rather than small specific aspects, if there is ever going to be an understanding of how plants operate as integrated wholes. This is not an easy task as there are a number of inter-acting factors which produce the final response. The final response can also be temporary and changes can occur as environmental conditions change. All in all it is a daunting, but challenging task.

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CHAPTER 6 : REFERENCES

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