# THE EFFECTS OF WIND AND SHAKING ON THE MORPHOLOGY, GROWTH, GAS EXCHANGE AND WATER RELATIONS OF *Pinus contorta* Douglas

by

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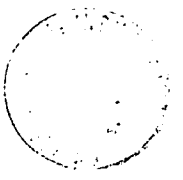

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## DECLARATION

This thesis has been composed by myself from the results of my own work except where acknowledged to the contrary.

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List of Symbols

| | |
|---|---|
| A | leaf area |
| b | regression coefficient |
| c | specific heat of dry air |
| C | sensible heat flux by convection, |
| $D_w$ | diffusion coefficient of water |
| $D_c$ | diffusion coefficient of $CO_2$ |
| $e_a$ | air vapour pressure |
| $e_s(T_s)$ | saturation vapour pressure at $T_s$ |
| $e_s(T_a)$ | saturation vapour pressure at $T_a$ |
| $e_s(T_n)$ | saturation vapour pressure at $T_n$ |
| E | transpiration rate |
| F | flux rate; net photosynthetic rate |
| $g_n$ | needle conductance to water vapour flux |
| $g_s$ | stomatal conductance to water vapour flux |
| $g_c$ | cuticular conductance to water vapour flux |
| G | heat flux by conduction |
| J | flow rate |
| K | transfer coefficient |
| L | leaf area ratio |
| $L_d$ | long-wave radiation flux from sun and sky (downward) |
| $L_e$ | long-wave radiation flux from environment |
| $L_s$ | long-wave radiation flux from surface |
| LWR | leaf weight ratio |
| P | chemical storage term |
| PhAR | photosynthetically active radiation |

| | |
|---|---|
| $r_a$ | boundary layer resistance to $H_2O$ flux |
| $r'_a$ | boundary layer resistance to $CO_2$ flux |
| $r_s$ | stomatal resistance to $H_2O$ flux |
| $r'_s$ | stomatal resistance to $CO_2$ flux |
| $r_l$ | leaf resistance to $H_2O$ flux |
| $r_n$ | needle resistance to $H_2O$ flux |
| $r_c$ | cuticular resistance to $H_2O$ flux |
| $r_r$ | 'residual' resistance to $CO_2$ flux |
| $r_R$ | 'radiative' resistance to radiative heat flux |
| $r_E$ | combined resistance to radiative heat flux and convective heat flux through the boundary layer |
| R | relative growth rate |
| $R_L$ | relative leaf growth rate |
| $R_a$ | absorbed radiation |
| $R_e$ | emitted radiation |
| $R_n$ | net radiation |
| $R_{ni}$ | isothermal net radiation |
| Re | Reynolds number |
| RWC | relative water content |
| RWR | root weight ratio |
| $s^2$ | variance |
| S | storage term |
| $S_t$ | diffuse and direct shortwave radiation from the sun and sky |
| $S_e$ | diffuse and direct shortwave radiation from the environment |
| Sh | Sherwood number |
| t | time |
| $T_a$ | temperature of air |

$T_s$ temperature of surface

$T_n$ temperature of needle

$U$ unit leaf rate

$V_o$ volume of water in tissue at full turgor

$V_p$ volume of water in tissue at incipient plasmolysis

$V_e$ volume of water expressed from tissue

$V_b$ volume of 'bound' water in tissue

$Y$ Young's modulus of elasticity

$W$ dry weight

$\Delta$ rate of change of saturation vapour pressure with temperature

$\epsilon$ emissivity of a surface; bulk modulus of elasticity of shoot or needle

$\zeta$ ratio of photon flux density at 660 nm. to photon flux density at 730 nm.

$\gamma$ psychrometer constant

$\gamma^*$ modified psychrometer constant ( $\gamma(r_a + r_s)/r_a$ )

$\lambda$ latent heat of vapourisation of water

$\rho$ reflection coefficient, density of dry air

$\Phi$ ratio of far-red phytochrome to total phytochrome

$\chi_a$ absolute humidity of air

$\chi_s(T_n)$ saturated absolute humidity at $T_n$

$\psi$ total water potential

$\psi_s$ solute water potential

$\psi_p$ pressure water potential

$\psi_{s,o}$ solute water potential at full turgor

$\psi_{s,p}$ solute water potential at incipient plasmolysis

Abstract

(1) Subjecting two year old Pinus contorta to high winds in a controlled environment wind tunnel, or to continuous shaking by a specially constructed shaking rig, caused a 20% reduction in extension growth of leader and lateral stems. Rates of needle extension were reduced 11% by shaking and 30% by exposure to high wind. Radial growth of the stem was not affected.

(2) Microscopic investigation of cell size and number revealed that the reduced growth of leader stems was due primarily to a reduction in cell division. Cell extension was also slightly reduced.

(3) The reduced extension growth caused by shaking was accompanied by large reductions in dry weight. Relative Growth Rate and Unit Leaf Rate were reduced, but Leaf Area Ratio was unaffected; suggesting that the reduced growth was due to a decrease in net photosynthesis, or to an increase in dark respiration.

(4) Subjecting P. contorta to high winds had no effect on net photosynthesis, determined with an Infra-Red Gas Analyser, but significantly increased dark respiration.

(5) Whole-plant and detached-needle transpiration rates were determined gravimetrically. High winds and shaking had no effect on stomatal or cuticular conductances. Total water potential, determined with a needle pressure-bomb, was slightly increased by wind and shaking. Solute and pressure potentials of individual needles, determined by the pressure-volume technique, were not affected. It is concluded that mechanical stress does not affect the growth of P. contorta via an effect on water relations.

(6) It is postulated that mechanical stress causes an increase in 'maintenance respiration', with a resultant decrease in respiratory

substrate for growth. The consequent reduction in cell division and extension leads to a decrease in extension growth and dry weight growth. It is accepted that the links between these various processes are unclear.

# Chapter 1. Introduction

In this thesis, some effects of wind and shaking on Pinus contorta are examined. The effects of wind on plants has been relatively neglected by botanists interested in the general topic of the plant-weather relationship, presumably due to the experimental difficulties involved. In the field, sites differing in windspeed also vary in other environmental parameters, such as temperature (2.1.2). Experimental manipulation of windspeed by erecting shelterbelts also has general effects on the plant microenvironment, other than just reducing windspeed (2.1.2). In the laboratory, the expense of some sort of wind tunnel may be prohibitive. Yet the results of such experiments, with all their attendant difficulties, indicate that wind may have considerable effects on plant growth and physiology (2.1.2 - 2.1.6).

The stunted, wind swept appearance of trees on mountains is perhaps the most extreme effect of wind on plants. The reduced growth of trees in 'exposed' situations implies that high winds are detrimental to growth, in as much as windspeed is generally high in 'exposed' situations (2.1.2). Similarly, the effects of shelter on plant growth and yield imply an effect of wind on plant growth (2.1.2).

Exposing plants to artificial winds in wind tunnels has shown considerable effects of wind on plant growth and physiology (2.1.3 - 2.1.6). It seems likely, therefore, that wind may be an important environmental factor affecting the growth, morphology and physiology of P. contorta.

The practical significance of such effects on P. contorta are difficult to assess. P. contorta is widely used by foresters in Britain, U.S.A. and Canada (2.2.1), so the effects of the weather, and in this case of wind, on the growth of P. contorta is a matter of considerable

interest. Wind is considered a major limiting factor to British forestry (MacDonald 1951, Palmer 1968), but the major concern of these authors is with the uprooting and 'windthrow' of trees. Despite this, at the symposium entitled 'Wind effects on the forest', edited by Palmer (1968), the effects of wind on the growth of herbaceous plants were discussed by Whitehead (1968), as there was little information available on the effects of wind on tree growth.

Neel and Harris (1971) observed that shaking Liquidambar styraciflua for just 30 seconds a day caused large reductions in growth. An obvious effect of wind is that it shakes plants to and fro; perhaps this mechanical stimulation is an important aspect of the effects of wind on plants.

Changes in windspeed have varied and complex effects on the plant's microenvironment. These effects, discussed in 2.13, must be distinguished from effects of wind on the plant itself, in order to understand how wind affects plant growth.

In chapter 2, the literature on the effects of wind and shaking on plants is reviewed. The effects of wind on the plant microclimate is evaluated and relevant aspects of the considerable literature on P. contorta are summarised.

Materials and methods used throughout this thesis are discussed in Chapter 3, as is the preparation of the plant material.

The effects of wind and shaking on the extension growth and radial growth of P. contorta are described and compared in Chapter 4.

In Chapter 5, the effects of wind and shaking on longtitudinal cell division and extension are evaluated.

The effects of shaking on the dry weight production of P. contorta is described in Chapter 6 and the effects of wind on the photosynthesis and respiration of P. contorta are described in Chapter 7.

The water relations of *P. contorta* subjected to high winds and shaking are examined in Chapter 8.

The effects of shaking on the subsequent year's growth of *P. contorta* is described in Chapter 9 and the effects of a brief period of shaking per day on the extension growth of *P. contorta* is described in Chapter 10.

Chapter 11 is a final discussion and summary chapter.

# Chapter 2 Literature Review

The literature pertinent to this thesis falls into two main categories. The effects of wind and shaking on plants are discussed in sections 2.1.1 - 2.1.7. The choice of species is discussed in 2.2.1 and problems arising from the complex growth cycle of conifers are discussed in 2.2.2. The objectives of this project are discussed in 2.3.

## 2.1.1 Deformation of trees by the wind

One of the most dramatic effects of wind on plants is the wind-training of trees. Putnam (1948) provides a detailed classification of such 'flag' trees. Such classifications have been used by several authors to determine wind direction and velocities (Yoshino 1967, Holroyd 1970, Hewson et al 1977).

The mechanisms involved in tree deformation have not been studied but are thought to involve lignification of the young branches during or after a 'heavy blow' (Putnam 1948) and abrasion of windward parts by windborne snow and ice (Daubenmire 1959).

## 2.1.2 Exposure and shelter

The inclemency of the aerial environments in upland situations has long been considered an important limiting factor to tree growth (Lines & Howell 1963). The term 'exposure' has often been used in a semi-quantitative way to express the complex of weather factors that affect plant growth, including windspeed and gustiness, air temperature and humidity (Lines and Howell 1963, Grace 1977). British foresters have estimated 'exposure' by (i) the 'topex' method in which the angle to the skyline for each of the 16 principal compass directions is determined (Howell and Neustein 1965),

(ii) by the rates of tatter of standard cotton flag (Lines and Howell 1963), or (iii) subjectively (e.g. Malcolm and Studholme 1972). Booth (1976) estimated exposure by determining windspeeds over a detailed model of the Kintyre peninsula in a wind tunnel. The relationship between all of these 'exposure' estimates and actual weather conditions are unclear, yet significant negative correlations between height growth of conifers and all of these different types of estimate have been obtained (Lines and Howell 1963, Malcolm and Studholme 1972, Savill 1974, Booth 1976). This suggests that exposure may be an important ecological factor although the meaning of exposure in terms of measurable environmental conditions is unclear. Millar (1964) describes an upland, 'exposed' area: windspeeds and rainfall were higher than a more sheltered site, whereas air temperature, number of frost-free and snow-free days, number of sunshine hours and potential evapotranspiration were all lower. All of these factors may affect plant growth. Near the seashore, salt deposition onto vegetation by the wind may also affect plant growth (Boyce 1954).

To counteract the effects of exposure it has long been the practice in horticulture to erect windbreaks in order to provide artificial shelter (Caborn 1965). This has almost always resulted in an increased yield (Grace 1977). The complex effects of shelter upon local microclimate have been reviewed by Marshall (1967) and Grace (1977). In general, shelter results in reduced windspeeds, increased soil and air temperatures and increased soil moisture. The yield improvement cannot therefore be attributed to any one single environmental factor. However, in both expsoure and shelter experiments, high windspeeds are associated with reduced plant growth, suggesting that wind may be an important ecological factor.

### 2.1.3 Effects of wind on the plant microenvironment

As discussed above, field observations suggest that wind may affect plant growth. To understand how this may occur, the effects of wind on the microclimate of plants must be considered.

At any interface between a solid and the atmosphere, i.e. at any surface, there is a thin skin of air of reduced velocity, called the boundary layer. The exchange of water, $CO_2$ and other gases, and of momentum between the atmosphere and the surface are all affected by the properties of the boundary layer. A laminar boundary layer is one in which the streamlines of flow are almost parallel to the surface. In such a boundary layer, gaseous exchange is by diffusion. As the flowrate increases, the flow breaks down to a chaotic pattern producing a turbulent boundary layer, in which exchange of gases is by turbulent mixing: small parcels of air are transferred to and from the surface. Irrespective of the type of flow, the flowrate at the surface must be zero; hence there is always a thin, laminar sub-layer even in a turbulent boundary layer.

The transfer of any entity between a surface and the atmosphere can be described by a generalised form of Fick's equation (Jarvis 1971);

$$F = -K \frac{dE}{dz} \qquad (2.1)$$

where F is the flux rate;
K is the transfer coefficient and
dE/dz is the concentration gradient.

The resistance to transfer of an entity across the boundary layer can be defined in terms of the diffusion pathlength and the transfer coefficient of the entity in question (Jarvis 1971):

$$r_a = \int_{z_1}^{z_2} \frac{dz}{K} = \frac{Z_2 - Z_1}{K} \qquad (2.2)$$

and hence

$$F = \frac{E_2 - E_1}{r_a} \qquad (2.3)$$

where $r_a$ is the boundary layer resistance;

$Z_2 - Z_1$ is the diffusion pathlength and

$E_2 - E_1$ is the concentration gradient.

The transfer coefficient, K, for momentum, heat, water vapour and $CO_2$ by molecular diffusion at 0°C are .133, .181, .212 and .219 $cm^2\ s^{-1}$ respectively (Monteith 1973). In turbulent flow all entities are transferred by turbulent mixing and the appropriate values for K may vary from .2 to 1000 $cm^2\ s^{-1}$ above a vegetation canopy (Monteith 1973). Transfer is obviously much faster and $r_a$ much lower in conditions of turbulence. The work of Parlange et al (1971), Pearman (1972), Grace and Wilson (1976) and Grace (1978) suggest that the boundary layer over leaves in natural, turbulent airflows is usually turbulent. $r_a$ for laminar boundary layers varies with the inverse square root of the windspeed (Monteith 1973), but no such simple relationship holds in turbulent boundary layers, where an increase in windspeed gives a greater decrease in $r_a$ than would occur in laminar flow (Grace and Wilson 1976).

A decrease in $r_a$ due to increased windspeed will result in increased fluxes of heat, $CO_2$ and water vapour and so may affect photosynthesis, surface temperatures and transpiration.

(i) Photosynthesis.

$r_a$ is only one of several resistances governing $CO_2$ flux rates (Jarvis 1971):

$$F = \frac{CO_{2\,a} - CO_{2\,chl.}}{r_a' + r_s' + r_r} \qquad (2.4)$$

$CO_{2a}$ and $CO_{2\,chl}$ are the $CO_2$ concentrations in the atmosphere and at the chloroplast, respectively;

$r_s'$ is the stomatal resistance to $CO_2$ transfer and

$r_r$ is the 'residual' resistance to $CO_2$ transfer.

Holmgren et al (1965) found that the stomatal resistances of a number of species ranged from .3 to 18 s $cm^{-1}$ while 'residual' resistances ranged from 2 to 10 s $cm^{-1}$. $r_a'$ is usually of the order of .1 - 1 s $cm^{-1}$ (Monteith 1973) and so is generally only a small part of the total resistance. Changes in windspeed thus have little affect on $CO_2$ fluxes via $r_a'$. Only in assimilation chambers (where $r_a'$ may be very large without mechanical mixing) has flowrate been reported to have considerable effects on photosynthesis (Decker 1947, Warren Wilson and Wadsworth 1958, Parkinson 1968).

(ii) Surface temperature.

Surface temperatures differ from air temperatures to an extent governed by the radiation absorbed and lost from the surface, by latent heat exchange and by convective heat exchange.

The net radiation gain or loss $R_n$, can be found by determining the components of the radiation balance (Monteith 1973) :

$$R_n = (1-\rho)(S_r + S_e) + \epsilon(L_d + L_e - 2L_s) \qquad (2.5)$$

$\rho$ is the reflection coefficient of the surface;

$S_r$ is the diffuse and direct shortwave radiation from the sun and sky;

$S_e$ is the diffuse and direct shortwave radiation from the environment;

$\epsilon$ is the emissivity of the body;

$L_d$ is the long-wave radiation transmitted by the atmosphere;

$L_e$ is the long-wave radiation transmitted by the environment;

$L_s$ is the long-wave radiation transmitted by the surface itself.

$S_r$, $S_e$, $L_d$, $L_e$ and $L_s$ are all expressed here on a projected area basis.

(2.5.) can be simplified:

$$R_n = R_a - R_e \qquad (2.6)$$

where: $$R_a = (1-\rho)(S_r + S_e) + \epsilon(L_d + L_e) \qquad (2.7a)$$

and $$R_e = 2\,L_s = 2\epsilon\sigma T_s^4 \qquad (2.7b)$$

$R_a$ is the absorbed radiation,

$R_e$ is the emitted radiation;

$\sigma$ is the Stefan-Bolzman constant;

$T_s$ is the surface temperature.

(2.6) and (2.7b) show that net radiation is itself dependent on surface temperature. To remove $T_s$ from $R_n$, Monteith (1973) introduces $R_{ni}$, the isothermal net radiation, defined as the net radiation of the body if it were at air temperature, $T_a$:

$$R_{ni} = R_a - 2\epsilon\sigma T_a^4 \qquad (2.8)$$

From (6), (7b) and (8):

$$R_n = R_{ni} - 2\epsilon\sigma(T_s^4 - T_a^4) \qquad (2.9)$$

Monteith (1973) defines the 'radiative resistance', $r_R$, as:

$$r_R = \frac{\rho c}{4\epsilon\sigma T^3} \qquad (2.10a)$$

and shows that $$(T_s^4 - T_a^4) = \rho c \frac{(T_s - T_a)}{r_R} \qquad (2.10b)$$

where $\rho$ is the density of dry air,

and c is the specific heat of dry air at constant pressure

From (2.9) and (2.10b):

$$R_n = R_{ni} - 2\rho c \frac{(T_s - T_a)}{r_R} \qquad (2.11)$$

Equation (2.11) is necessary to solve the energy balance equation for surface temperature.

The energy balance equation states that in steady-state conditions (Gates 1962):

$$R_n + C + \lambda E + G + S + P = 0 \qquad (2.12)$$

when C is the sensible heat flux by convection

$\lambda E$ is the latent heat flux;

G is the heat flux by conduction;

S is a storage term;

and P is a chemical storage term, e.g. photosynthesis.

In many conditions, and for this discussion, it can be assumed that G, S and P can be ignored (Monteith 1973). (2.12) now reduces to:

$$R_n = C + \lambda E \qquad (2.13a)$$

In 'dry systems', where latent heat exchange is negligible (2.13a) reduces t

$$R_n = C \qquad (2.13b)$$

Sensible and latent heat fluxed are affected by windspeed through it's effect on $r_a$ (Monteith 1973):

$$C = \frac{\rho c(T_s - T_a)}{r_a} \qquad (2.14)$$

$$\lambda E = \frac{\rho c(e_s(T_s) - e_a)}{\gamma(r_a + r_l)} \qquad (2.15)$$

where $e_s(T_s)$ is the saturation vapour pressure at $T_s$;

$e_a$ is the air vapour pressure;

$\gamma$ is the psychrometer constant;

$r_l$ is the leaf resistance to latent heat flux.

Plant buds and stems can be considered 'dry systems', so the simplified energy balance equation (2.13b) can be solved for these structures:

From (2.13b) and (2.14):

$$R_n = \frac{\rho c(T_s - T_a)}{r_a} \qquad (2.16)$$

Insert (2.11):

$$R_{ni} = \frac{\rho c(T_s - T_a)}{r_a} + 2\rho c \frac{(T_s - T_a)}{r_R}$$

$$\Rightarrow \quad R_{ni} = \rho c(T_s - T_a)\left[\frac{1}{r_a} + \frac{2}{r_R}\right] \qquad (2.17)$$

Define: $$\frac{1}{r_E} = \frac{2}{r_R} + \frac{1}{r_a} \qquad (2.18)$$

Insert (2.18) into (2.17):

$$T_s = T_a + \frac{r_E R_{ni}}{\rho c}$$

$$\Rightarrow \quad T_s = T_a + \frac{r_E}{\rho c}(R_a - 2\varepsilon\sigma T_a^4) \qquad (2.19)$$

Equation (2.19) shows that surface temperature of dry systems differs from air temperature by an amount determined by the radiative environment and the geometry of the organ (which determine $R_a$ and $r_E$). Increasing wind-speed decreases $r_E$ through it's effect on $r_a$ (equation 2.17) and so decreases the right-hand term of (2.19), bringing $T_s$ closer to $T_a$. Landsberg et al (1974) provide experimental data for apple buds and blossoms demonstrating this.

It should be noted that for elements with a small characteristic dimension, such as buds, twigs or stems of small herbaceous plants, $r_a \ll r_R$ and so to a first approximation, $r_E = r_a$. For large elements such as tree trunks and branches, the much larger $r_a$ approaches the magnitude of $r_R$ and so $r_E \neq r_a$ (Monteith 1973).

For 'wet systems', such as plant leaves, latent heat flux must be taken into account. Factors affecting leaf temperature are air temperature, the radiation balance (equation 2.11), sensible heat flux (equation 2.14) and latent heat flux (equation 2.15). From (2.13a), (2.14), (2.15) and (2.11):

$$R_{ni} = \frac{\rho c(T_s - T_a)}{r_a} + \frac{2\rho c(T_s - T_a)}{r_R} + \frac{\rho c(e_s(T_s) - e_a)}{\gamma(r_a + r_l)} \qquad (2.20)$$

From (2.18):

$$R_{ni} = \frac{\rho c(T_s - T_a)}{r_E} + \frac{\rho c(e_s(T_s) - e_a)}{\gamma(r_a + r_l)} \qquad (2.21)$$

The leaf-air vapour pressure deficit $(e_s(T_s) - e_a)$ can be related to the leaf-air temperature difference and the air vapour pressure deficit by the Penman substitution (Campbell 1977):

$$e_s(T_s) - e_a = e_s(T_a) - e_a + \Delta(T_s - T_a) \qquad (2.22a)$$

$$\Rightarrow \quad T_s - T_a = \frac{e_s(T_s) - e_s(T_a)}{\Delta} \qquad (2.22b)$$

where $e_s(T_a)$ is the saturation vapour pressure at $T_a$;
and $\Delta$ is the rate of change of saturation vapour pressure with temperature.
Insert (2.22a) into (2.21);

$$\frac{R_{ni}}{} = \frac{\rho c(T_s - T_a)}{r_E} + \frac{\rho c\left[e_s(T_a) - e_a + \Delta(T_s - T_a)\right]}{\gamma(r_a + r_l)}$$

$$\Rightarrow \quad \frac{R_{ni}}{\rho c} = \frac{(T_s - T_a)}{r_E} + \frac{\Delta(T_s - T_a)}{\gamma(r_a + r_l)} + \frac{(e_s(T_a) - e_a)}{\gamma(r_a + r_l)}$$

$$\Rightarrow \quad \frac{R_{ni}}{\rho c} - \frac{(e_s(T_a) - e_a)}{\gamma(r_a + r_l)} = \frac{(T_s - T_a)}{r_E}\left[1 + \frac{r_E.\Delta}{\gamma(r_a + r_l)}\right] \qquad (2.23)$$

Define: $\gamma^* = \gamma(r_a + r_l)/r_E \qquad (2.24)$

Insert (2.24) into (2.23) and rearrange:

$$\frac{R_{ni}\, r_E}{\rho c} - \frac{(e_s(T_s)-e_a)}{\gamma^*} = (T_s-T_a)\left[\frac{\gamma^*+\Delta}{\gamma^*}\right]$$

$$\Rightarrow \quad T_s - T_a = \left[\frac{r_E R_{ni}}{\rho c} - \frac{(e_s(T_a)-e_a)}{\gamma^*}\right]\left[\frac{\gamma^*}{\gamma^*+\Delta}\right]$$

$$\Rightarrow \quad T_s = T_a + \left[\frac{\gamma^*}{\gamma^*+\Delta}\right]\left[\frac{r_E(R_a-2\varepsilon\sigma T_a^4)}{\rho c} - \frac{(e_s(T_a)-e_a)}{\gamma^*}\right] \qquad (2.25)$$

Equation (2.25) is the same as that given by Campbell (1977) and shows that leaf temperature is strongly dependant on air temperature, radiation balance and air vapour pressure deficit. (I am grateful to A. Miranda for his assistance with this derivation). Leaf temperature is dependant on windspeed, via $r_a$, in a complex way, as $r_a$ appears as both numerator and denominator. Decreasing $r_a$ can cause either an increase or decrease in leaf temperature, depending on specific environmental conditions. The graphical analysis of Gates and Papian (1971) show that in conditions of high absorbed radiation and moderate air temperature, $T_s > T_a$ and an increase in windspeed decreases leaf temperature. This has been shown experimentally by Yamaoka (1958), Mellor et al (1964) and Drake et al (1970).

In conditions of low or negative radiation balance, or at high air temperature, $T_s < T_a$ and increasing windspeed increases leaf temperature (Gates and Papian 1971).

(iii) Transpiration

The effects of windspeed on transpiration rate has been discussed in detail by Monteith (1965), Gates (1968), Gates and Papian (1971), Haseba and Takechi (1972), Monteith (1973), Hinshiri (1973), Gates (1976)

and Grace (1977). The following discussion is based on those of Monteith (1965), Hinshiri (1973) and Campbell (1977).

The major factors affecting latent heat flux are the resistances to latent heat flux (equation 2.15), the radiation balance (equation 2.5 and 2.11) and surface temperature (affected by sensible heat flux and radiative heat loss, equations 2.14 and 2.11). The energy balance equation (2.13a) can be solved for latent heat flux:

From (2.13a), (2.14), (2.11) and (2.18):

$$R_{ni} - \lambda E = \frac{\rho c(T_s - T_a)}{r_E} \tag{2.26}$$

Eliminate $T_s$ using the Penman substitution (2.22b):

$$R_{ni} - \lambda E = \frac{\rho c}{r_E}\left[\frac{e_s(T_s)-e_s(T_a)}{\Delta}\right] \tag{2.27}$$

Rearrange (2.15):

$$e_s(T_s) = \frac{\gamma \lambda E(r_l + r_a)}{\rho c} + e_a \tag{2.28}$$

Insert (2.28) into (2.27) to eliminate $e_s(T_s)$ :

$$R_{ni} - \lambda E = \frac{\rho c}{\Delta r_E}\left[\gamma\lambda E\frac{(r_l+r_a)}{\rho c} + e_a - e_s(T_a)\right]$$

$$\Rightarrow \quad \Delta\lambda E + \frac{\gamma(r_l + r_a)\lambda E}{r_E} = \Delta R_{ni} + \frac{\rho c}{r_E}(e_s(T_a)-e_a)$$

$$\Rightarrow \quad \lambda E(\Delta + \gamma^*) = \Delta R_{ni} + \rho c(e_s(T_a)-e_a)/r_E$$

$$\Rightarrow \quad \lambda E = \frac{\Delta R_{ni} + \rho c(e_s(T_a)-e_a)/r_E}{\Delta + \gamma^*}$$

$$\Rightarrow \quad \lambda E = \frac{\Delta(R_a - 2\varepsilon\sigma T_a^4) + \rho c(e_s(T_a)-e_a)/r_E}{\Delta + \gamma^*} \tag{2.29}$$

Equation (2.29) is essentially similar to that of Campbell (1977) and differs from that of Monteith (1965) only in that instead of net radiation, $R_n$, the more detailed term $(R_a - 2\varepsilon\sigma T_a^4)$ is used, and that $\gamma^* = \gamma(r_a + r_l)/r_E$ instead of $\gamma(r_a + r_l)/r_a$. As Monteith (1973) points out, $r_E \approx r_a$ for all but very large leaves.

Inspection of (2.29) shows that transpiration rate ( $\lambda E$) is strongly dependant on the radiation balance, humidity and temperature (as $\Delta$ and $e_s(T_a)$ are strongly temperature-dependant). $\lambda E$ is only weakly dependant upon $r_a$ as this occurs as both numerator and denominator. An increase in windspeed can increase or decrease transpiration, depending on environmental conditions.

By introducing the 'isothermal' or 'climatic' resistance, $r_i$, rewriting (2.29) nondimensionally and differentiating it with respect to $r_a$, Monteith (1965) shows that $\lambda E$ is independant of $r_a$ when:

$$r_l = (1 + \gamma/\Delta)\, r_i \qquad (2.30a)$$

or

$$\lambda E/C = \Delta/(\Delta+\gamma) \qquad (2.30b)$$

where $r_i$ is defined as

$$r_i = \frac{\rho c(e_s(T_a)-e_a)}{\gamma C} \qquad (2.31)$$

($r_i$ is thus a property of the environment in terms of a diffusive resistance).

In the case of a plant with low $r_l$ and a low radiation balance, as on a cloudy day, $r_i$ is large (as C is small without high $R_n$) and so $r_l \leq (1 + \gamma/\Delta)r_i$. A decrease of $r_a$ causes an increase in $\lambda E$ at the expense of C, i.e. transpiration rate increases. Conversely, on a sunny day with high $R_n$, C is large and so $r_i$ is small, so $r_l$ may exceed $(1 + \gamma/\Delta)r_i$. A decrease in $r_a$ results in a decrease in $\lambda E$.

The graphical analysis of Gates (1968), Gates and Papian (1971) and Grace (1977) show that only at low irradiances, when $T_s$ does not differ greatly from $T_a$, does an increase in windspeed cause an increase in transpiration. At high irradiances and moderate air temperatures, $T_s > T_a$ and an increase in windspeed can often decrease transpiration, as shown experimentally by Satoo (1951 a,b,c), Mellor et al (1964) and Drake et al (1970).

The above analyses show that changes in windspeed always result in changes in the plant's microenvironment. Changes in temperature and water use in particular are likely, when $r_a$ is altered. Such changes should be taken into account in any experiments on the effects of wind on plants. Unfortunately, very few studies have included monitoring leaf or bud temperatures. It has often been stated that the effect of wind on plant growth is due to it's 'drying effect', e.g. Tansley (1946), Daubenmire (1947, 1959), Venning (1949), Green (1964) and Willis (1973), yet as shown above, increasing windspeed may often have the opposite of a 'drying effect'.

Table 2.1 Effects of Wind on Plant Growth

| Species | Dry Weight Growth | Leaf Area Growth | Extension Growth | Radial Growth | Root/Shoot Ratio | Author |
|---|---|---|---|---|---|---|
| *Calendula officinalis* | d | | | | | Finnell (1928) |
| *Helianthus annuus* | d | d | d | d | | Martin and Clements (1935) |
| *Setaria italica* | d | | d | d | | Rao (1938) |
| *Apium graveolens* | | | d | | | Venning (1949) |
| *Brassica napus* | d | d | | | | Wadsworth (1959) |
| *Brassica napus*, *Pisum sativum*, *Hordeum vulgare* in solution culture | n | n | | | | Wadsworth (1960) |
| *Robinia pseudoacacia* | d | d | d | d | | Satoo (1962) |
| *Helianthus annuus* | d | d | d | | i | Whitehead (1962) |
| *Zea mays* | d | | d | i | i | Whitehead & Luti (1962) |
| *Larix laricinia* | | | d | i | | Larson (1965) |
| *Phaseolus vulgaris* in solution culture | d | d | | | d | Kalma and Kuiper 1966 |
| *Juglans nigra* | d | n | n | n | n | Heiligmann and Schneider (1974) |
| *Lolium perenne* | d | d | d | | i | Russell and Grace (1979) |
| *Festuca arundinacea* | d | d | | | i | |
| *Populus tremula* | | d | | | | Fluckiger et al (1978) |

d = decrease i = increase n = no effect

## 2.1.4 Effects of wind on plant growth and development

The effects of wind on plant growth has been investigated by several authors over the past 50 years, some results are summarised in table 2.1. Dry weight growth, leaf area growth and height growth were reduced in practically every species studied. Diameter growth is decreased in H. annuus, S. italica and A. graveolens; increased in Z. mays and L. laricinia, and unaffected in J. nigra. Root/shoot ratio is increased in H. annuus and Z. mays; decreased in P. vulgaris in water culture and unaffected in J. nigra. The observation of Wadsworth (1960) that wind exposure did not affect plant growth in water culture led him to conclude that wind affects plant growth via an effect on water relations. In contrast, Kalma and Kuiper (1966) found that wind did affect the growth of P. vulgaris in water culture.

Various developmental effects have been noted: Martin and Clements (1935) found that H. annuus exposed to continuous wind developed an increased number of stomata per unit area and decreased number of xylem vessels in the stem. Rao (1938) noted a decrease in tillering and root volume in S. italica. Venning (1949) observed a large increase in cross-sectional area of collenchyma bundles in the petioles of A. graveolens. Satoo (1962) noted a decrease in leaf production and root length in R. pseudoacacia. Whitehead and Luti (1962) found that although the leaves of Z. mays were shorter in wind-grown plants, they were also broader and thicker, had a greater number of stomata per unit area, a greater number of leaf veins, larger phloem elements and more sclerenchyma fibres. Grace and Russell (1977) found that leaves of F. arundinacea grown in continuous wind were thinner, had more stomata per unit area, more marginal sclerenchyma cells, a greater number of epidermal hairs and a

higher Young's modulus of elasticity than controls. In contrast, Russell and Grace (1978a) found none of these effects in L. perenne.

Various experiments have been carried out on the effects of wind-blown particles on plants. Much shorter periods of exposure are required to produce similar amounts of abrasive damage when the wind contains particles of sand or soil (Dewey et al 1956, Armbrust et al 1974). For instance, 15 to 20 minutes exposure to wind of 13.5 m $s^{-1}$ plus 5 to 15 kg of sand were used by Armbrust et al (1974). Such exposures have been shown to reduce dry weight growth and yield of Triticum aestivum (Woodruff 1956, Armbrust et al 1974), P. vulgaris (Skidmore 1966), Gossypium hirsutum (Armbrust 1968) and Lycopersicon esculentum (Armbrust et al (1969).

Finally, there are a few field observation of relevance here. Bright (1928) found that the fronds of Pteridium aquilinum were smaller at the top of an exposed slope than lower down the slope; cells were thicker and there was a greater per cent of sclerenchyma fibres in the petioles. Helmers (1943) found that needles of wind-deformed Pinus ponderosa had thicker cuticles and hypodermes, thinner epidermes, decreased cross-sectional area and increased numbers of stomata per unit area than needles from undeformed trees on the same ridge. These effects cannot be attributed unambiguously to wind, however.

Turner (1971) divided an experimental area in the Dischma valley, Switzerland, into regions of mean windspeed class and irradiance class. He found that height growth and survival of young Larix decidua and Pinus montana arborea were significantly negatively correlated with windspeed class in areas of high irradiance, but not in areas of low irradiance. Hewson et al (1977) classified various mountainous sites as 'windy' and

'non-windy' and found that the height/diameter ratios of *P. ponderosa* and *Pseudotsuga menziesii* were significantly lower in the windy sites. Again, it is likely that environmental variables other than wind may also vary within these classifications.

Fluckiger et al (1978) compared the leaf area growth of several species placed in the dividing strip or by the side of a motorway with the growth of plants 200m away from the motorway. Traffic gusts of wind were up to 5 m $s^{-1}$ in the central reservation and up to 1 m $s^{-1}$ by the side of the motorway, providing 'additional windiness' for the plants. Leaf area growth of *Populus tremula*, *Fraxinus excelsior*, *Betula pendula*, *Cornus sanguinea*, *Lonicera xylosterum* and *Quercus robur* was reduced by proximity to the motorway, the biggest effect being in the central dividing strip. This effect, while consistent with that of wind on plants, cannot be ascribed solely to wind.

There is thus a considerable body of evidence that wind can have marked effects on plant growth and development. Various explanations have been put forward to account for this; these are reviewed in subsequent sections.

### 2.1.5 Effects of wind on plant water relations.

The effects of wind on plant water use via the boundary layer resistance are discussed in 2.1.3. The modified Penman equation (2.29) is strictly only applicable to steady-state conditions. If the leaf resistance changes with windspeed, there will be changes in transpiration not predicted by (2.29). The leaf resistance, $r_l$, is composed of the stomatal resistance $r_s$ and cuticular resistance $r_c$ in parallel:

$$\frac{1}{r_l} = \frac{1}{r_s} + \frac{1}{r_c} \qquad (2.32)$$

There is evidence in the literature that both $r_s$ and $r_c$ are affected by windspeed. Martin and Clements (1935) found that although transpiration of H. annuus increased with increasing windspeed, a fairly rapid stomatal closure followed, partially reducing the increase in transpiration. Satoo (1962) demonstrated a decline in stomatal aperture with increasing windspeed in Quercus acutissima. Tranquillini (1969) subjected various species to increasing windspeed and found that, in the same environmental conditions, transpiration of Alnus viridis and Larix decidua increased with increasing windspeed whereas that of Picea abies, Pinus cembra, Sorbus aucuparia and Rhododendron Ferrugineum decreased with increasing windspeed. This implies a response of $r_l$ to windspeed in at least one of these groups. Davies et al (1974) found that increasing windspeed increased stomatal aperture in Fraxinus americanus, decreased stomatal aperture in Acer saccharum and had no affect on Pinus resinosa. Heiligmann (1974) found that wind had no effect on stomatal aperture of J. Nigra. Davies et al (1978) found that stomata of a coastal, prostrate ecotype of *Cytisus scoparius* closed with increasing windspeed, whereas the stomata of an upright, inland provenance opened with increasing windspeed. However, Davies et al (1978) did not control air vapour pressure and noted that the increase in windspeed was accompanied by a two-fold increase in air vapour pressure deficit. With the exception of Tranquillini (1969) the other workers listed above do not mention humidity. Grace et al (1975) found that increasing windspeed had no effect on transpiration rate of Picea sitchensis and attributed this to a stomatal response to vapour pressure deficit. They pointed out that the increased flux of water vapour away from the leaf surface (in their environmental conditions) would reduce the vapour pressure sensed at the leaf surface, and showed that the stomata of P. sitchensis responded directly to changes in air vapour

pressure deficit. It has now been established that many species show a stomatal response to air vapour pressure deficit (Jarvis et al 1974, Burrows and Milthorpe 1976, Beadle 1976, Hall et al 1976). Such a response may have confounded the results of some of the above cited work. Despite this, there clearly is evidence that $r_s$ may well change with changing windspeed, causing changes in $r_l$.

$r_c$ is usually much greater than $r_s$ and so, to a first approximation, $r_l = r_s$ (equation 2.32). Large changes in $r_c$ would be required to significantly affect transpiration rate.

Grace (1974) investigated the effects of wind on cuticular and stomatal resistances of grasses. Exposure of Festuca pratense, Lolium multiflorum and Dactylis glomerata to 3.5 m $s^{-1}$ for 48 hours caused marked decreases in cuticular and stomatal resistances. Thompson (1974) showed that this wind exposure resulted in a loss of structure of epicuticular waxes and rupture of epidermal cells where leaves had collided with one another in the wind. Mackerron (1976a) examined the wind lesions of Fragaria x ananassus leaves and found a collapse of the periclinal walls of epidermal cells. Wilson (1978) made detailed examinations of the lesions of Acer pseudoplatanus leaves resulting from wind-induced abrasion. She noted crushing of epidermal and mesophyll cells, disruption of epicuticular waxes and reported a linear relation between per cent macroscopic damage and cuticular conductance.

It appears that $r_s$ and $r_c$ both vary with windspeed. Bearing in mind that increasing windspeed may decrease the potential transpiration from the plant and that the stomata of at least some species close in response to high winds, it is by no means certain that high winds will cause a water stress. Recourse to experiments where plant water status is actually

measured must be made. According to the van den Honert (1948) model of water movement through the soil-plant-air continuum, an increase in transpiration will be accompanied by a decrease in water potential (Weatherley 1976). In those experiments mentioned above where an increase in transpiration was reported, there was presumably an accompanying fall in water potential. Unfortunately there have been very few actual measurements of water status.

Satoo (1962) found that the uptake of water by C. japonica lagged behind the increase in transpiration rate obtained on increasing the windspeed and inferred that a water stress had been imposed. Grace and Russell (1977) grew F. arundinacea in continuous wind or drought. They found that wind-exposed and droughted plants had more negative water potentials at any given relative water content than control plants. This was interpreted as an adaptive response to water stress: less total water need be transpired to establish a given water potential gradient between soil and leaves. Droughted plants also showed the adaptive response of increased leaf resistance. Wind-exposed plants, however, had decreased leaf resistances. Despite these changes, the wind exposed plants, which were freely supplied with water, showed only slightly greater water stress (-1.2 MPa) than controls (-1.0 MPa.)

Continuing their experiments in a controlled environment wind tunnel, Russell and Grace (1978b) were again unable to detect any effects of wind on water potentials of F. arundinacea and L. perenne, although leaf resistances and leaf area growth were reduced.

To date, there is no convincing evidence that wind-induced water stresse are important to plant growth. The importance of damaged cuticles in situations of limited water supply has not been examined. Yet considerable

effects of wind on plant growth have been observed in situations of plentiful water supply, suggesting that wind-induced water stresses may not be an important factor in the effects of wind on plant growth.

2.1.6 Effects of wind on photosynthesis and respiration

Tranquillini (1969) exposed a variety of species to increasing windspeeds and found that the photosynthetic rate of L. decidua and P. cembra showed a maximum at 4 m $s^{-1}$; S. aucuparia and A. viridis showed a maximum at 1.5 m $s^{-1}$; and R. ferrugineum and P. abies decreased above .5 m $s^{-1}$. Caldwell (1970) extended these experiments and showed that the decrease in photosynthesis of R. ferrugineum with increasing windspeed was due to increasing stomatal closure, whereas that of P. cembra was due to increasing mutual shading as the plant bent over in the wind.

Yabuki et al (1970) also found that photosynthesis of Cucumis satiuas showed a maximum at .5 m $s^{-1}$. These reported increases in photosynthetic rate at low windspeeds are presumably due to the decrease in boundary layer resistance as windspeed is increased.

Grace and Thompson (1973) reported a decrease in net photosynthesis of F. arundinacea following exposure to 3.5 m $s^{-1}$; but Russell and Grace (1978b) were unable to detect any effect of windspeed in F. arundinacea and L. perenn This may be due to the difference in techniques used: Grace and Thompson (1973) measured net photosynthesis of whole plants whereas Russell and Grace (1978b) measured gross photosynthesis of single, newly expanded leaves.

MacKerron (1976b) found that the photosynthetic rate of wind-damaged F. x ananassus leaves was lower than that of undamaged leaves.

Wilson (1978) showed that the net photosynthesis of A. pseudoplatanus was increased by exposure to a high windspeed, if calculated on a viable

leaf area basis. She attributed this to the effects of loss of leaf area on photosynthetic rate as reported by Wareing et al (1968).

Armbrust et al (1974) also found an increase in net photosynthesis calculated on a viable leaf area basis when T. aestivum were subjected to brief periods of wind-blown particle exposure.

Grace and Thompson (1973) and Wilson (1978) found that wind had no effect on dark respiration rate. Todd et al (1972) however, demonstrated large, rapid increases in dark respiration upon exposing 8 different species to high windspeeds. Respiration rate rapidly returned to normal when calm conditions were restored. Armbrust et al (1974) and Mackerron (1976b) also found increased respiration rates in wind exposed plants.

Table 2.2. Effects of Motion on Plant Growth

| Species | Treatment | Extension Growth | Radial Growth | Author |
|---|---|---|---|---|
| Pinus radiata | g | n | i | Jacobs (1954) |
| Gossypium hirsutum | sh,h | d | | Frizzel et al (1960) |
| Bryonica dioica | h | d | | Boyer (1967) |
| Liquidamlar styraciflua | sh | d | i | Baillaud (1967)<br>Neel and Harris (1971a) |
| Zea mays | sh | d | | Neel and Harris (1971b) |
| Cucurbita melopepo | sh | d | i | Turgeon and Webb (1971) |
| Pinus taeda | g | n | i | Burton and Smith (1973) |
| Hordeum vulgare<br>Bryonia dioica<br>Cucumis sativus<br>Phaseolus vulgaris<br>Mimosa pudica<br>Ricinus communis | h | d | | Jaffe (1973) |
| Cucumis pepo<br>Pisum sativum<br>Triticum aestivum | h | n | | Jaffe 1973 |
| Liquidambar styraciflua | sh | d | n | Phares et al (1974) |
| Juglans nigra | | | | Phares et al (unpublished) |
| Acer saccharinum | | | | |
| Lycopersicon esculentum<br>Pisum sativum | sh,h | d | | Mitchell et al (1975) |
| Pinus resinosa | sh | d | d | Quirk and Freese (1976) |
| Pseudotsuga menziesii | sh | d | n | Kellogg and Steucek (1977) |
| Zea mays | h | d | | Beardsell (1977) |
| Festuca arundinacea | sh | d | | Russell and Grace (unpublished) |

g - guying
sh - shaking
h - handling
n - no effect
d - decreased
i - increased

## 2.1.7 Effects of shaking on plants

Although the effects of wind on plant growth are clear, effects on plant water relations and carbon budget are not so clearcut. Perhaps the effect of wind on plant growth is due to the shaking that it causes.

Various types of mechanical stimulus have been applied to plants, and their effects on growth studied. Jacobs (1954) and Burton and Smith (1973) guyed trees to prevent them swaying in the wind; Boyer (1967), Jaffe (1973) and others handled plants, while Neel and Harris (1971 a,b) and others shook plants for 30 seconds daily. Growth in plant height and diameter have been studied; results are summarised in table 2.2. In nearly all the 21 species studied, the mechanical stimuli reduced extension growth, and where studied, increased radial growth.

Virtually all the authors listed in table 2.2 hypothesise that plant hormones are involved in this response, with a majority in favour of ethylene. The only evidence for a role of hormones is that of Boyer (1967) who found marked decreases in the indole acetic acid/gibberellic acid fraction of handled plants.

Parkhurst and Pearman (1971), in a critique of Neel and Harris (1971), point out that although shaking might affect plant hormone distribution and activities, it might also have effects on the plant's water relations or carbon budget. The only work to date on water relations is that of Kahl (1951) and Beardsell (1977). Kahl (1951) found that shaking increased transpiration of Rhoeo discolor, Taraxacum officinalis and Lactuca sativa. Beardsell (1977) could detect no effect of handling on the transpiration of Z. mays.

Asher (1968) observed that deflecting the fascicles of various pine species induced an action potential in the stem. Pickard (1971) found that stroking pea epicotyls also gave rise to action potentials. Both authors commented on the similarity of the response to that of the Mimosas and carnivorous plants, which also show depolarisation upon mechanical stimulation (Sibaoka 1969). In these plants and others, this depolarisation is associated with rapid movement, such as closing of leaves or coiling of tendrils. For instance, Jaffe and Galston (1968) showed that the coiling of pea tendrils in response to a mechanical stimulus is accompanied by an efflux of electrolytes, $H^+$ and $^{14}C$ label. They proposed that the mechanical stimulus is transduced into an electrolyte efflux, resulting in an efflux of water with a consequent loss of turgor, and contraction. Zimmerman (1978), in his discussion of the electromechanical model of turgor maintenance, proposes that changes in the geometric dimensions of the plasmalemma, due to turgor pressure changes, are transformed into changes of ion concentrations and electric field distribution. If, as the work of Asher (1968) and Pickard (1971) suggests, sensitivity of the plasmalemma to mechanical stimuli are common amongst plants, perhaps the mechanical stimuli observed to reduce plant growth do so through an effect on the turgor of the plant. It must be emphasised that there is no evidence for this.

There is direct evidence for an effect of mechanical stimuli on components of the carbon budget. Kahl (1951) found that shaking detached leaves of L. sativa caused a 60% increase in respiration and a 52% decrease in net photosynthesis. Audus (1935), Barker (1935), Godwin (1935) and Audus (1939) showed that rubbing and flexing detached leaves of a variety of species caused large, sustained increases in respiration rate. Phares et al (unpublished) examined the effects of shaking on dry weight and leaf

area growth of 3 species of tree. Total dry weight and leaf area ratio of J. nigra were significantly reduced, but not significantly affected in L. styraciflua or A. saccharum. They concluded that shaking has little effect on photosynthetic parameters, at least in the latter two species.

In conclusion, a variety of mechanical stimuli have been shown to affect plant growth, but the physiological details of this effect are still unclear.

### 2.2.1 Lodgepole Pine

The species chosen for experimentation in this project was Pinus contorta, or Lodgepole Pine. P. contorta is of considerable importance both economically and aesthetically. Over 13 x $10^6$ acres, 49 x $10^6$ acres and 73,000 hectares had been planted with P. contorta by 1975 in U.S.A., Canada and Great Britain respectively (Wellner 1975, McDougal 1975 and Lines 1976). The North American Indians used P. contorta for teepee poles, currently it is used for light construction, interior panelling, ports, poles and railway ties (Wellner 1975). It's economic importance is further reflected by the considerable amount of research dealing with this species. Lotan and Sweet (1975) list 1155 references of work on P. contorta over the period 1954-1973.

Forest managers and landscape architects consider P. contorta of considerable aesthetic value (Litton Jr. 1975). Herrington (1975) and Despain (1975) point out that P. contorta is of great value to outdoor recreationists as it frequently occurs in many of the fairly rigorous climatic conditions often found in scenic situations. However, Despain (1975) also notes that the general population do not recognise P. contorta as a particular species and 'those that can recognise the species usually complain about it'.

P. contorta has an ecological range of 30° of latitude (California to Alaska) and from sea level to 11,000 feet in it s natural environment (Lines 1966). It is divided into many provenances on the basis of appearance, growth rate, fruiting habit and ability to withstand 'exposure' (Lines 1966). The major division is between inland and coastal populations. (Lines 1966, Cannell 1974), although Critchfield (1957) recognises 4 subspecies.

The full botanical classification of the provenance used in this work is Pinus contorta Douglas ex. Loudon ssp. contorta Critchfield, provenance 73 (7972) 1, also known as Long Beach provenance. This South Coastal provenance is of considerable importance to British Forestry because of it s rapid growth rate even on poor soils (Lines 1966).

2.2.2 The growth cycle of conifers, with particular reference to P. conto

The growth cycles of most conifers are relatively complex, as differentiation and development are temporally separated. A considerable amount of detailed descriptive work on the growth cycle of P. contorta is available. Van Den Berg and Lanner (1971), Cannell & Willett (1975), Owens and Molder (1975), Lanner and Van Den Berg (1975), Cannell and Willett (1976) and Cannell (1976) have all thoroughly described the various stages of the growth cycle of P. contorta.

Buds and needles initiated in year n remain as primordia throughout year n and do not elongate into the mature structures until year n + 1, or in some cases, n + 2. Owens and Molder (1975) provide the following account of bud development of P. contorta in Victoria, British Columbia.

Cell division in the bud apex, pollen cone primordia and needle primordi begins in early March. The bud apex initiates sterile cataphyll primordia until the second half of April, when fertile catophylls (i.e. those bearing axillary buds) begin to be initiated. Initiation rates do not peak

until well after shoot elongation is completed. Axillary bud primordia remain small until August when they undergo repeated cell divisions to form two-needled dwarf shoot primordia or lateral branch primordia.

This calendar of events agrees well with that of Cannell and Willett (1975) for P. contorta grown in Scotland.

In unicyclic buds these structures elongate in year n + 1. However, Van Den Berg and Lanner (1971) found that many buds of P. contorta are polycyclic. Polycyclic buds produce more than one whorl of lateral bud primordia. Second-cycle lateral bud primordia may develop dwarf shoot primordia in year n, or these may not develop until n + 1. Third-cycle lateral bud primordia are usually small by the end of year n and continue development as buds during n + 1, not extending until n + 2. Doak (1935) coined the useful term 'stem unit' to describe a single internode plus node plus nodal appendage, i.e. a dwarf shoot, whether telescoped in the bud or elongated in the shoot.

The number of stem units is fixed in year n, and so sensitive to the environment only of year n.

Development and maturation of the bud structures are also temporally separated in n + 1. Thompson (1974) and Cannell and Willett (1976) provide complete descriptions of the growth (as opposed to differentiation) of P. contorta in Scotland. Bud elongation commences in mid-April to May, increases throughout May, peaks in June and is finished by early July. Needles (borne on the dwarf shoots) commence elongation in June and are fully extended by September. Root growth occurs in April, but mainly in July to October. Increase in girth occurs May to August. If growing conditions are favorable in August, some further shoot extension may occur. This 'lammas' growth consists of extension of latterly developed

stem units (Cannell et at 1976).

The amount of height growth in n + 1 is a function both of the number of stem units formed in year n and the extension per stem unit in year n + 1. As a result of this, various researchers have found that conifer shoot extension may be affected more by the environment of the previous year than of the current year, e.g. Mikola (1962), Kozlowski (1962 and 1971).

Pollard and Logan (1977) found that primordia production in Picea mariana and Picea glauca was markedly sensitive to temperature, but surprisingly insensitive to light intensity or duration, or to mild water stress. The sensitivity of conifer growth cycles to an environmental stress in years n and n + 1 is most clearly shown by the work of Garrett and Zahner (1973). They subjected P. resinosa trees to drought in either the early, middle or late periods of the growing season for two consecutive years. They found that shoot extension was equally affected by drought in June and July of year n and April and May of year n + 1; but needle length was affected by drought in June and July of year n + 1 only.

This sensitivity of growth to previous environments obviously complicates any attempt to determine the effect of an environmental stress in the current year on conifer growth. This is further discussed in 4.1.

## 2.3 Objectives

The negative correlation observed between 'exposure' and height growth of *P. contorta* observed by Lines and Howell (1963) suggests that wind may adversely affect the growth of *P. contorta*. This is also suggested by the work of Lines (1976) who found that the extension growth of *P. contorta* was increased by up to 56% by artificial shelter.

As discussed in 2.1.2, the effects of exposure and shelter on plants cannot be attributed to wind alone. To establish whether wind, and wind alone, does reduce the growth of *P. contorta*, controlled environment experiments are necessary. The pros and cons of controlled environment studies are discussed in the next chapter. Principally, the results of controlled environment studies can only show whether the experimental variable is *potentially* important in the field.

The primary objective of this thesis was to establish whether wind, as distinct from other correlated environmental variables, such as temperature, humidity and salt spray, actually does affect the growth of an economically important conifer, *P. contorta*.

Subsidiary objectives were: (i) to determine whether shaking has similar effects on the growth of *P. contorta* as wind, and so to assess the role of shaking in any wind effect; (ii) to investigate the effects of wind and shaking on the dry weight production, photosynthesis, respiration and water relations of *P. contorta*, in an attempt to determine how wind and shaking affect plant growth.

# Chapter 3. Materials and Methods

In this chapter, materials and methods used in this thesis are described. Controlled environment studies have been heavily relied upon; the rationale for their use is discussed in 3.1. The wind tunnel, growth room and shaking frames are described in 3.2, 3.3 and 3.4. Basic instrumentation used in describing the controlled environments are discussed in 3.5. Use of the controlled environments is discussed in 3.6. Preparation of the plant material is described in 3.7.

## 3.1 The rationale of controlled environments

Went (1963) points out that conditions in a controlled environment are often very far removed from those experienced by a plant in the natural environment. The contrasts between the constant growth room environment and the continually changing out-of-doors environment are marked and considerable. Yet to understand the biological responses of plants to specific environmental factors, controlled environment studies are extremely useful. The correlation of environmental factors with one another and the continual variation of not only environmental factors themselves but also combinations of environmental factors out-of-doors render it difficult to relate a plant response to a specific environmental factor.

The use of a controlled environment can firmly establish a plant response to a given environmental factor, in a given set of conditions. Extrapolation of such experiments to field conditions must be circumspect, however, as variation in other environmental factors might modify the response (Evans 1963).

The limitations of 'exposure' and shelter experiments are discussed in chapter 2. These experiments suggest that wind might have an effect on plant growth, but because other environmental factors could not be controlled, cannot firmly establish such an effect. Controlled environment studies, on the other hand, can examine the effects of wind, and wind alone, on plant growth. The two types of experiments are complementary and if they give similar results can form the basis of a very strong argument.

In this thesis, controlled environments and shaking frames have been used. The controlled environment wind tunnel provides a means of varying windspeed independantly of other environmental factors. The

shaking frames provide a means of investigating the effects of plant motion, such as that caused by wind, but virtually without the wind's effect on mass transfer through the boundary layer. The regular, continuous mode of shaking is unlike that seen in the natural wind, but can be standardised and repeated in successive experiments.

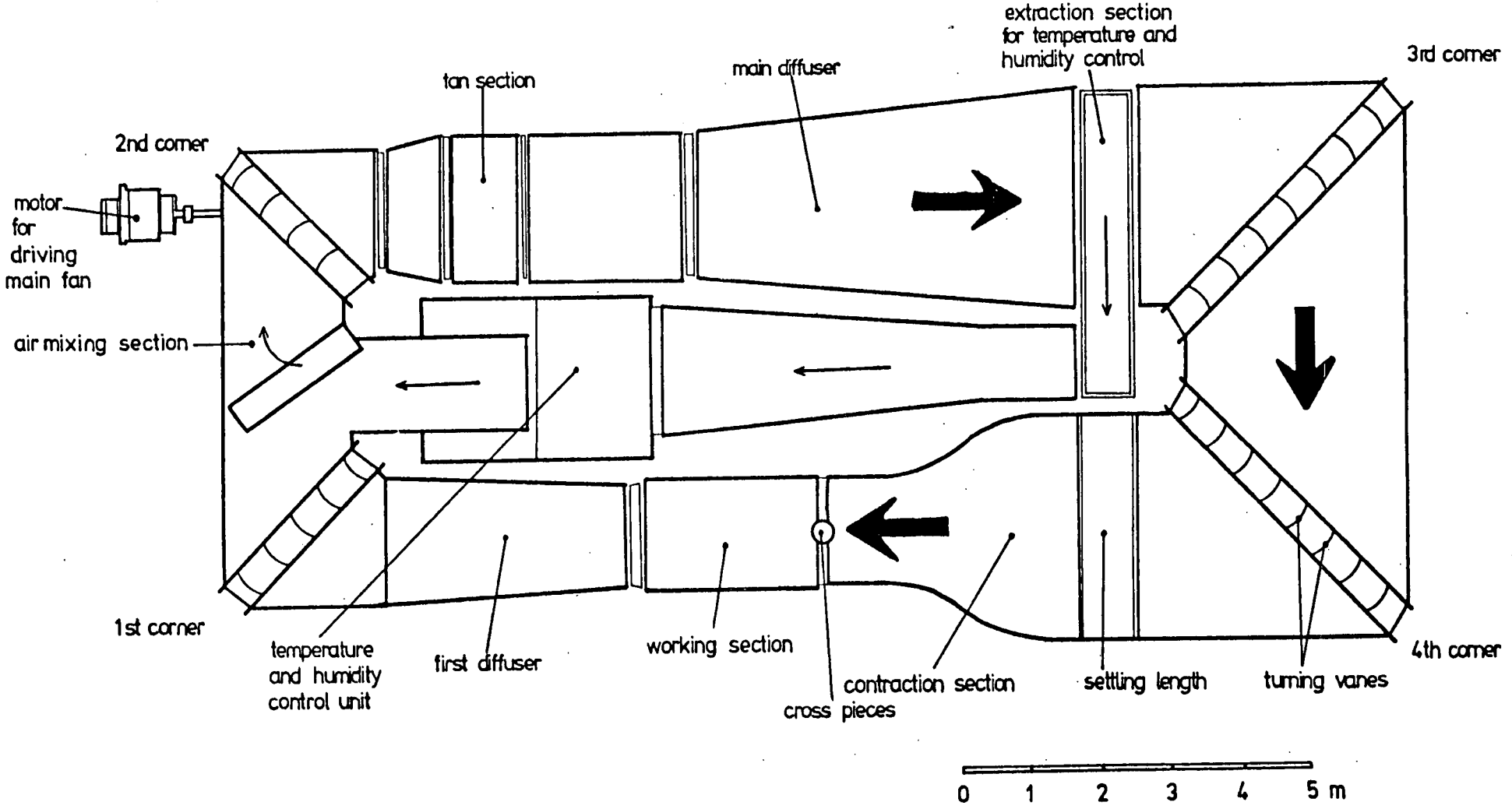


Figure 3.1 Controlled Environment Wind Tunnel ( from Thompson 1975 )

## 3.2 The wind tunnel

The following brief description of the controlled environment wind tunnel is based on that of Thompson (1975).

A plan of the wind tunnel, which is of the closed circuit or Prandtl type is given in figure 3.1. Air flow is driven by the main fan situated at the second corner. Turning vanes at the corners and the smooth finished surface of the wind tunnel restrict the development of turbulence. The walls of the rectangular cross-section tunnel are constructed of two layers of marine plywood sandwiching expanded polystyrene, mounted on a steel framework.

Part of the air is extracted at the third corner for temperature and humidity control. Heating and refrigeration units mounted outside the wind tunnel provide a wide, stable range of air temperatures. Humidity is regulated by the injection of steam into the air.

Cylindrical cross-pieces mounted in the throat of the wind tunnel generate artificial turbulence within the working section.

The 1.8 m x .9 m working section can be raised and lowered by electromechanical means for access. The internal glass walls are lined with silver-coated polyester to increase irradiance. Nine 400 W metal-halide lamps and six 60 W tungsten lamps mounted above the glass ceiling provide an irradiance of ca. 250 $\mu E\ m^{-2}\ s^{-1}$ in the 400–700 nm. range at a height of 30 cms., just above the plants. At this level of photosynthetically active flux density, the net photosynthetic rate of Long Beach P. contorta should be about half the maximal light-saturated rate (chapter 7). In the 300–3000 nm. range (using a Kipp's solarimeter), irradiance is about 140 $W\ m^{-2}$. For a 17-hour day, this gives a daily total of 8.7 $MJ\ dy^{-1}$. Data collected over four years on the roof of the

Department of Forestry and Natural Resources show an average of 13.8 MJ $dy^{-1}$ for April to September (Caborn, pers. comm.). Plants in the wind tunnel thus receive approximately 60% of the short wave radiation received outdoors.

The turbulence in the wind tunnel was sufficient to cause considerable small-scale movements of the pine stems and needles, at high windspeeds. Even at low windspeeds there was slight plant movement. Large-scale movements, as occur in a gusty wind, did not occur in the wind tunnel.

## 3.3 The growth room

The growth room is a small room with walls coated in silver coated polyester. Plants are placed on a 1.6 m x 1.0 m bench of adjustable height, situated beneath the lights. Fifteen 400 W metal-halide and twelve 60 W tungsten lamps are mounted above the glass ceiling of the growth room. Control of air temperature is provided by heating and refrigeration units mounted in a duct outside the room through which air is circulated. Water droplets are introduced into the air by a 'Defensor' humidifier (Defensor Ltd.) to regulate air vapour pressure.

The room was modified by Mr. R. Lawson in an attempt to increase the windspeed. Plyboards coated with silver-lined polyester were placed along the long sides of the bench. A large fan placed at one end blew air across the table, through perforated plyboard, figure 3.2. Windspeed was considerably increased, but somewhat uneven across the bench, figure 3.3. This modification had the considerable advantage of improving the humidity control system: water droplets evaporated into the air before leaving the fan and the previous 'mist' of water droplet was eliminated.

Irradiance levels were reduced in the growth room to match those in the wind tunnel.

Figure 3.2 Pinus contorta in the modified growth room. A large fan behind the perforated plyboard provides an increase in windspeed.

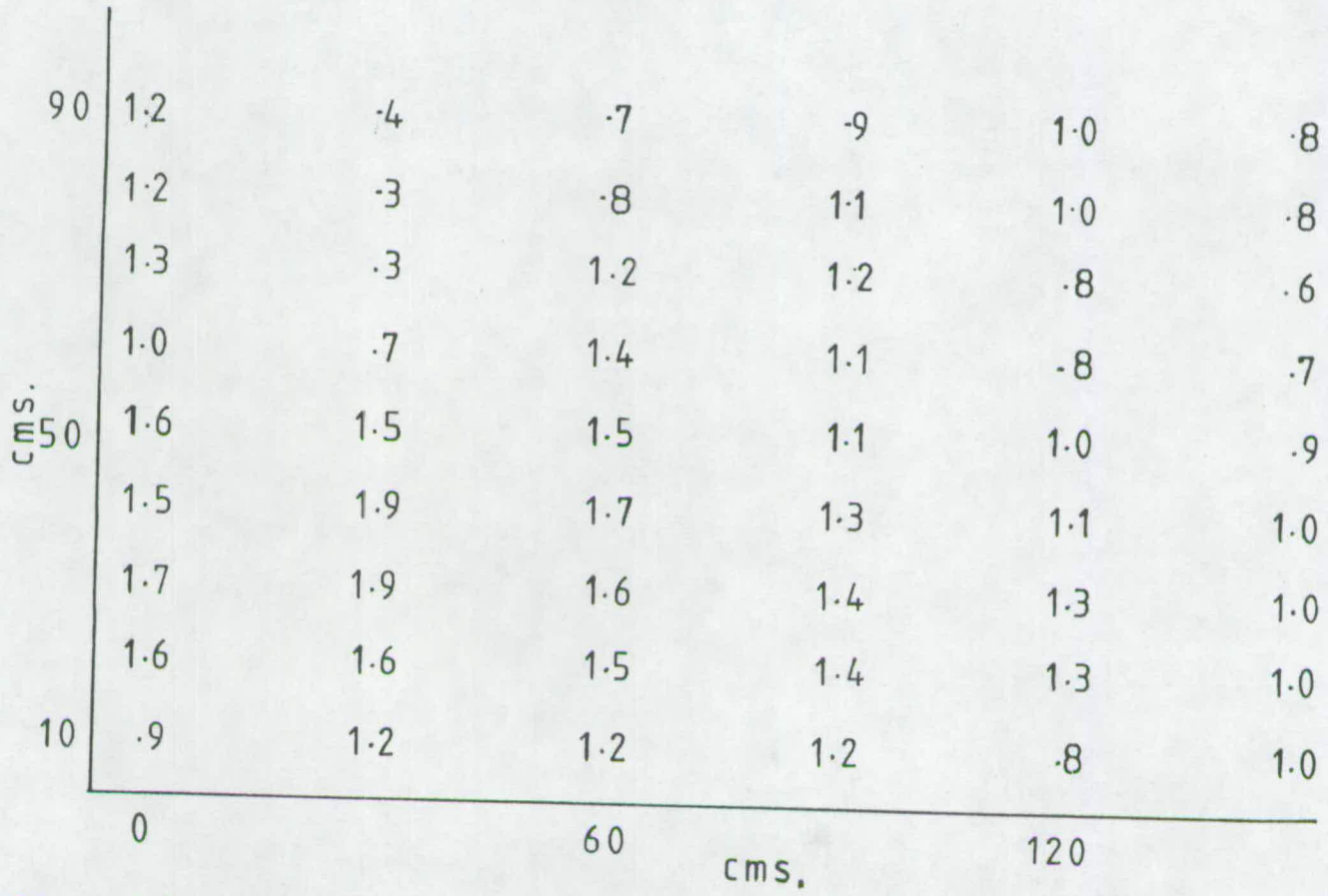


Figure 3.3 Windspeed over the working section of the modified growth room, with no plants present, $ms^{-1}$. The fan is situated at -30 cms on the x-axis, in this diagram.

## 3.4 The shaking frames

Plants were shaken by shaking frames outdoors in cold frames. A lightweight rectangular frame constructed from Dexion was mounted on wheels on a Dexion base. This frame was moved back and forth by a Citenco electric shaking motor, figure 3.4. The force was transmitted to the plants by wooden stakes tied to the moving frame figure 3.5. Plants were frequently examined for signs of damage to the stem where they were in contact with the wooden stakes. No damage to the stem other than a gradually increasing 'shininess' of the bark at the point of contact was observed.

The frequency of shake was quite low: 1-2 Hz. It should be noted that the control plants, which stood nearby in the cold frames were not often completely stationary. Windspeed was reduced in the cold frames, but often strong gusts would cause considerable motion of the control plants.

Figure 3.4 The shaking frame.

Figure 3.5 The movement of the Dexion frame is transmitted to the plants by wooden stakes.

## 3.5 Measurement of the environment

To characterise the various environments in which the plants were grown, net radiation, photosynthetically active radiation (PhAR), air temperature and vapour pressure, needle and bud temperatures (where necessary) and windspeeds were monitored.

Net radiation was measured with a polythene-shielded, Funk net radiometer, model ME-1, produced by Swissteco Pty. Ltd., Australia. PhAR was measured with a quantum-sensor, model LI-1905R produced by Lambda Instruments Co. Ltd., U.S.A. Wet-bulb and dry-bulb air temperatures were measured with an Assman psychrometer (Cassella Ltd., England). Windspeed was measured with a 5 cm diameter, vane anenometer (Airflow Developments Ltd., England).

Thermocouples were simply manufactured by tying 42 S.W.G. copper and constantan wires together; to produce a knot of not more than 1 mm diameter. These thermocouples were tightly coiled around needles and buds, to provide good thermal contact. In the wind tunnel, temperatures were measured and recorded with a mark II temperature recorder, manufactured by Kent Control Systems Ltd., England. This recorder incorporates an electronic reference junction. In the growth room and outdoors, an ice/water mixture was used as the reference junction, and the temperature-induced e.m.f. was measured using a D. C. millivoltmeter, type 1201, produced by Comark Instruments Ltd., England.

## 3.6 Procedures

The aim in using the wind tunnel and growth room was to produce two environments differing only in windspeed. To do this, PhAR and net radiation were measured over the working section of the wind tunnel at a 'plant height' of 30 cms. above the working surface. Metal halide and tungsten bulbs were removed and the bench height adjusted in the growth room, until PhAR and net radiation levels were as close as possible to those in the wind tunnel. Air temperatures and vapour pressures were initially set using the Assman psychrometer, and then recorded using the monitoring equipment supplied with the wind tunnel and growth room. Windspeeds immediately in front of each plant were measured. Mean windspeed in the wind tunnel was adjusted to equal the mean windspeed in the growth room, where required.

The high windspeed treatments in the wind tunnel differed between experiments in the windspeeds used, from 7 m $s^{-1}$ to 9 m $s^{-1}$. The lowest mean windspeed, 7 m $s^{-1}$, was used when there were 40 small, 1 year old plants, in the wind tunnel, as this was the highest windspeed possible without blowing the leading plants over. 9 m $s^{-1}$ was measured when there were only 6 plants in the wind tunnel. The objective of the high windspeed was to produce the maximum amount of plant movement possible in the absence of a 'gusty' airflow. The plant movement produced by these windspeeds may be approximately compared with natural windspeed by use of the Beaufort Scale. The plant movement in the wind tunnel at high windspeed correspond to about Beaufort numbers 3-5, which are not uncommon in Scotland (Caborn 1957). Plants in the growth room were moved very gently by the wind, corresponding approximately to Beaufort number 1.

Night temperatures were the same as day temperatures in all experiments, as there is no facility for lowering night temperature in the wind tunnel.

Photoperiods were adjusted to promote or prevent shoot extension. During the extension growth experiment, the photoperiod was 17 hrs. During the water relations experiment, the photoperiod was 10 hrs.

In the shaking experiments, control plants were placed immediately adjacent to the shaking frames in the cold frames. Although the cold frames greatly reduced windspeed, control plants were often moved by occasional gusts of wind.

As the new shoots extended, the height of shaken plants was adjusted relative to the shaking frame when it was judged that the motion of the extending shoots were such as to cause breakage of the shoot. Despite this, several shoots were broken by the shaking treatment.

## 3.7 Preparation of the plant material

Two year old Long Beach and Hazelton provenances of P. contorta ((73(7972)1 and (65(7114)3) and one year old Long Beach were provided by the Forestry Commission (courtesy of Mr. R. Lines) in January and February 1977 and 1978. These were immediately potted into U. C. Mix IV D compost (Baker 1957) and stood out in the cold frames. Plants remained in the cold frames until their removal to the various experiments. The lowest branches of the plants were removed in order to (i) enable plants to be tied into plastic bags for gravimetric determination of transpiration rate and (ii) to improve the water status of the plants (which would have lost considerable amounts of roots when uplifted by the Forestry Commission).

From the beginning of the growing season onwards, nutrients were added to the plant in the form of a liquid feed once per week. The 'Solufeed Standard' powder consists of 22% nitrate, 19% soluble phosphate and 16% potash, weight for weight (S.A.I. Horticulture Ltd., Technical Division, pers. comm.). When made up as directed the plant is supplied with 4.0, 3.5 and 2.9 mg $l^{-1}$ of nitrate, phosphate and potash, respectively.

In late March, the length and width of the plant stems and leader buds, and number of lateral buds were determined for all the plants. These measurements were used to provide groups of plants as uniform as possible for experimentation. (This is further discussed in 4.1).

# Chapter 4 The effects of wind and shaking on the morphology of P. contorta

## 4.1 Introduction

As discussed in 2.1.2 exposure and shelter experiments suggest that wind may have an adverse effect on conifer growth. Controlled environment experiments show an adverse effect of wind on plant growth in a variety of species (2.1.4). Shaking has been shown to reduce extension growth of several species of trees and other plants (2.1.7) and both increases and decreases in radial growth have been reported. It is possible that any effect of wind on plant growth is due to the shaking it causes.

Experiments reported in this chapter describe the effects of high winds and shaking on the growth and form of P. contorta. Parameters examined are extension of leader and lateral shoots, 'apical control', extension of needles, radial growth and stem elasticities.

As discussed in 2.2.2, conifer shoot extension is a function both of the number of stem units formed in the previous year and of extension per stem unit. Many authors have found extension growth better related to the previous year's environment than to the current year's environment (Kozlowski 1962, 1971). However, Clements (1970) demonstrated that the reduced extension growth of Pinus resinosa in year n, due to water stress imposed in year n-1, was clearly heralded by a reduction in bud size at the beginning of year n. Kozlowski et al (1973) showed that shoot elongation of Pinus strobus is highly correlated with initial bud lengths and widths. These experiments suggest that the effect of the previous year's environment can be estimated by determining initial bud

dimensions. By ensuring that all experimental groups of plants have the same mean bud sizes, differential affects of environmental history may be reduced avoided. (This can be checked at the end of the experiment by determining fascicle numbers). Current year elongation has also been related to the previous year's elongation (Kozlowski 1962), suggesting that including stem lengths and widths in initial measurements, and ensuring that experimental groups also have the same mean stem sizes, is advisable.

Measurement of elongating lateral shoots, as well as leader shoots, allows determination of the apical dominance exerted by the leader. Brown et al (1967) pointed out that the control exerted by leading shoots on laterals must be very different from that exerted by apical buds on axillary buds and introduced the term 'apical control' to describe this. Little (1970) measured 'apical control' in Pinus strobus as the ratio of the length of the longest lateral shoot to the length of the leading shoot, whereas Cannell (1974) used the ratio of mean lateral shoot length to leader length. In the work to be described here, 'apical control' is estimated by the method of Cannell (1974) as this is probably more robust.

Leaf area growth is as sensitive as height growth to wind, or more so (2.1.4). But conifer needle extension has a considerably different cycle of growth to that of most broadleaved species (2.2.2), so the effects of wind and shaking on needle extension in P. contorta were also observed.

Jacobs (1954) and Burton and Smith (1973) found that after several years guying, trees of Pinus radiata and Pinus taeda were no longer stable in normal winds. This suggests that the wind-induced motion increased the rigidity of the non-guyed trees, either through increasing the

Young's modulus of elasticity (equation 4.2) or simply by the effect on radial growth (equation 4.3). An increase in Young's modulus could possibly come about by the laying down of compression wood in response to motion. The recent review of reaction wood by Wilson and Archer (1977) shows that stems and branches are sensitive to their orientation with respect to the vertical and if displaced from their natural position, will produce reaction wood in order to bend back into the original position. Subjecting plants to motion might induce reaction wood formation though Neel and Harris (1971a) and Burton and Taylor (1973) found no evidence of this. The effects of shaking on stem elasticity was determined, to investigate these points.

## 4.2 Materials and Methods

Treatment of the plant material is described in 3.7. Two year old saplings of Long Beach provenance (73(7972)1) of P. contorta were used in experiments 4.3.1, 4.3.2 and 4.3.3. One year old saplings were used in experiment 4.3.4. Measurement of environmental conditions and plant temperatures, are described in 3.4.

Length of extending shoots were measured to the nearest mm. from the point of insertion of the shoot into the main stem. Stem widths were measured with calipers to the nearest 0.25mm. At the end of each experiment, needles were removed from leader stems and fascicle numbers were determined. The number of fascicle scars per contact parastichie from apex to base were counted, and multiplied by the number of contact parastichies (Baxter and Cannell 1978). Needle length of three needles per plant near the apical bud were measured to the nearest mm.

In experiment 4.3.1, environmental conditions in the wind tunnel and growth room were matched as closely as possible, as described in 3.4. The environmental conditions are detailed in table 4.1. Plants were measured and removed to the wind tunnel and growth room on 6/4/78. Initial plant measurements are recorded in table 4.2. For the first nine days the windspeed in the wind tunnel was kept at the same low windspeed as that in the growth room, and subsequently it was increased.

In experiments 4.3.2. and 4.3.3, plants were measured on 31/3/78 and 3/4/78 respectively and subjected to continuous shaking at 1-2 Hz by shaking machines in the cold frames (as described in 3.3). Their growth was compared to nearby control plants in the cold frames, Air, bud and needle temperatures, net radiation and water potential were measured over

a two day period in June, as described in 3.4 and 8.3.4. Initial plant measurements are detailed in tables 4.4 and 4.6. Experiment 4.3.3 continued throughout the growing season. Needle lengths and stem diameters were monitored over this period.

In experiment 4, needle extension of groups of 40 one year old P. contorta over 17 day periods in the wind tunnel at either low windspeed or high windspeed were compared with needle extension of plants in the growth room. Environmental conditions are detailed in table 4.8.

The Young's modulus of elasticity (Y) of new leader stems of Long Beach and of Hazelton (65(7114)3) provenances were measured at the end of the 1977 growing season (October). Plants subjected to continuous shaking were compared with controls. At the end of experiment 4.3.2 described above, Y of plants subjected to continuous shaking was compared with those of controls (July).

Young's modulus of elasticity (Y) was determined by applying known weights to horizontally clamped stems and measuring the resulting vertical deflections (Morley 1953). After Morley (1953), the moment of inertia (I) and Young's modulus of elasticity (Y) can be found from:

$$I = \frac{\pi d^4}{64} \qquad (4.1)$$

where d is the cylinder (stem) diameter.

$$Y = \frac{l^3}{3I} \cdot \frac{w}{v} \qquad (4.2)$$

where $l$ is the cylinder length,

and v is the vertical deflection resulting from the applied weight, w.

The gradient (b) of the relationship between v and w for a series of weights (w) was calculated by linear regression. (4.2) now becomes:

$$Y = \frac{l^3}{3Ib} = \frac{64\, l^3}{3\pi d^4\, b} \qquad (4.3)$$

'Rigidity' is here defined as the deflection per unit load for observed stem lengths and width, i.e. b or v/w. 'Rigidity' is proportional to length cubed:

$$b = k\, l^3 \Rightarrow \frac{b_1}{l_1^3} = \frac{b_2}{l_2^3} \qquad (4.4)$$

'Rigidities' of actual stem lengths were calculated from (4.4), where $b_1$ and $l_1$ refer to the rigidity of the length of stem used in the determination, and $b_2$ and $l_2$ refer to the calculated 'rigidity' for the actual stem length of the plant.

## 4.3 Results

### 4.3.1 Effects of high wind on the morphology of P. contorta

Initial measurements of plants and environmental conditions in the wind tunnel and growth room are detailed in tables 4.1 and 4.2. The extension of leader and lateral shoots in the two environments are shown in figure 4.1. During the low windspeed period in the wind tunnel, there were no differences in extension growth between the two groups. When the windspeed was raised to 8.5 m $s^{-1}$, extension of leader and lateral buds in the wind tunnel were reduced compared to controls. Final measurements on the plants are shown in table 4.3. Extension of leader and lateral shoots were reduced 22% and 17% respectively, by high windspeed. Widths of new and basal stems, and 'apical control' were unaffected. The number of fascicles in the leaders did not differ significantly between the two groups, so the differences in final extension can be attributed to current season differences in environment, i.e. to the differences in windspeed.

Figure 4.2 shows two plants from the wind tunnel and two from the growth of similar initial measurements.

Although there was a 1.2°C difference in bud temperature and a .2°C difference in needle temperatures between the two groups, it is unlikely that this could account for the differences in extension. This point is discussed further in the discussion, 4.4.1.

Table 4.1 Environmental conditions in the wind tunnel and growth room

| | Daylength hrs. | Net radiation $W\ m^{-2}$ | Photosynthetically Active Radiation $\mu E\ m^{-2}\ s^{-1}$ | Temperature Air °C | Bud °C | Needle °C | Air Vapour Pressure mb | Windspeed $m\ s^{-1}$ |
|---|---|---|---|---|---|---|---|---|
| Growth Room | 17 | 174 | 260 | 15 | 16.2 | 15.6 | 12 | .6 |
| Low Wspd. Wind Tunnel | 17 | 164 | 257 | 15 | 16.9 | 15.8 | 12 | 8.5 |
| High Wspd. Wind Tunnel | 17 | 164 | 257 | 15 | 15.3 | 15.0 | 12 | .6 |

Table 4.2 Wind tunnel/growth room experiment. Initial plant measurement, means and standard errors

| | Stem | | Leader Bud | | No. of Lateral Buds | No of Plants |
|---|---|---|---|---|---|---|
| | width mms. | length mms. | width mms. | length mms. | | |
| Wind Tunnel Group | 5.3 ± .12 | 184 ± 6.1 | 4.75 ± .09 | 27.8 ± 2.8 | 3.9 ± .30 | 18 |
| Growth Room Group | 5.5 ± .23 | 183 ± 5.5 | 4.86 ± .13 | 26.6 ± 2.6 | 4.2 ± .39 | 17 |

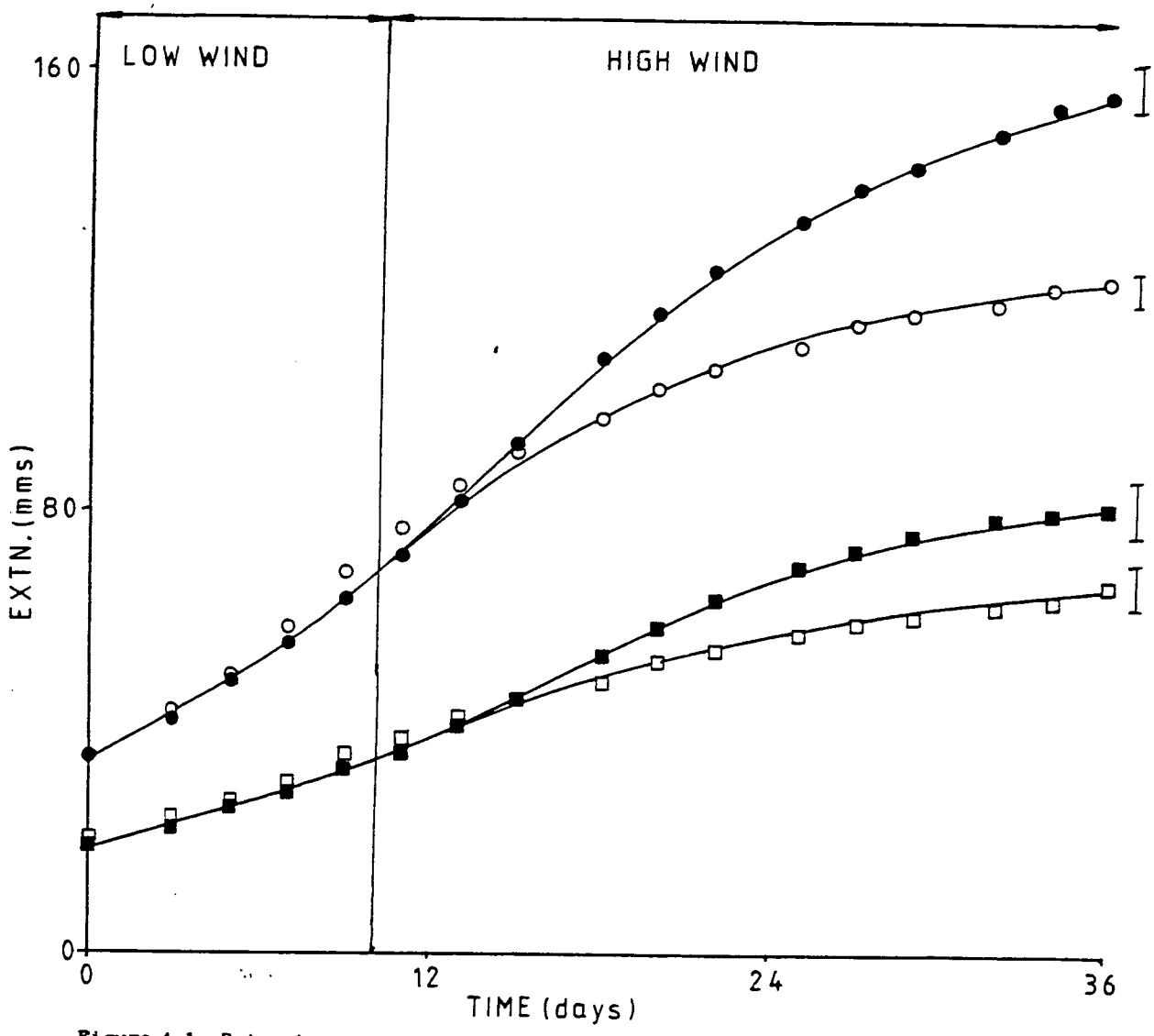


Figure 4.1 Extension growth of P. contorta in the growth room( low windspeed throughout ; solid symbols ) or in the wind tunnel ( low windspeed days 1-9, subsequently high windspeed open symbols ). Other environmental conditions similar in the two environments.
Circles : mean leader extension ; Squares : mean lateral extension
Bars are two standard errors.

Table 4.3 Effects of high wind on morphology of P. contorta

Final measurements. Means and standard errors.

| | Leader | | Basal | Mean Lateral | Apical | Fascicle No. |
|---|---|---|---|---|---|---|
| | Length mms | Width mms | Width mms | Length mms | Control * % | on Leader |
| Wind Tunnel | 113.2 | 5.4 | 6.8 | 81.4 | 52.0 | 239 |
| Group | ± 5.81 | ± .13 | ± .14 | ± 4.58 | ± 1.58 | ± 14.0 |
| Growth Room | 145.1 | 5.5 | 6.7 | 67.3 | 55.5 | 259 |
| Group | ± 7.43 | ± .29 | ± .24 | ± 3.90 | ± 1.58 | ± 10.7 |
| level of statistical significance | .001 | NS | NS | .05 | NS | NS |
| % change | -22% | - | - | -17% | - | - |

* Apical control = mean lateral stem length as a % of leader length

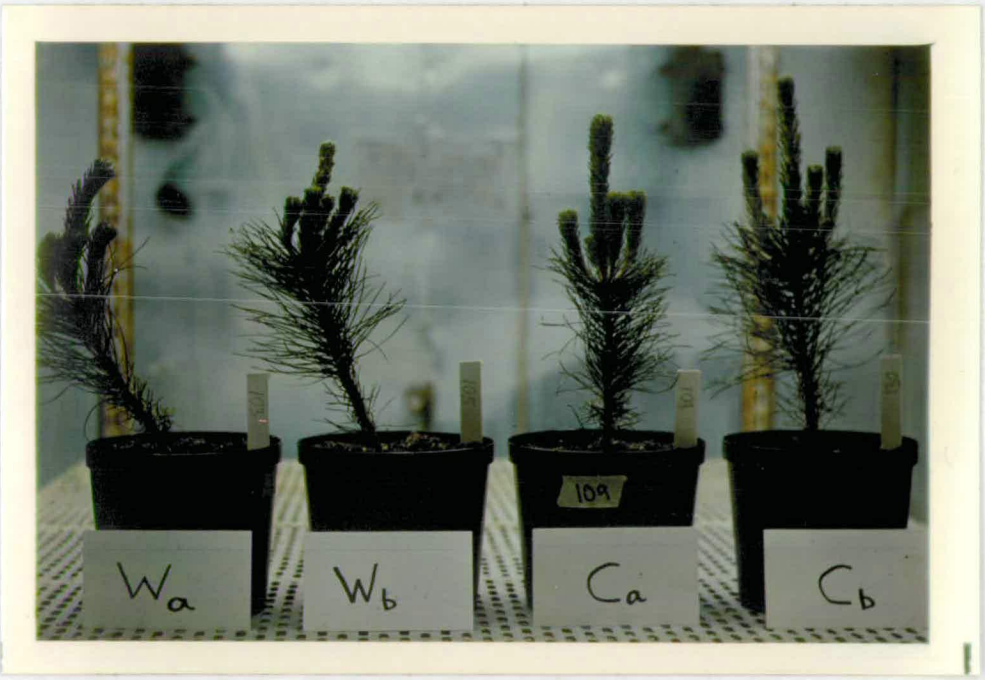


Figure 4.2 P. contorta grown in the wind tunnel at high windspeed (W), or in the growth room at low windspeed (C). Plants with subscript $_a$ had the same initial measurements, as did plants with subscript $_b$.

### 4.3.2 Effects of shaking on the morphology of P. contorta

Four of the eighteen plants subjected to shaking in the outdoor cold-frames were damaged by the shaking stress. Although all plants received the same applied force from the shaking frame at a plant height of ca. 12 cms. the force experienced by the leader stem during acceleration and deceleration is proportional to the length of the leader, and in the case of four plants, caused breakage of the young extending leader shoots.

Initial and final plant measurements are detailed in tables 4.4 and 4.5. Extension of leader and lateral shoot are shown in figure 4.3. Shaking reduced both leader and lateral extension by 18%. Apical control and stem width growth were not affected by shaking. Fascicle numbers, predetermined in the previous year, were not significantly different between the two groups.

Diurnal changes in net radiation, air, bud and needle temperature, water potentials and leader extension of five plants of each of the two groups over a two-day period are presented in figure 4.4. No significant or continuous differences in air, bud or needle temperatures were observed. Water potentials of the shaken plants tended to be less negative then those of the control plants, but the differences were not statistically significant. Leader extension mainly occurred during the night when water potentials were least negative.

Table 4.4 Initial plant measurements. Means and standard errors

| | Stem | | Leader Bud | | No. of lateral | No. of |
|---|---|---|---|---|---|---|
| | width mms | length mms | width mms | length mms | Buds | Plants |
| Shaking Group | 5.23 ± .182 | 176 ± 5.6 | 4.71 ± .208 | 27.4 ± 2.25 | 4.5 ± .25 | 14* |
| Control Group | 5.38 ± .035 | 176 ± 5.4 | 4.64 ± .122 | 23.8 ± 1.95 | 4.1 ± .27 | 18 |

* Leader stems of four plants broke due to excessive shaking

Table 4.5 Final measurements. Means and standard errors

| | Leader | | Basal | Lateral | Apical | Fascicle No. |
|---|---|---|---|---|---|---|
| | length mms | width mms | width mms | Extension mms | Control* % | on Leader |
| Shaking Group | 181 ± 6.8 | 6.0 ± .30 | 7.5 ± .21 | 97.8 ± 5.27 | 49.6 ± 2.30 | 271 ± 13.6 |
| Control Group | 220 ± 7.3 | 5.9 ± .14 | 7.1 ± .19 | 118.7 ± 6.38 | 50.3 ± 2.06 | 288 ± 8.1 |
| level of statistical significance | .001 | NS | NS | .02 | NS | NS |
| % change | -18% | | | -18% | | |

* Apical control = mean lateral stem length as a % of leader length

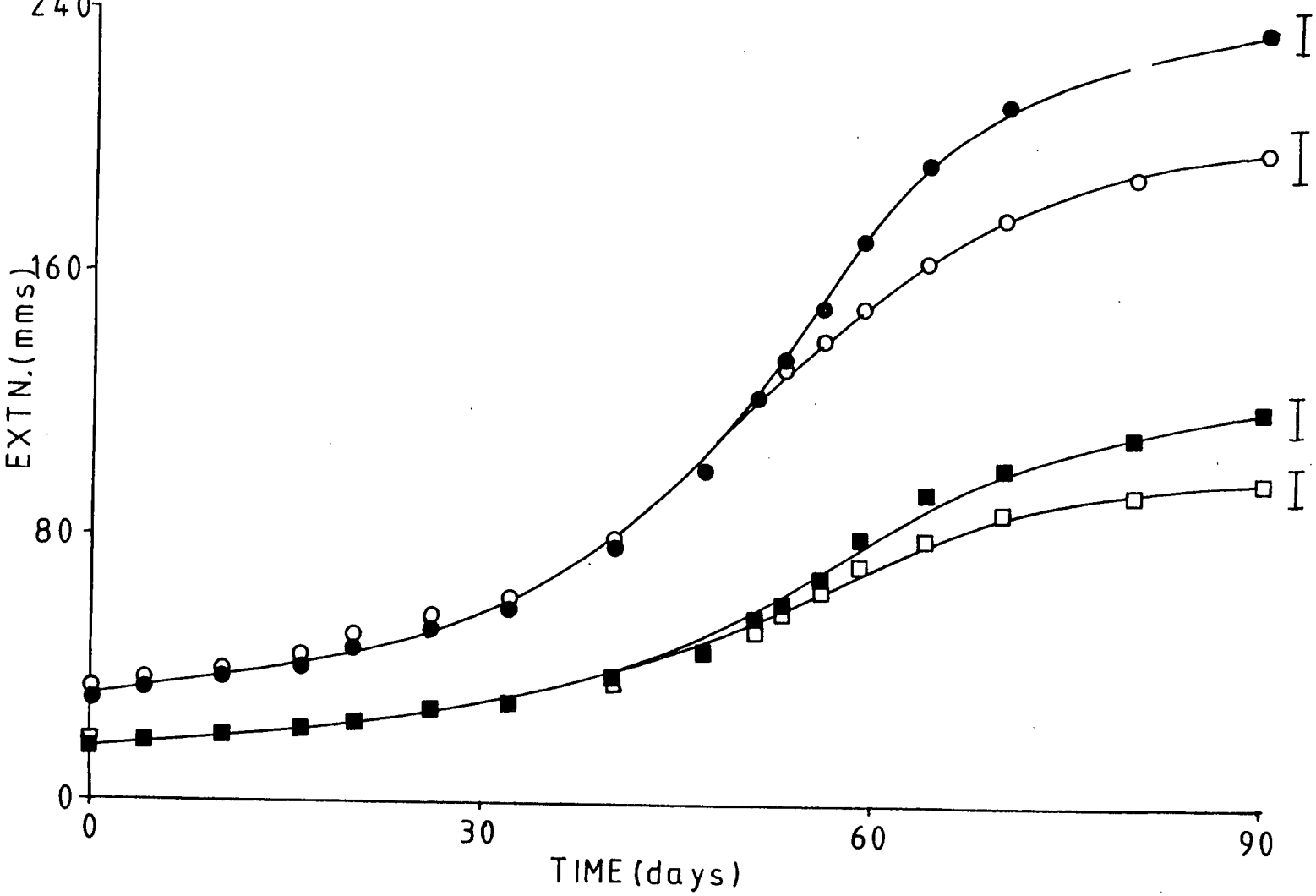


Figure 4.3 Extension growth of control ( solid symbols ) and shaken ( open symbols) P. contorta.
Circles : mean leader extension ; Squares : mean lateral extension
Bars are 2 standard errors.

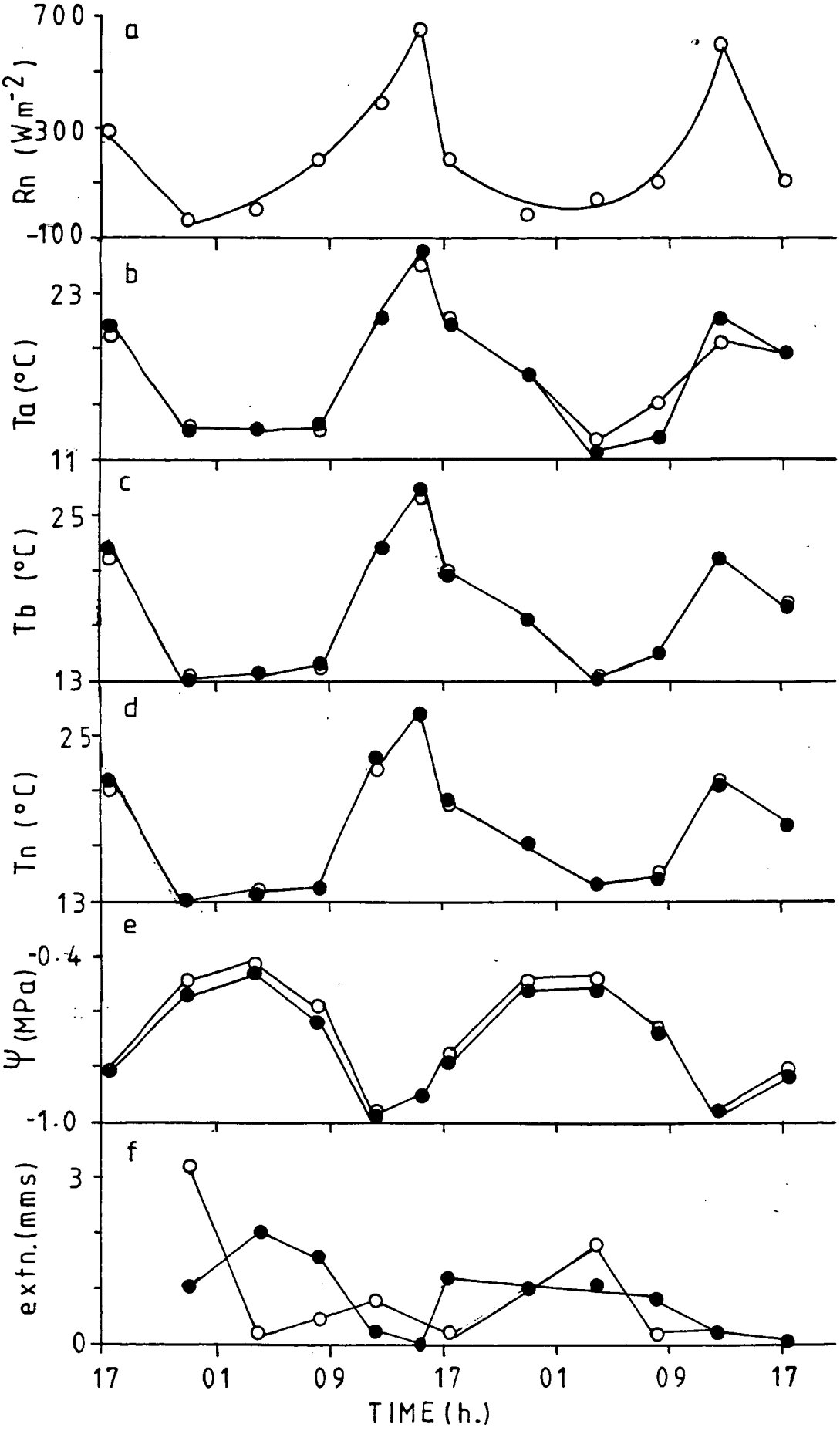


Figure 4.4 Environmental measurements in the cold frames, 4/6/78 - 6/6/78
a Net radiation ; b Air temperature ; c Bud temperature ;
d Needle temperature ; e Water potential ; f leader extension.
Solid symbols are Control plants, open symbols are shaken plants.

### 4.3.3 Effects of shaking on the morphology of *P. contorta*

In this experiment, the extending leader stem of only one shaken plant broke due to excessive shaking. Initial and final measurements are detailed in tables 4.6 and 4.7. Extension of leader and lateral buds of the two groups are presented in figure 4.5.

As observed in the other experiments, extension of both leader and lateral shoots was reduced by 21%. Stem width growth and 'apical control' of the two groups were again unaffected. Differences in fascicle number were not statistically significant.

Needle lengths and stem diameters throughout the growing season are presented in figure 4.6. Even at the very first measurement of needle lengths, those of the shaken plants were significantly less than those of the control plants, and at the end of the growing season, the mean needle length of the shaken plants was 10% less than that of the controls. The rate of needle extension was reduced by 11% by shaking. Growth in stem width was unaffected even by shaking over the whole growing season.

Figure 4.7 shows a shaken and a control plant at the end of the growing season. These plants had the same initial measurements.

Table 4.6 Initial plant measurements. Means and standard errors

| | Stem | | Leader Bud | | No. of lateral | No. of |
|---|---|---|---|---|---|---|
| | width mms | length mms | width mms | length mms | Buds | Plants |
| Control Group | 4.26 ± .124 | 130 ± 3.5 | 4.18 ± .090 | 21.3 ± 1.2 | 3.4 ± .27 | 17* |
| Shaking Group | 4.37 ± .173 | 129 ± 3.1 | 4.40 ± .163 | 21.5 ± 1.5 | 3.0 ± .35 | 18 |

* Extending leader stem of one plant broken due to excessive shaking

Table 4.7 Final measurements. Means and standard errors

| | Leader | | Basal | Lateral | Apical | No. of |
|---|---|---|---|---|---|---|
| | Length mms | width mms | width mms | Extension mms | Control * % | Fascicles on leader |
| Control Group | 203 ± 6.1 | 7.2 ± .20 | 8.8 ± .20 | 109.6 ± 5.80 | 54.4 ± 2.73 | 218 ± 11.2 |
| Shaking Group | 160 ± 5.6 | 7.5 ± .26 | 8.3 ± .22 | 86.8 ± 6.60 | 53.6 ± 2.66 | 222 ± 10.5 |
| level of statistical significance | .001 | NS | NS | .02 | NS | NS |
| % change | -21% | | | -21% | | |

* Apical control = mean lateral length as a % of leader length

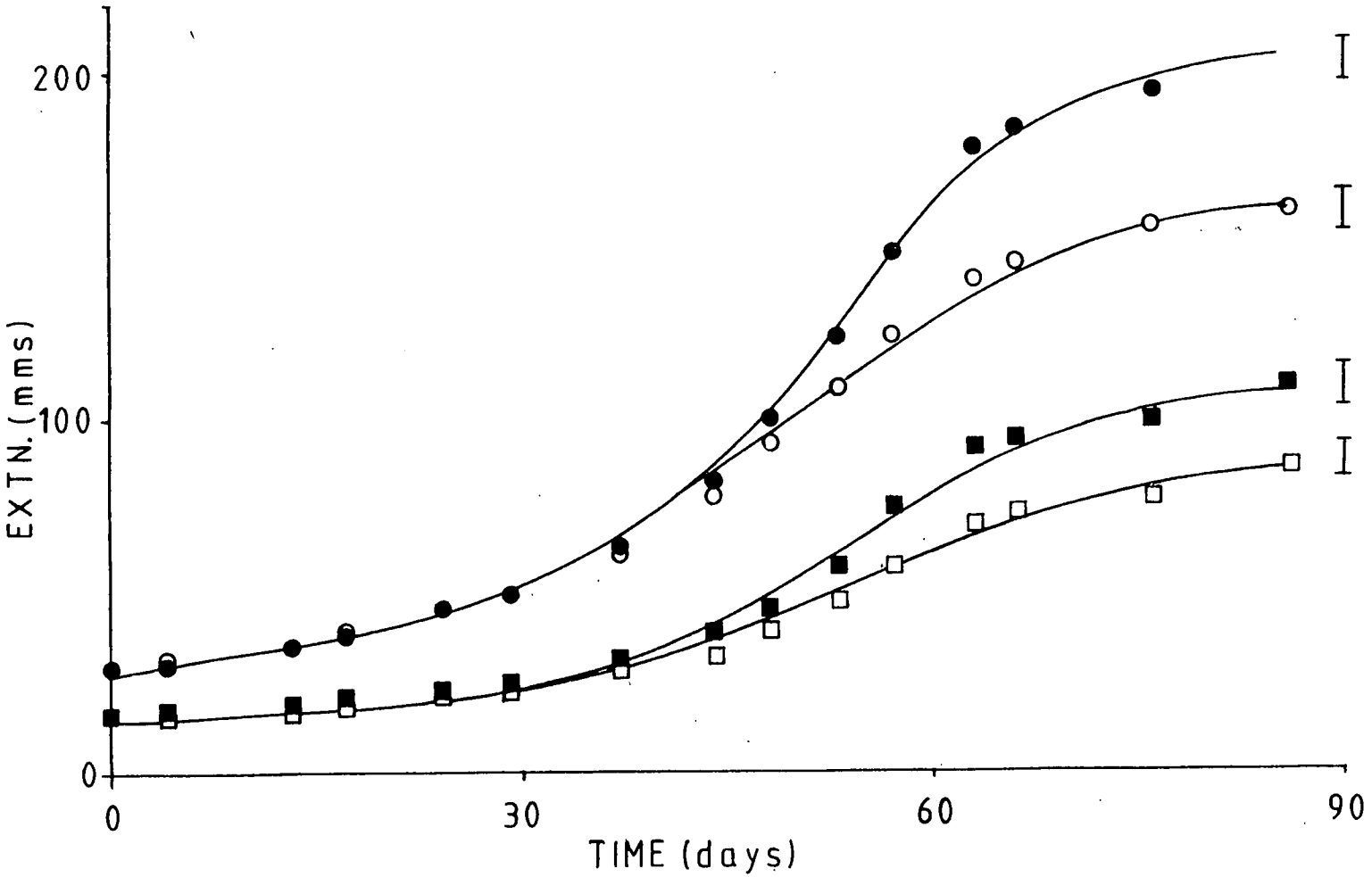


Figure 4.5 Extension growth of control ( solid symbols ) and shaken ( open symbols ) P. contorta.
Circles : mean leader extension ; Squares : mean lateral extension
Bars are 2 standard errors.

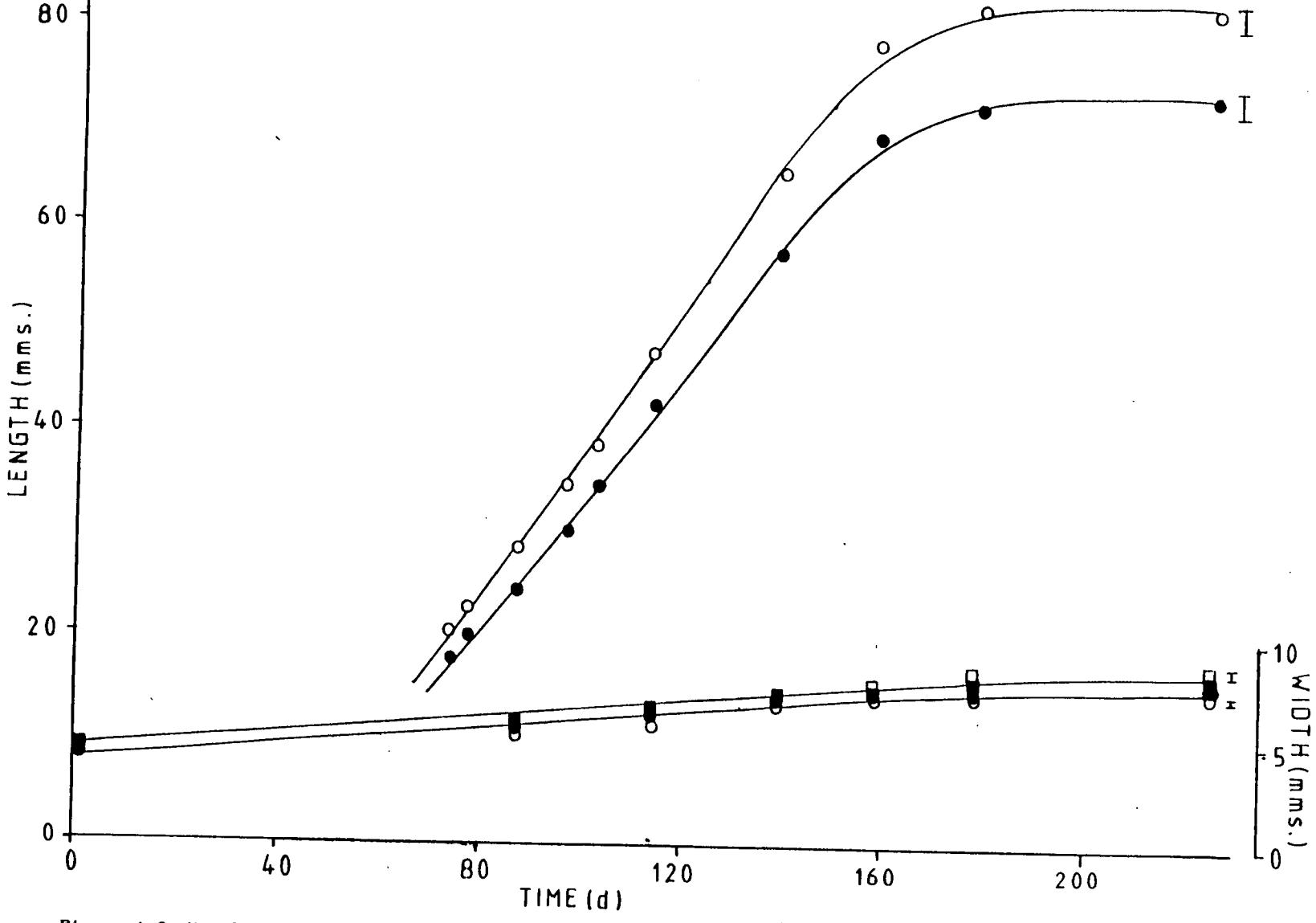


Figure 4.6 Needle extension (circles) of P. contorta and on radial growth of basal stems (squares) and leader stems (circles). Open symbols : Control plants ; Closed symbols : Shaken plants. Bars are 2 standard errors.


Figure 4.7 This shaken (Sh) plant had the same initial measurements at the beginning of the growing season as this control (C) plant.

### 4.3.4 Effects of high wind on needle extension

Needle extension of forty one year old P. contorta in the wind tunnel was compared with that of forty plants in the growth room. Environmental conditions are detailed in table 4.8.

When the windspeed in the wind tunnel was the same as that in the growth room, there were no differences in needle extension (Figure 4.8). When P. contorta was subjected to a high windspeed in the wind tunnel ($7\ m\ s^{-1}$), the rate of needle extension was reduced 30% compared to control plants in the growth room. Needle temperatures were 0.5 °C lower at the high windspeed.

Table 4.8 Environmental conditions in the wind tunnel and growth room

| | Daylength | Net Radiation | Photosynthetically Active Radiation | Temperature | | Air Vapour Pressure | Windspeed |
|---|---|---|---|---|---|---|---|
| | | | | Air | Needle | | |
| | h. | $W\ m^{-2}$ | $\mu E\ m^{-2}\ s^{-1}$ | $^{o}C$ | $^{o}C$ | mb | $m\ s^{-1}$ |
| Wind tunnel High Windspeed | 18 | 136 | 292 | 17 | 17.1 | 13.6 | $7\ m\ s^{-1}$ |
| Wind tunnel Low Windspeed | 18 | 136 | 292 | 17 | 17.6 | 13.6 | $.4\ m\ s^{-1}$ |
| Growth Room | 18 | 157 | 284 | 17 | 17.8 | 13.6 | $.4\ m\ s^{-1}$ |

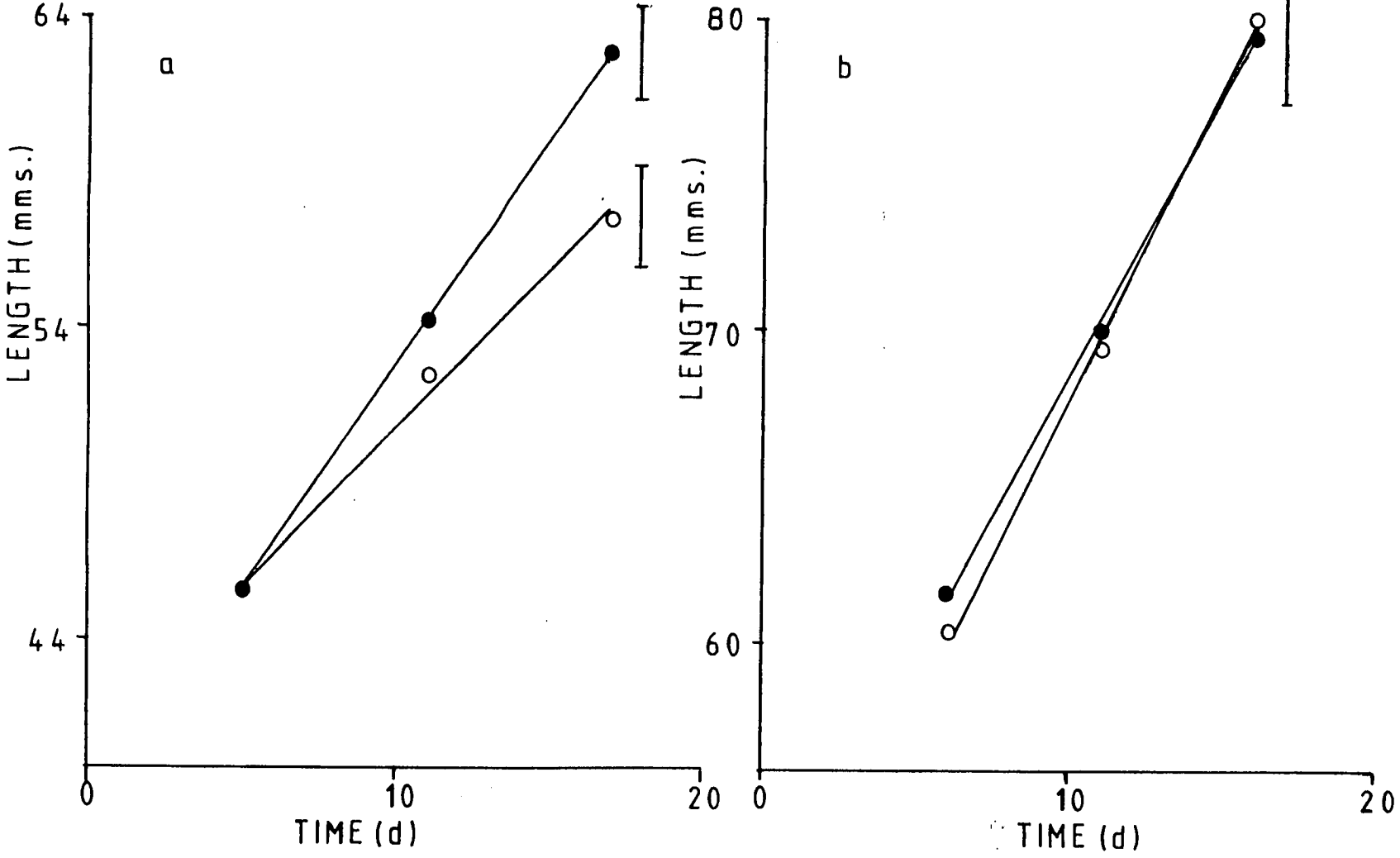


Figure 4.8 Needle extension of P. contorta in the low windspeed growth room ( solid symbols ) and in the wind tunnel ( open symbols ). a wind tunnel windspeed 7 $ms^{-1}$ ; b wind tunnel windspeed matched to that of growth room (.4 $ms^{-1}$ ) Bars are 2 standard errors.

### 4.3.5 Effects of shaking on stem elasticity

Table 4.9 shows the Young's modulus of elasticity and 'rigidities' of Long Beach and Hazelton provenances, measured at the end of the growing season, when stem development would be completed for that year. The differences between provenances and treatments are not statistically significant, but in the case of both provenances, the shaken plants have lower elasticities than controls. Despite this, the shaking treatment had no effect on 'rigidities' calculated for actual stem length and widths of the plants. The large differences between provenances in 'rigidity' were due to differences in the length and width growth of the two provenances, not to differences in elasticity.

Table 4.10 shows that stem elasticities of recently extended leader shoots (July) is much less than at the end of the growing season. Structural strength is presumably developed in the form of lignified and thickened cell walls over the growing season.

The 30% reduction in elasticity of new leader shoots due to shaking is statistically significant ($P<.01$). The much smaller reduction in elasticity of basal stems is not statistically significant, but once again elasticity of shaken stems is somewhat less than that of controls. Despite the large differences in elasticity of the new leader stems, differences in 'rigidity' are not statistically significant, due primarily to the reduced extension growth caused by shaking.

Table 4.9 Mean Young's modulus of elasticity and deflection per unit load (adjusted to actual stem length and diameter) of Long Beach and Hazelton provenances of P. contorta at the end of the growing season (October).

| | | Young's Modulus MN $m^{-2}$ | 'Rigidity'* mm $g^{-1}$ | No. of plants |
|---|---|---|---|---|
| Long Beach Provenance | shaken | 42.8 ± 4.05 | .86 ± .220 | 8 |
| | control | 49.3 ± 4.70 | .95 ± .147 | 9 |
| Hazelton Provenance | shaken | 43.4 ± 5.95 | 2.49 ± .460 | 7 |
| | control | 55.2 ± 4.18 | 2.50 ± .295 | 8 |

* Rigidity = deflection per unit load

Table 4.10 as Table 4.9 for current year stems and basal stems of Long Beach provenance of P. contorta, at the end of extension growth (July).

| | | Young's Modulus $MN\ m^{-2}$ | 'Rigidity' $mm\ g^{-1}$ | No. of Plants |
|---|---|---|---|---|
| Leader Stem | shaken | 9.6 ± 1.14 | 3.81 ± .375 | 14 |
| | control | 15.1 ± 1.10 | 4.29 ± .292 | 18 |
| Basal Stem | shaken | 50.2 ± 4.07 | .25 ± .036 | 14 |
| | control | 53.1 ± 2.82 | .19 ± .022 | 18 |

## 4.4 Discussion

### 4.4.1 The involvement of temperature in the wind and shaking effect.

Extension of leader shoots and needles was reduced by 20% and 10% respectively, by both high wind and shaking. Needle and bud temperatures were slightly lower in the high windspeed than controls; but were unaffected by the shaking treatment. The similarity between the effects of high wind and shaking suggest that they can be attributed to continuous motion rather than to the small temperature differences.

Malcolm and Pymer (1975) grew Picea sitchensis in a series of controlled air temperatures and found that a reduction in day temperature of 4°C and in night temperature of 2°C was required to produce a 20% reduction in extension. Assuming that bud temperatures closely followed the changes in air temperature, this suggests that the 0.9°C difference in bud temperatures reported here would have only a small effect on extension growth. In a similar experiment with grasses, Russell and Grace (1979) also argued that the observed small apical temperature difference was insufficient to produce the reduction in extension seen at high windspeed.

### 4.4.2 Effects of continuous motion on the morphology of P. contorta

Extension of leader and lateral shoots was reduced by ca. 20% by both high wind and shaking, confirming that as with other species, continuous motion has an adverse effect on the growth of P. contorta. The ratio of mean

lateral length to leader length, or 'apical control', was not affected by continuous motion induced by either method. Wind and shaking thus did not affect the branching habit, or 'bushiness', of P. contorta.

The rate of needle extension of the shaken and control outdoor plants was .62 and .69 mms $day^{-1}$ respectively. The rates of needle extension of P. contorta in the wind tunnel at high windspeed and of growth room controls were 1.00 and 1.45 mms $day^{-1}$ respectively. Needle extension proceeded at a considerably greater rate in the favourable growing conditions in the controlled environments. Needle extension rates were reduced 11% by shaking and 30% by high windspeed. The greater effect of wind is probably partly due to the greater extension rates in the controlled environments.

Radial growth of the stems was also unaffected by continuous motion of either type. As reviewed in table 2.2, guying and shaking caused increased radial growth of four of the seven species studied so far, including two species of Pinus. There is only one report in the literature that shaking reduces radial growth, and two reports that shaking has no effect on radial growth (table 2.2). Extension growth was reduced, so the relationship between stem length and width in these experiments must be affected. Little (1970) reported a linear relation between stem length and width in Pinus strobus, as did Malcolm and Studholme (1972). The latter authors also found that the height/diameter ratio of Picea sitchensis and Larix decidua decreased with elevation and 'exposure'. Hewson et al (1977) also found a reduced height/diameter ratio in 'windy' places.

Stem length is plotted against stem diameter in figure 4.9 for forty Long Beach P. contorta taken at random from the initial measurements made on the plants. The correlation coefficient is statistically significant

($P < .01$) and the data confirm a linear relationship between length and width for this species. In table 4.11 the regression equations between width and length for the three experiments reported here are listed. In all cases the relationship between width and length is significant. Covariance Analysis (Snedecor and Cochran 1967) reveal that high wind and shaking have significantly altered the relationships between width and length.

The Young's modulus of elasticity of stems subjected to shaking was lower than that of controls, suggesting that thickening and lignification of cell walls may have been affected. However, the increased width/length ratios of shaken plants greatly reduced the differences in 'rigidity' between the two groups, i.e. the deflection per unit load of the two groups was not greatly affected by shaking.

Putnam (1948) reported that after high winds, conifer shoots are often seen to be bent into the wind, rather than with the wind, as might be expected. Shoots exposed to a high windspeed in the wind tunnel behaved similarly, figures 4.2 and 4.10. It was noted that as a result of the shoot curvature, the shoot apexes were in an approximately vertical position as the plant bent over in the wind. This suggests that a phototrophic or gravimorphic response (Zimmerman and Brown 1971) was acting to maintain the plant apex in a vertical position.

These experiments confirm that wind, as distinct from other correlated environmental variables, can affect the growth morphology of P. contorta. The qualitatively and quantitatively similar results of the shaking and high wind experiments suggest that wind-induced plant motion may be an important aspect of the effects of wind on plants.

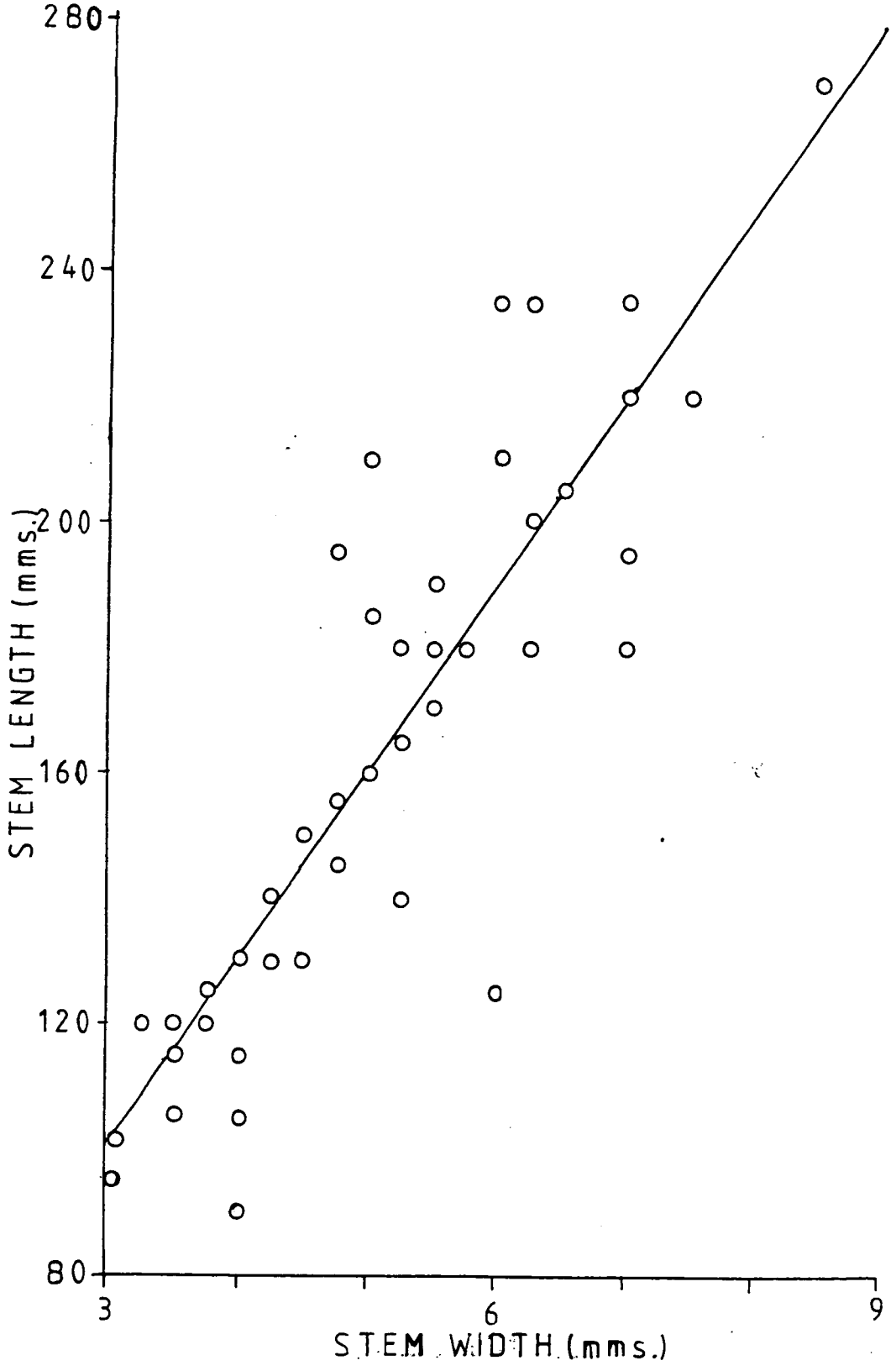


Figure 4.9 Relationship between stem length and width of 40 2 year old P. contorta.

Figure 4.10 Curvature of extending buds of *P. contorta* into the wind.

## 4.5 Summary

(i) Subjecting *P. contorta* to a high windspeed (8.5 m $s^{-1}$) or to continuous shaking resulted in a 20% reduction in leader and lateral shoot extension. 'Apical control' (the ratio of mean lateral shoot length to leader length) and stem width growth were not affected by wind and shaking. The stem width/length ratio was thus significantly increased by wind and shaking.

(ii) The rate of needle extension was reduced by 11% by shaking throughout the growing season and by 30% by high windspeed in a short-term experiment in the controlled environments. The greater effect of wind was probably partly due to the greater extension rates of the plants in the controlled environments.

(iii) Shaking caused a reduction in stem elasticity, but because of the altered stem width/length ratios, stem 'rigidity' (deflection per unit load) was much less affected.

(iv) The similarity of the effects of wind and shaking on *P. contorta* suggests that wind-induced shaking may be an important aspect of the effects of wind on plants.

# Chapter 5 Effects of wind and shaking on longitudinal cell growth

## 5.1 Introduction

A reduction in shoot length implies a decrease in cell number, or cell size, or both. Neel and Harris (1971a) found that the xylem vessels and fibres of Liquidambar styraciflua were shorter in shaken plants than in controls, indicating that cell extension had been reduced. The observations of Grace and Russell (1977), that wind reduces leaf length, but has apparently no effect on abaxial epidermal cell length, suggests a reduction in cell division in F. arundinacea.

In chapter 4, it was shown that subjecting P. contorta to continuous motion reduced the extension growth of leader and lateral shoots. Cell division, cell extension, or both, must have been reduced. To determine which of these aspects of cell growth had been affected, leader stems of P. contorta subjected to high wind or low wind in controlled environments, and leader stems of control and shaken plants were sectioned and examined microscopically.

## 5.2 Materials and methods

At the end of the experiments described in 4.3.1 and 4.3.2, the leader shoots were labelled with different coloured cotton threads and fixed in 50% Formyl Acetic Acid, made up as described in Purvis, Collier and Walls (1964). When the material was sufficiently soft, it was dehydrated and wax-embedded. The dehydration and embedding schedule, based on Purvis, Collier and Walls (1964), is described in table 5.1.

To find how cell size and number varied with distance from the growing point, stems from the various treatments were cut into 20 mm. sections, labelled with different coloured cotton threads, dehydrated and embedded. Apical and basal segments only were examined in subsequent stems.

Longitudinal sections, 20$\mu$m. thick, were cut on a rotary microtome (Baird and Tatlock Ltd., London). Sections from the centre of the stem, with a distinct tracheid layer, were stained as described in table 5.2 and examined microscopically. The lengths and numbers of parenchymatous cells of the stem cortex were determined.

The number of cells in sequential 435$\mu$m longitudinal transects along each section were determined and the mean number of cells per mm. and mean cell length for each stem segment were calculated. The number of cells per stem were calculated as described in 5.3.

Table 5.1 Dehydration and embedding schedule

| Chemical | Time | Chemical | Time |
|---|---|---|---|
| Wash out FAA overnight with water | Day 1 | | Day 2 |
| | | 2 absolute alchohol:1 chloroform | 0900-1000 |
| Alchohol 15% | 0900-0930 | 1 " " 1 " | 1000-1100 |
| " 30% | 0930-1000 | 2 " " 3 " | 1100-1130 |
| " 50% | 1000-1030 | 1 " " 2 " | 1130-1200 |
| " 60% | 1030-1130 | 2 " " 5 " | 1200-1230 |
| " 70% | 1130-1230 | chloroform | 1230-1300 |
| " 80% | 1230-1330 | " | 1300-1330 |
| " 90% | 1330-1430 | chloroform/wax | 1330-1400 |
| " 95% | 1430-1530 | wax | 1400-1430 |
| " 'commercial' | 1530-1600 | wax | 1430-1500 |
| " " | 1600-1630 | wax | 1500-1530 |
| | | wax | 1530-1600 |
| " absolute | 1630-1700 | | |
| | | Embed | |
| " " | overnight | | |

Table 5.2 Staining Schedule

| Chemical | Time |
|---|---|
| Xylene | 3-4 minutes |
| Xylene | 3-4 " |
| Absolute Alchohol | 3 " |
| 95% " | 3 " |
| 85% " | 3 " |
| 70% " | 3 " |
| 60% " | 3 " |
| 50% " | 4 " |
| Safranin Alchohol * | 10 " |
| Acid Alchohol * | 3 " |
| 70% " | 2 " |
| 80% " | 3 " |
| 90% " | 3 " |
| Absolute Alchohol | 3 " |
| " " | 3 " |
| Xylene | 3 " |

* Made up as described in Purvis et al (1964).

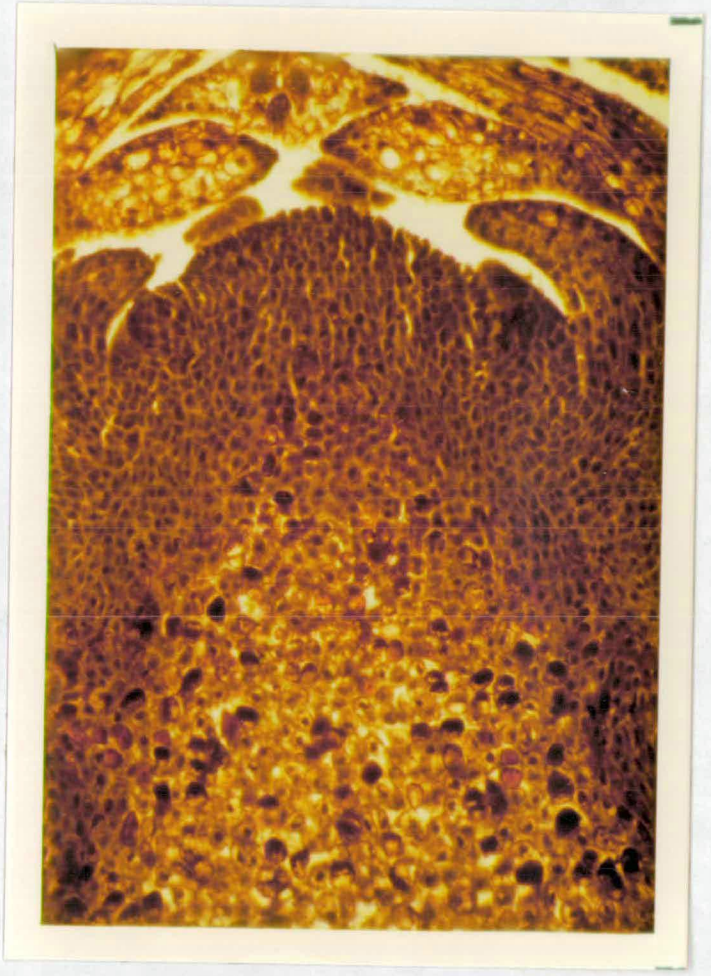

Figure 5.1 Typical long itudinal section of apex of P. contorta stem. X 100 magnification.

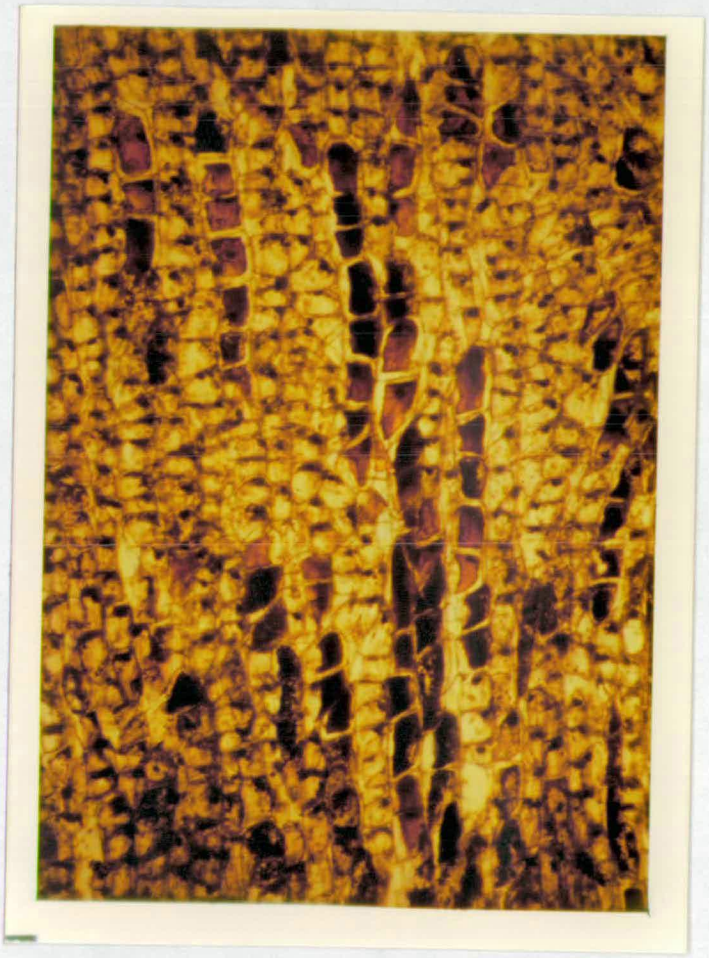

Figure 5.2 Typical longitudinal section of parenchymatous cells of the stem cortex of P. contorta in the basal region of the leader stem. X 100 magnification.

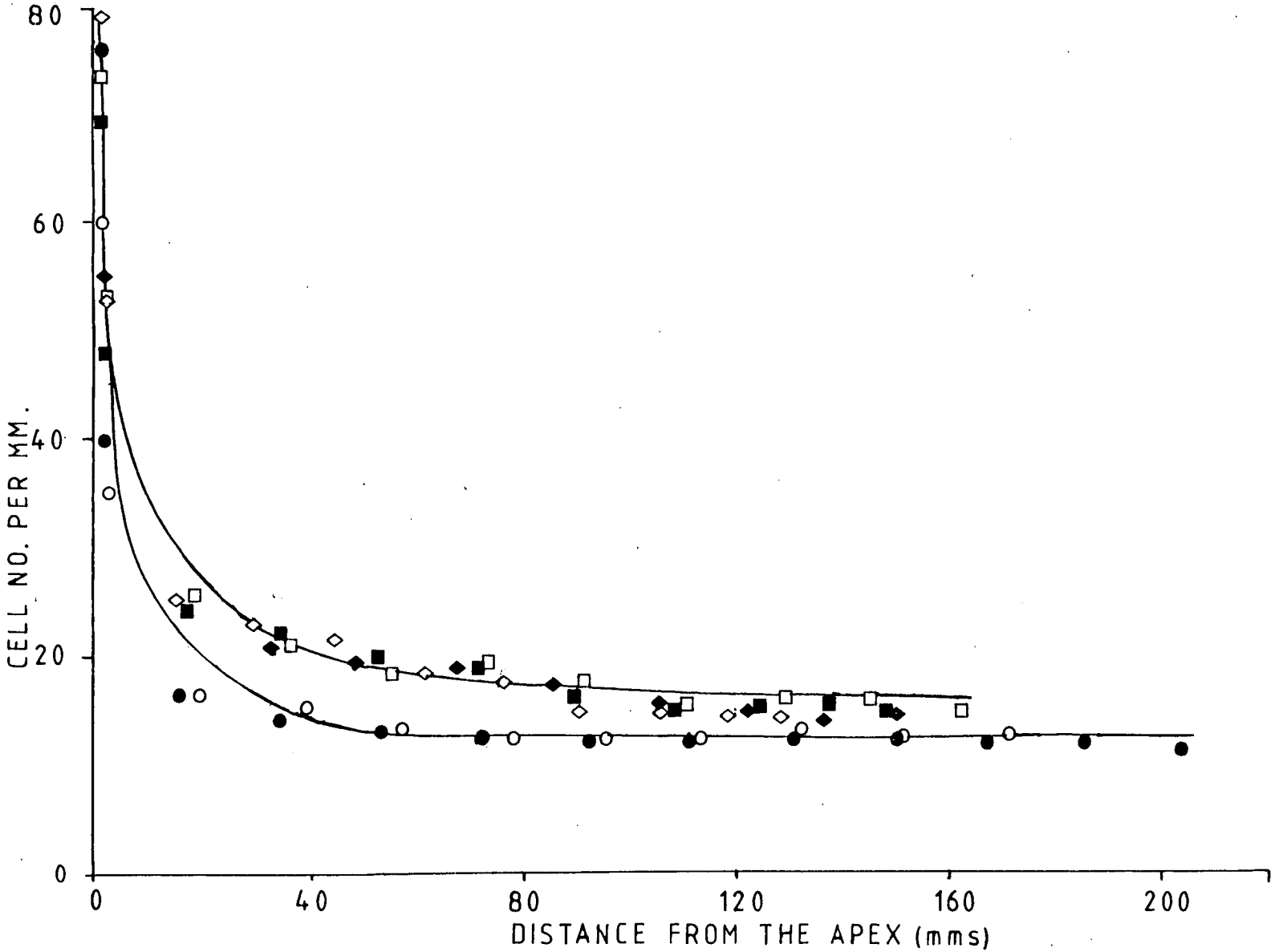


**Figure 5.3** Variation in number of cells per mm with distance from the stem apex. Squares, diamonds : plants from the controlled environments ; circles : outdoor plants.

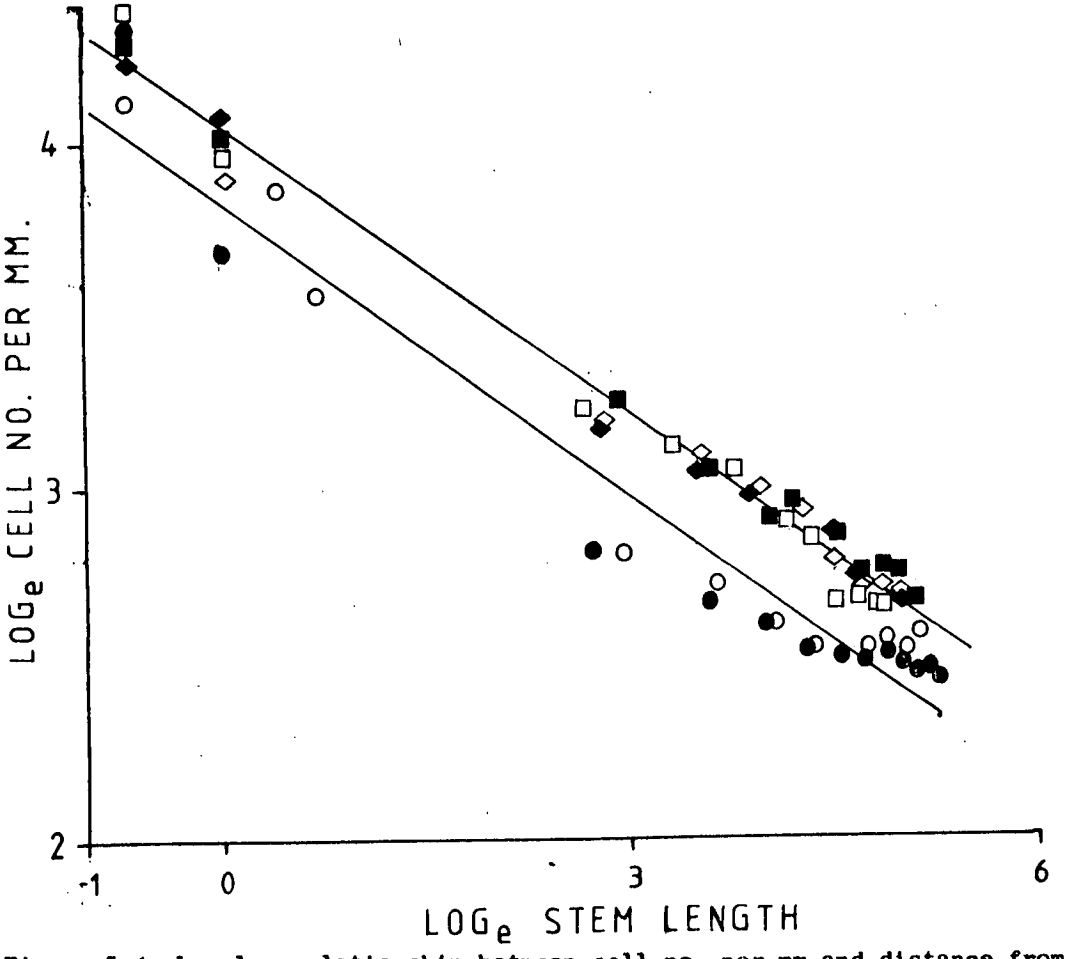


**Figure 5.4** Log-log relationship between cell no. per mm and distance from apex ( stem length ). Same data as in fig. 5.3

## 5.3 Results

Figures 5.1 and 5.2 show typical apical and basal sections of current year P. contorta stems.

### 5.3.1 The relationship between cell number and distance from the stem apex.

Figure 5.3 shows the number of cells per mm. at various points along stems taken from P. contorta exposed to high and low winds, from P. contorta exposed to continuous shaking, and their controls. The area below such a curve represents the total number of cells in a longitudinal file from the apex to the base of the stem, N, i.e.:

$$N = \int_0^z f(x)\, dx \qquad (5.1)$$

where z is the distance from the stem apex (at 0) to the stem base i.e. stem length,

and $f(x)$ is the relationship between cell no. per mm. and distance from the stem apex.

N is a measure of the number of longitudinal cell divisions.

Figure 5.4 shows that a log - log function closely describes the relationship between cell no. per mm. and distance from the apex i.e.:

$$\log_e n = b \log_e x + a \qquad (5.2)$$

Where n is the no. of cells per mm. at x;

b is the gradient of the log - log line,

x is the distance from the stem apex,

and a is the intercept of the log - log line.

(5.2) implies : $n = x^b e^a$ (5.3)

Insert (5.3) into (5.1) :

$$N = \int_0^z (x^b e^a)\, dx = e^a \int_0^z x^b\, dx = e^a \left[ \frac{x^{(1+b)}}{1+b} \right]_0^z$$

$$= \frac{e^a z^{(1+b)}}{(1+b)} \qquad (5.4)$$

N can thus be calculated if z, a and b are known.

Having shown that a log-log relationship held for the six specimens taken at random shown in figures 5.3 and 5.4, microscopic examination of subsequent stems was restricted to four standard positions at the apex and base. Even with this limited data, $\log_e$ cell no. per mm was significantly correlated with $\log_e$ distance from the apex at at least $P < .05$ in each case. The parameters a and b were calculated from the data for each stem by linear regression and the no. of cells in a longtitudinal file from apex to base, N, calculated.

Cell lengths were calculated directly from the counts of cell no. per 435 $\mu$m. Analysis of variance tests were performed on the counts per 435 $\mu$m for apical sections (excluding the first 2 mms, where cell lengths vary rapidly with distance from the apex) and for basal sections.

### 5.3.2 Effects of wind and shaking on cell division and cell extension

In table 5.3, the mean number of cells in a longtitudinal file from stem apex to base, as calculated by equation 5.4, are presented.

Exposure to both high winds and shaking caused a ca. 15% reduction in cell number, implying a 15% reduction in total cell division.

In tables 5.4 and 5.5, analyses of the data on cell lengths are summarised. The 10% reduction in cell length (i.e. increase in cell no. per 435 $\mu$m) caused by high wind is statistically significant ($P < 0.025$) for cells near the apex, but for cells near the base, the 3% reduction is significant only at $P < 0.1$. Variation in cell length between plants is highly significant. The 11% reduction in cell length of cells near the apex caused by shaking is significant at only $P < 0.1$ while for the basal cells, the 3% reduction is significant at $P < 0.01$. It can be concluded that wind and shaking have a significant effect on cell extension, ranging from a 10% reduction near the apex to a 3% reduction for basal cells. The average reduction for the whole stem cannot be determined from the data, but must lie between 10% and 3%. Cell division appears to be more sensitive to continuous motion than cell extension, but both are reduced.

Table 5.3 Effect of wind and shaking on cell division

No. of cells in longitudinal files from stem apex to base

| | Controlled Environments | | Outdoors | |
|---|---|---|---|---|
| | High Wind Wind Tunnel | Low Wind Growth Room | Shaking | Control |
| no. of stems | 8 | 8 | 6 | 6 |
| Mean No. | 2412 | 2903 | 2588 | 2964 |
| Standard Error | 190.0 | 91.9 | 125.1 | 105.0 |
| level of statistical significance * | .05 | | .01 | |
| % change | -17% | | -13% | |

* Using the t - test (Steel and Torrie 1960)

Table 5.4a Effects of wind on the no. of cell per 435 $\mu$m. (cell counts)

Analysis of variance with subsamples (Steel and Torrie 1960)

| Test | Source | d.f. | S.S. | M.S. | F | P |
|---|---|---|---|---|---|---|
| | Among plants | 15 | 767.6 | | | |
| | Among treatments | 1 | 244.6 | 244.6 | 6.6 | 0.025 |
| apical sections | Among plants within treatments | 14 | 523.0 | 37.4 | 14.5 | 0.01 |
| | Among counts within plants | 795 | 2047.3 | 2.6 | | |
| | Total | 810 | 2814.9 | | | |
| | Among plants | 16 | 83.7 | | | |
| | Among treatments | 1 | 14.4 | 14.4 | 3.1 | 0.1 |
| Basal | Among plants within treatments | 15 | 69.3 | 4.6 | 3.5 | 0.001 |
| sections | Among counts within plants | 1047 | 1466.0 | 1.4 | | |
| | Total | 1062 | 1480.4 | | | |

Table 5.4b Mean no. of cells per 435 $\mu$m and corresponding cell length

| Section | Treatment | Mean cell no. per 435 $\mu$m $\pm$ standard errors | Cell lengths $\mu$m. | % diff. |
|---|---|---|---|---|
| apical | High wind | 9.9 $\pm$ .23 | 44 | -10% |
| sections | Low wind | 8.8 $\pm$ .23 | 49 | |
| basal | High wind | 6.8 $\pm$ .07 | 64 | - 3% |
| sections | Low wind | 6.6 $\pm$ .07 | 66 | |

Table 5.5a Effect of shaking on the no. of cells per 435 μm (cell counts)
Analysis of variance with subsample (Steel and Torrie 1960)

| Test | Source | d.f. | S.S. | M.S. | F. | P |
|---|---|---|---|---|---|---|
| apical sections | Among plants | 11 | 341.7 | | | |
| | Among treatments | 1 | 100.7 | 100.7 | 4.2 | 0.1 |
| | Among plants within treatments | 10 | 241.0 | 24.1 | 8.0 | 0.001 |
| | Among counts within plants | 619 | 1883.3 | 3.0 | | |
| | Total | 630 | 2225.0 | | | |
| basal sections | Among plants | 11 | 41.1 | | | |
| | Among treatments | 1 | 21.7 | 21.7 | 11.2 | 0.01 |
| | Among plants within treatments | 10 | 19.4 | 1.9 | 1.6 | NS |
| | Among counts within plants | 879 | 1052.9 | 1.2 | | |
| | Total | 890 | 1094.0 | | | |

Table 5.5b Mean no. of cells per 435 μm and corresponding cell lengths

| Section | Treatment | Mean cell no. per 435 μm ± standard errors | Cell lengths, μm | % diff. |
|---|---|---|---|---|
| Apical sections | Shaken | 7.4 ± .21 | 59 | -11% |
| | Control | 6.6 ± .21 | 66 | |
| Basal Sections | Shaken | 5.4 ± .05 | 81 | -5% |
| | Control | 5.1 ± .05 | 85 | |

## 5.4 Discussion

Over 130 years ago, Harting (1845) found that the differences in length between long and short shoots of *Tilia parviflora* were due to differences in cell number rather than to differences in cell length (quoted in Sachs 1965). This was extended to conifers by Baxter and Cannell (1978) and implies that cell division, rather than cell extension, is the process regulated by apical dominance mechanisms (Baxter and Cannell 1978).

Lam and Brown (1974) found that the reduction in shoot length of *Liquidambar styraciflua* caused by short photoperiods was due to a reduction in cell number. Cell extension was not affected. Campbell (1976), working with the same species, found that cell extension was slightly reduced by short photoperiods and by water stress, but that cell division was much more sensitive.

The results reported in this thesis, that cell division is more sensitive to motion than cell extension, and the work quoted above suggest that cell division is generally more sensitive to the environment than cell extension. However, the difference in lengths between the controlled environment plants and the outdoor plants is almost entirely due to a difference in cell length (compare tables 5.4 and 5.5).

There is considerable literature on the hormonal regulation of cell growth (e.g. Rost and Gifford 1977). It is possible that the reduction in cell growth caused by motion is due to an alteration of the tissue hormone balance. However, cell division and cell extension are complex processes and any alteration in the general metabolism may be expected to affect cell growth.

The effects of wind and shaking on the carbon budget and water relations of P. contorta are examined in subsequent chapters. Cell extension and division are sensitive to mild water stress (Hsiao 1974, Hsiao et al 1976); if motion causes a water stress this would explain the results reported here. Similarly, if the carbon available for growth is reduced, cell growth would be reduced, although the links between the carbon budget and cell growth have not been studied as such.

## 5.5 Summary

(i) Leader stems of P. contorta were sectioned and examined microscopically. The variation in the number of parenchymatous cells of the stem cortex per mm. was examined. An empirical function describing the relationship between cell no. per mm. and distance from the stem apex was derived. From measurements on apical and basal sections, values for the parameters of this relationship were determined and the total number of cells in longitudinal file from stem apex to base calculated.

(ii) Both wind and shaking caused a ca. 15% reduction in the number of cells in a longitudinal file from apex to base. Cell length was reduced by 10% near the apex, and 3% at the stem base, by both wind and shaking.

(iii) It is concluded that the major effect of continuous motion on longitudinal cell growth is on cell division, though cell elongation is also slightly reduced.

# Chapter 6 The effects of shaking on the dry weight production of *P. contorta*

## 6.1 Introduction

It was shown in chapter 4 that wind and shaking reduce the extension growth of *P. contorta*. This may reflect a decrease in plant dry weight, or may be due to a relocation of assimilates.

In those few experiments where the dry weight of conifers have been determined it appears that height growth generally does parallel changes in dry weight (Wareing 1970, Cannell et al 1976).

The effects of shaking on the 'growth efficiency', 'assimilatory efficiency' and distribution of assimilates are examined in this chapter by means of growth analysis (Evans 1972 and others).

The extension and radial growth of the plants used in this growth analysis experiment are described in 4.3.3.

## 6.2.1 Materials and methods

The growth of two year old Long Beach P. contorta subjected to continuous shaking in the cold frames throughout the 1978 growing season was compared to that of controls. Plants harvested in April 1978 provided reference values of mean dry weight and leaf area at time 0. The leading shoot of one plant was broken by the shaking treatment (4.3.3). The rest of the plants were harvested after 219 days growth.

Soil was carefully washed from the roots and the plants divided into needles, stems and roots. Dry weights of these organs were determined ater 48 hours drying at 80 C. Projected areas of the (fresh) needles were determined using an LI-3100 area meter (Lambda Insts. Corp. U.S.A.).

## 6.3.1 Calculations

The following calculations are based on Radford (1967), Květ et al (1971), Evans (1972) and Hunt (1978).

Relative growth rate, R, is the rate of increase in dry weight, W, per unit dry weight per unit time, t:

$$R = \frac{1}{W} \frac{dW}{dt} \qquad (6.1)$$

Mean relative growth rate, $\bar{R}$, from harvest 1 at time 1, $t_1$ to harvest 1 at time 2, $t_2$ is thus:

$$\bar{R} = \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} \frac{1}{W} \frac{dW}{dt} \cdot dt = \frac{\log_e \bar{W}_2 - \log_e \bar{W}_1}{t_2 - t_1} \text{ day}^{-1} \qquad (6.2)$$

where $\bar{W}_1$ and $\bar{W}_2$ are mean total dry weights at times $t_1$ and $t_2$.

Unit leaf rate, U, is the rate of increase in dry weight per unit leaf area, A, per unit time:

$$U = \frac{1}{A} \frac{dW}{dt} \tag{6.3}$$

Assuming A is linearly related to W, mean unit leaf rate, $\overline{U}$, is

$$\overline{U} = \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} \frac{1}{A} \frac{dW}{dt} \, dt = \frac{\overline{W}_2 - \overline{W}_1}{t_2 - t_1} \cdot \frac{\log_e \overline{A}_2 - \log_e \overline{A}}{A_2 - A_1} \; g \; m^{-2} \; dy^{-1} \tag{6.4}$$

where $\overline{A}_2$ and $\overline{A}_1$ are mean leaf areas at $t_2$ and $t_1$.

Leaf area ratio, L, is the ratio of leaf area to total plant dry weight.

$$L = A/W \tag{6.5}$$

Radford (1967) shows that a mean value for L cannot be satisfactorily determined, so instantaneous mean values of leaf area ratio, $\overline{L}$, are used in this experiment:

$$\overline{L} = \overline{A}/\overline{W} \; m^2 \; g^{-1} \tag{6.6}$$

From 6.1, 6.3 and 6.5 it can be seen that, instantaneously,

$$R = U.L \tag{6.7}$$

A change in R must be reflected in either U or L.

Leaf weight ratio, LWR, stem weight ratio, SWR and root weight ratio, RWR are the ratios of the organ concerned to total dry weight:

$$LWR = W_L/W \tag{6.8}$$

$$SWR = W_S/W \tag{6.9}$$

$$RWR = W_R/W \tag{6.10}$$

where W is total dry weight and $W_L$, $W_S$ and $W_R$ are leaf, stem and root dry weights.

L may be divided into LWR and specific leaf area, SLA, where SLA is:

$$SLA = A/W_L \; m^2 \; g^{-1} \tag{6.11}$$

then

$$L = LWR \; . \; SLA \; m^2 \; g^{-1} \tag{6.12}$$

A change in L must be reflected in either SLA or LWR.

Relative leaf growth rate, $R_L$, is the rate of increase in leaf area per unit leaf area per unit time:

$$R_L = \frac{1}{A}\frac{dA}{dt} \qquad (6.13)$$

Mean relative growth rate, $\bar{R}_L$, is thus:

$$\bar{R}_L = \frac{1}{t_2-t_1}\int_{t_1}^{t_2}\frac{1}{A}\frac{dA}{dt}\,dt = \frac{\log_e \bar{A}_2 - \log_e \bar{A}_1}{t_2 - t_1} \text{ day}^{-1} \qquad (6.14)$$

6.3.2 Statistical analysis of relative growth rate and unit leaf rate

I am grateful to C.A. Glasbey of the Agricultural Research Council Unit of Statistics, University of Edinburgh for the following statistical discussion.

The variance of $\bar{R}$ can be approximated, by Taylor's theorem, by:

$$s_R^2 \approx \frac{1}{(t_1-t_2)^2}\cdot\left[\frac{s_{W1}^2}{\bar{W}_1^2} + \frac{s_{W2}^2}{\bar{W}_2^2}\right] \qquad (6.15)$$

where $s_R^2$ is the variance of $\bar{R}$;

$(t_2-t_1)$ is the time interval between successive harvest;

$s_{W1}^2$ and $s_{W_2}^2$ are the variances of the dry weights at $t_1$ and $t_2$ respectively;

$\bar{W}_1$ and $\bar{W}_2$ are the mean dry weights at $t_1$ and $t_2$

Variance, $s^2$, is used here as:

$$s^2 = \frac{1}{n(n-1)}\sum_{i=1}^{i=n}(x_i - \bar{x})^2 \qquad (6.16)$$

The variance of $\bar{U}$ defined by equation 6.4 is complex:

$$s_U^2 = \left(\frac{\partial U}{\partial W_1}\right)^2 s_{W1}^2 + \left(\frac{\partial U}{\partial W_2}\right)^2 s_{W2}^2 + \left(\frac{\partial U}{\partial A_1}\right)^2 s_{A1}^2 + \left(\frac{\partial U}{\partial A_2}\right)^2 s_{A2}^2 +$$

$$2\left(\frac{\partial U}{\partial W_1}\right)\left(\frac{\partial U}{\partial A_1}\right) s_{W1a1}^2 + 2\left(\frac{\partial U}{\partial W_2}\right)\left(\frac{\partial U}{\partial A_2}\right) s_{W2A2}^2 \qquad (6.17)$$

where $\left(\frac{\partial U}{\partial W_1}\right) = -1/(t_2-t_1)$ (6.18)

$$\left(\frac{\partial U}{\partial A_1}\right) = \frac{\bar{W}_2-\bar{W}_1}{t_2-t_1} \cdot \frac{(\log_e \bar{A}_2 - \log_e \bar{A}_1) - (\bar{A}_2-\bar{A}_1)/\bar{A}_1}{(\bar{A}_2-\bar{A}_1)^2} \qquad (6.19)$$

$$\left(\frac{\partial U}{\partial W_2}\right) = 1/(t_2-t_1) \qquad (6.20)$$

$$\left(\frac{\partial U}{\partial A_2}\right) = \frac{\bar{W}_2-\bar{W}_1}{t_2-t_1} \cdot \frac{(\bar{A}_2-\bar{A}_1)/\bar{A}_2 - (\log_e \bar{A}_2 - \log_e \bar{A}_1)}{(\bar{A}_2-\bar{A}_1)^2} \qquad (6.21)$$

$s_U^2$ is the variance of $\bar{U}$;

$s_{A1}^2$ and $s_{A_2}^2$ are the variances of A at $t_1$ and $t_2$, respectively;

$s_{W1A1}^2$ and $s_{W2A2}^2$ are the covariances of A and W at $t_1$ and $t_2$, respectively.

If there is no difference between the shaking and control plants then $\frac{R_S - R_C}{\sqrt{s_{RS}^2 + s_{RC}^2}}$ is 't'-distributed with (n-1) degrees of freedom (6.22)

where the subscripts $_S$ and $_C$ refer to shaken and control plants; and n is the smaller of $n_1$ and $n_2$ (when $n_1$ and $n_2$ differ only slightly), the numbers of plants in the final harvests.

In the experimental design used in this chapter, the same plants are used as reference values at $t_1$ for both shaken and control plants, hence $R_S$ and $R_C$ are not independent of one another.

The difference in R caused by shaking is:

$$\bar{R}_S - \bar{R}_C = \frac{\log_e \bar{W}_{2S} - \log_e \bar{W}_1}{t_2 - t_1} - \frac{\log_e \bar{W}_{2C} - \log_e \bar{W}_1}{t_2 - t_1}$$

$$= \frac{\log_e \bar{W}_{2S} - \log_e \bar{W}_{2C}}{t_2 - t_1} \qquad (6.23)$$

By analogy with equation 6.15, the variance of the difference in R is:

$$S^2_{S-C} = \frac{1}{(t_2 - t_1)} \left[ \frac{S^2_{W2S}}{\bar{W}^2_{2S}} + \frac{S^2_{W2C}}{\bar{W}^2_{2C}} \right] \qquad (6.24)$$

Equation 6.22 thus becomes :

$$\frac{\bar{R}_S - \bar{R}_C}{\sqrt{S^2_{S-C}}} \text{ is 't'-distribued with } (n-1) \text{ degrees of freedom} \qquad (6.25)$$

A similar argument can be used to simplify the 't'-test for $R_L$, but not for U. The unmodified 't'-test, equation 6.22 must be used to compare $\bar{U}_S$ and $\bar{U}_C$.

## 6.4 Results

Results are presented in table 7.1. Continuous shaking caused a statistically significant 14% decrease in relative growth rate and a 15% decrease in relative leaf growth rate. Leaf area ratio was not affected by shaking. Unit leaf rate was reduced by 24%, but the standard errors of $\overline{U}$ are so large that the differences cannot be formally declared significant. Large standard errors are to be expected for a term derived from four variables.

Equation 6.7 shows that, from the definitions of R, U and L, a change in R must be reflected by a change in U or L. In this experiment, $\overline{U}$ shows a 24% reduction due to shaking, while L is unaffected, so despite the large standard errors attached to $\overline{U}$, the reduction in $\overline{R}$ caused by shaking must be due to a reduction in $\overline{U}$.

Stem weight ratio was increased at the expense of root weight ratio, indicating a redistribution of assimilates from roots to stem. Despite this no effect of shaking on stem radial growth was detected (4.3.3).

Table 6.1 Effects of shaking on dry weight growth of P. contorta
(a) Basic data - means and standard errors

| Group | Needle area $cm^2$ | Dry weight g | | | | No. of Plants |
|---|---|---|---|---|---|---|
| | | needles | stem | roots | total | |
| Initial | 85.4 ± 8.77 | 2.21 ± .406 | 1.21 ± .098 | 1.14 ± .113 | 4.56 ± .595 | 18 |
| Control | 619.2 ±31.63 | 14.06 ± .623 | 8.33 ± .475 | 9.46 ±.538 | 31.86 ±1.518 | 18 |
| Shaking | 464.0 ±29.34 | 11.10 ± .805 | 6.63 ±.642 | 6.35 ±.481 | 24.39 ±1.723 | 17 |

(b) Growth analysis parameters, means and standard errors

| Group | $\bar{R}$ $day^{-1}$ | $\bar{U}$ g $m^{-2}$ $dy^{-1}$ | L* $m^2$ $g^{-1}$ | $\bar{R}_L$ $day^{-1}$ |
|---|---|---|---|---|
| Control | .00888 ±.000635 | 4.63 ± 3.106 | .00195 ±.000486 | .00905 ±.000524 |
| Shaking | .00766 ±.000693 | 3.50 ± 3.855 | .00193 ±.000420 | .00773 ±.000562 |
| level of statistical significance | 0.05 | NS | NS | 0.01 |
| % diff. | -14% | -24% | - | -15% |

(c) Growth analysis parameters - means and standard errors

| Group | SLA* $m^2$ $g^{-1}$ | LWR* | SWR* | RWR* |
|---|---|---|---|---|
| Control | .00439 ±.000050 | .444 ±.0084 | .260 ±.0062 | .296 ±.0067 |
| Shaking | .00422 ±.000070 | .456 ±.0078 | .284 ±.0076 | .259 ±.0084 |
| level of statistical significance | 0.1 | NS | 0.02 | 0.001 |
| % diff. | -4% | - | +9% | -13% |

* instantaneous values at final harvest

## 6.5 Discussion

### 6.5.1 Statistical analysis

The standard text on growth analysis, that of Evans (1972), entirely neglects the calculation of variances of growth parameters from the variance of the basic data. Květ et al (1971) provide a formula identical with equation 6.15 but do not consider the variance of unit leaf rate, other than to point out that the variance of a term derived from four variables is likely to be large.

Hunt (1978) briefly mentions the technique of 'pairing'. Plants are matched at time 0, one of each pair is harvested at time 0 and the other at the next harvest. Values of $\bar{R}$ and $\bar{U}$ are calculated for each pair and the means and variances of these individual values calculated. This is undoubtedly the simplest and most reliable method, but not always applicable, as in the experiment reported here.

The standard errors of $\bar{R}$, $\bar{R}_L$ and $\bar{U}$ calculated from equations 6.15 and 6.17 are large in comparison to $\bar{R}$, $\bar{R}_L$ and $\bar{U}$ themselves. If the unmodified 't'-test as defined in equation 6.22 were used for $\bar{R}$ and $\bar{R}_L$, the effect of shaking would be declared not significant. $\bar{U}_R$ and $\bar{U}_S$ are also positively correlated and an appropriate variance for the difference in $\bar{U}_R$ and $\bar{U}_S$ should strictly be used to compare these parameters, but this would be a complex calculation. This formal approach to the statistics of conventional growth analysis is probably only useful when dealing with $\bar{R}$ and $\bar{R}_L$.

### 6.5.2 Dry weight production

The reduction in relative growth caused by shaking resulted in a 25% decrease in dry matter production of the plants. This figure

compares well with the 21% reduction in extension growth of these plants reported in 4.3.3. The reduced growth appears to be due to an effect of shaking on unit leaf rate.

Unit leaf rate is dimensionally analagous to net photosynthetic rate. Evans (1972) discusses this in some detail and equates unit leaf rate to: daily net photosynthetic rate - dark respiratory rate plus daily mineral uptake plus overall metabolic balance, all expressed on a leaf area basis. Net photosynthesis and respiration are the two largest terms in this equality, so changes in unit leaf rate are usually taken to indicate changes in photosynthesis or respiration. The results of this experiment thus suggest that shaking decreases photosynthesis or increases respiration.

It should be noted that respiration is not merely a regrettable loss of carbon for the plant, as implied above, but a process vital to plant growth. This is discussed further in the next chapter.

Phares et al (pers. comm.) found that 30s. daily shake had little effect on the dry weight production of Liquidambar styraciflua and Acer saccharum, despite reducing extension growth by 70-80%. Dry weight growth of Juglans nigra, however, was significantly reduced. Beardsell (1977) found that handling Z.mays significantly reduced leaf and stem dry weights.

The effects of wind on dry weight growth are also relevant here. As noted in 2.1.4, there are reports that wind decreases dry weight production of plants (Finnel 1928, Martin and Clements 1935, Whitehead and Luti 1962, Whitehead 1962, Satoo 1962, Morse and Evans 1962 and others.) Heiligmann and Schneider (1974), also working with J. nigra, found that wind reduced dry weight production, but had no effect on height growth. Wadsworth (1959) found that above an optimum windspeed,

relative growth rates of a variety of species decreased, mainly due to an effect on unit leaf rate. Russell and Grace (1979) however, attributed the reduction in relative growth rate caused by wind to an effect on specific leaf area and showed that unit leaf rate increased to compensate. In Pinus contorta however, the results of this experiment show that the shaking-induced reduction in relative growth rate is due to a reduction in unit leaf rate.

## 6.6 Summary

(i) The 21% reduction in extension growth of P. contorta caused by shaking was accompanied by a 24% reduction in dry weight.

(ii) The reduction in relative growth rate is shown to be due to a reduction in unit leaf rate, suggesting an effect of shaking on photosynthesis or respiration.

(iii) Formal calculations of the variances of relative growth rate and unit leaf rate (derived by C. A. Glasbey) are presented.

# Chapter 7 Effects of wind on the $CO_2$ exchange of *P. contorta*

## 7.1 Introduction

The effects of wind on photosynthesis and respiration are reviewed in 2.1.6. The work of Tranquillini (1969), Grace and Thompson (1973) and MacKerron (1976b) suggest that exposure to high wind may cause a reduction in net photosynthesis. Armbrust et al (1974) and Wilson (1978) report an increase in net photosynthesis of the remaining live leaf tissue of their plants, following wind-induced abrasion. This does not preclude a reduction in net photosynthesis per plant, although this was not measured in their work.

Todd et al (1972), Armbrust et al (1974) and MacKerron (1976b) report increased respiration rates caused by wind. Grace and Thompson (1973) and Wilson (1978) were unable to detect an effect of wind on dark respiration of their plants.

Dark respiration rates and light-photosynthesis curves of *P. contorta* subjected to low and high winds are compared in this chapter.

## 7.2 Materials and Methods

### 7.2.1 Procedures

Long Beach P. contorta in their second growing season were brought into the wind tunnel ten days before the experiment started. Conditions in the wind tunnel were: 15°C air temperature: 12 mb vapour pressure, 275 $\mu$E $m^{-2}$ $s^{-1}$ PhAR, 12 hours daylength. Windspeed was maintained at 1.0 m $s^{-1}$ for the first six days, increased to 9.3 m $s^{-1}$ for the subsequent nine days and returned to 1.0 m $s^{-1}$ for the final six days.

A plant was removed each day before the lights came on and placed in the assimilation chamber, which was maintained at 15 $\pm$ 1°C and 12 $\pm$ 2 mb. $CO_2$ efflux in the dark was measured, then light intensity was increased in steps. 1-1½ hours were allowed for the plant to come to equilibrium at each light intensity.

### 7.2.2 The assimilation chamber

The assimilation chamber was a rectangular box measuring 20 x 20 x 25 cms., with perspex sides and lid and a highly polished aluminium base, figure 7.1. The lid closed about the horizontally placed plant on a neoprene seal. The sides of the chamber were lined with aluminium foil to increase the irradiance in the chamber and provide light from all directions. The chamber and plant pot were placed in a water-bath set at 15°C, to facilitate temperature control within the chamber. The pot was sealed within two plastic bags to prevent water entering the soil.

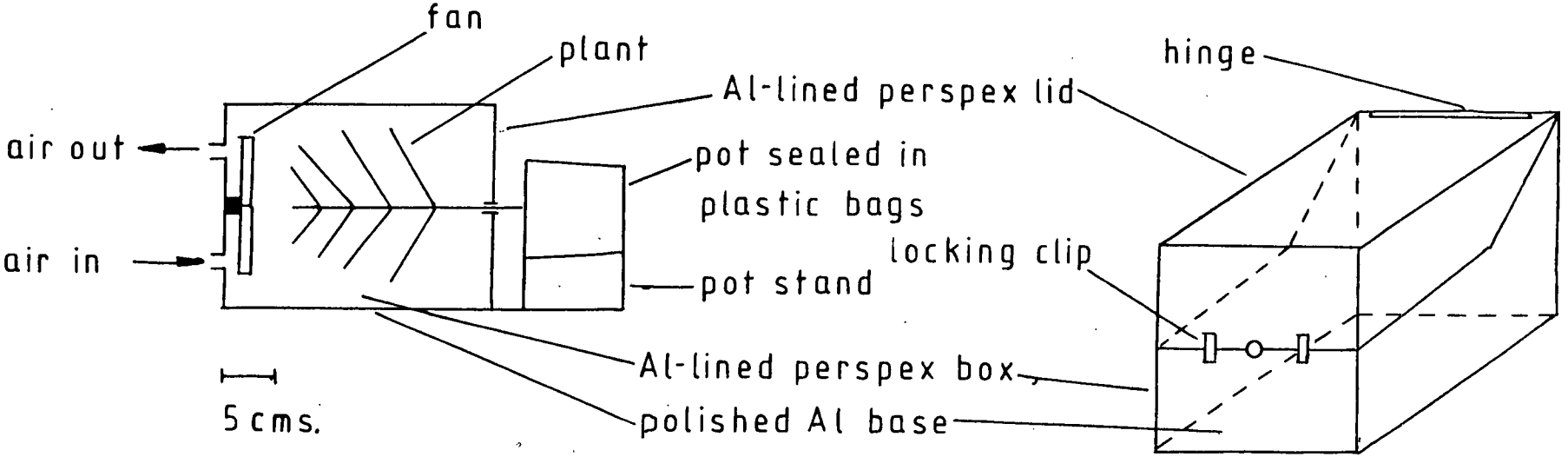


**Figure 7.1 The assimilation chamber.**

A large fan in the chamber provided adequate mixing; the boundary layer resistance, determined by the method of Landsberg and Ludlow (1970) was .13 s $cm^{-1}$ within the chamber.

Needle temperature of the plant in the chamber was determined using copper/constantan thermocouples as described in 3.4.

Whole plants were used in this experiment, with a leaf area of 200-300 $cm^2$. The maximum obtainable flowrate through the chamber was 12 l $min^{-1}$ and as a result the plants depleted the airstream of up to 50 ppm $CO_2$ at the highest light intensities. The maximum tolerated depletion is ideally 20 ppm (Larcher 1969), as higher depletions may reduce the rate of photosynthesis.

The light source was a 400 W metal halide lamp (Wotan HQ1-T). Approximately 75% of the output of this lamp is PhAR (Morison, pers. comm.) Photon flux density was altered by the use of neutral density cinemoid and cheesecloth filters at the chamber. The absorption spectrum of these filters is almost uniform in the 400-700 nm. waveband (Wilson 1978).

PhAR within the chamber was determined using a quantum sensor (LI-190SR, Lambda Insts. Corpn.).

### 7.2.3 The gas circuit

The gas circuit is shown diagrammatically in figure 7.2. Air is drawn in from outside the building (at 4th floor level) and passes through the air conditioning system, A. Air is split into 'dry' and 'wet' lines and the rates of flow are regulated by flowstats fs1 and fs2 and measured by flowmeters fm1 and fm2. By adjusting the relative rates of flow through the 'dry' and 'wet' lines, the vapour pressure of the air

Figure 7.2 key

p1 portal to outside (4th floor)

A air conditioning system

Fs1 flowstat regulating flow through 'dry' line
Fm1 flowmeter measuring flow through 'dry' line
d1 $CaCl_2$ drying tower
d2 $Mg(ClO_4)_2$ drying tower
Fs2 flowstat regulating flow through 'wet line'.
Fm2 flowmeter measuring flow through 'wet line'.
h humidifier - air bubbles through this vessel of water set in a water-bath at 30 °C.
c coil set in same water-bath as assimilation chamber

B 'chamber' and 'reference' lines

Fs3 flowstat regulating flow through assimilation chamber
Fm3 flowmeter measuring flow through assimilation chamber
ch assimilation chamber set in water-bath at 15 °C
Fm4 venting flowmeter - air escapes into atmosphere
Fs4 flowstat regulating flow along 'sample' line
Fm6 flowmeter measuring flow along 'sample' line
p2 portal connection between 'sample' line and measuring instruments
dph dew point hygrometer
fs5 flowstat regulating flow through 'reference' line
fm5 flowmeter measuring flow through 'reference' line

C Air-scrubbing system

d3,d4, $CaCl_2$ drying tower, $Mg(ClO_4)_2$ drying tower
s1, s2, s3, s4 'Carbasorb' $CO_2$-scrubbing towers
fs6 flowstat regulating flow of $CO_2$ - free air through p9 and $S_s$
p6, p5 portals into URAS-2 case; flushing it with $CO_2$ - free air

D The URAS-2
p3 portal to sample line
$S_l$,$S_s$ long and short sample tubes
p9 portal between long and short sample tubes
p4 portal to reference line
$R_l$ and $R_s$ long and short reference tubes
p7, p8 portals from reference and sample lines to atmosphere
b compressed-air bottle of known $CO_2$-concentration

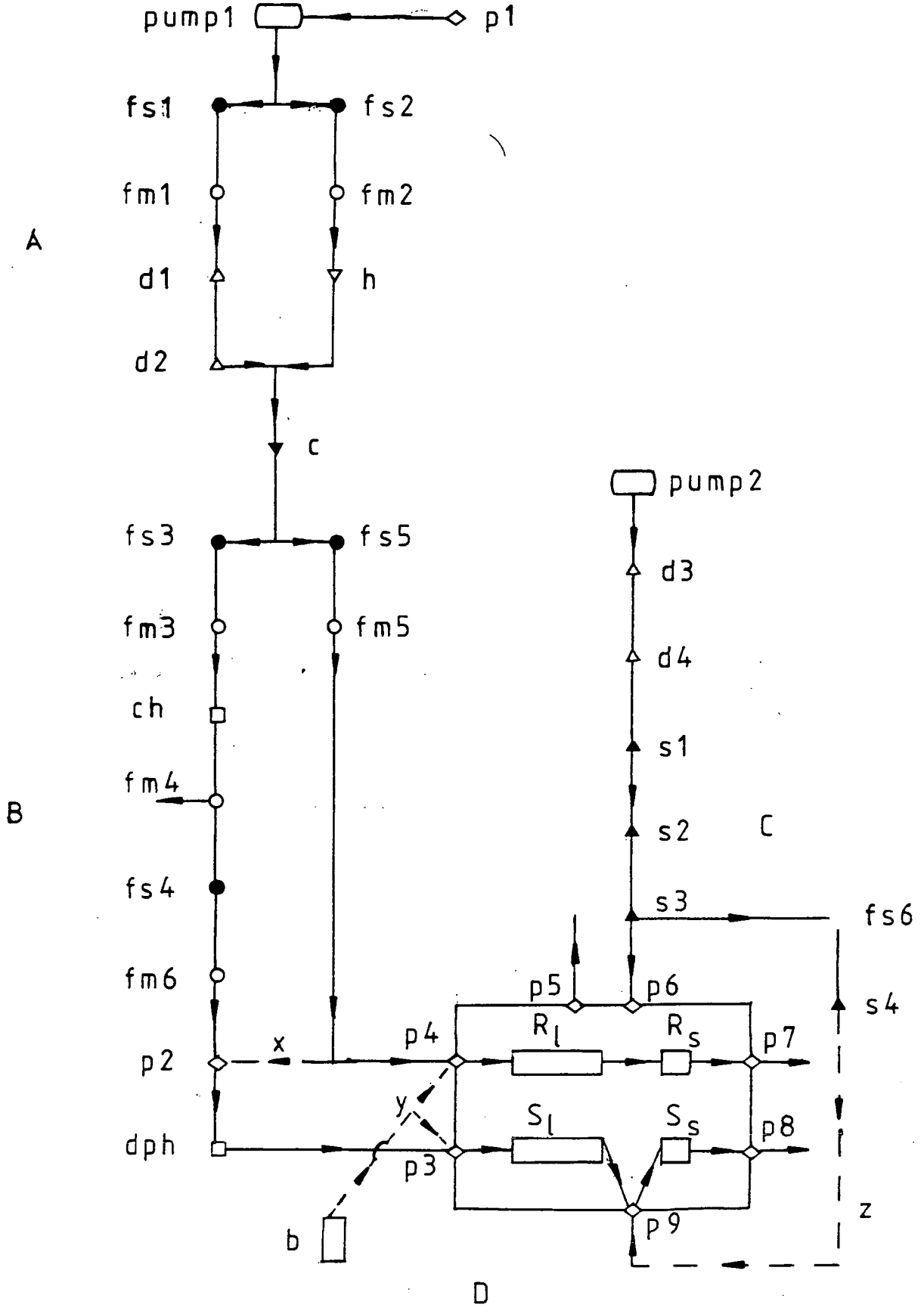


Figure 7.2 The gas flow system.

can be finely adjusted. The airflow is brought to the same temperature as the assimilation chamber in a copper coil in the assimilation chamber's water-bath and split into 'chamber' and 'reference' lines, B.

The rate of flow through the 'chamber' and 'reference' lines, B, is regulated and metered by fs3, fs5, fm3 and fm5. Air leaving the chamber is split into two lines, the majority vents to the atmosphere while the rest flows along the 'sample' line to the instruments. The flowmeter measuring flow into the chamber was calibrated against a precision wet test meter (Alexander Wright and Co.,Ltd., London).

In monitoring mode, air from the chamber flows through the instruments (solid line, figure 7.2). To determine the $CO_2$ concentration and water vapour pressure of the 'reference' line, pathway x is completed in figure 7.2. The sensitivity of the URAS-2 was determined as described in 7.2.4, by completing pathways y to z.

Ambient $CO_2$ concentrations were determined by comparing the 'reference' line with air of known $CO_2$ concentration from the gas bottle. The $CO_2$ concentration of the compressed air was determined using gas-mixing pumps arranged in cascade (Wösthoff oHG. types SA18, SA27, G27) as described by Sesták, Cătský and Jarvis (1971).

### 7.2.4 The infra-red gas analyser.

A URAS-2 infra-red gas analyser (Hartmann and Braun, W. Germany) in differential mode was used to measure differences in $CO_2$ concentration between the 'sample' and 'reference' lines. The URAS-2 was fitted with optical filters at the 2700 nm. waveband, rendering it insensitive to water vapour. A detailed description of the instrument is provided by Sesták et al (1971).

The reference and sample tubes of the URAS-2 are divided into long and short cells, figure 7.2. To determine the relative length of the sample short tube, the sensitivity of the instrument was calculated from the deflection resulting from air of different $CO_2$ concentrations flowing through the reference and sample lines. Passing air of a known $CO_2$ concentration through the long tubes and reference short tube (i.e. $R_1$, $R_s$, $S_1$ in figure 7.2) and air of a known, different $CO_2$ concentration through the sample short tube ($S_s$), gives a deflection from which the relative length of $S_s$ can be found, if the sensitivity is known (Sestàk et al 1971). Air of various known $CO_2$ concentrations was obtained using the Wösthoff gas-mixing pumps.

Whenever a reading was to be taken, the sensitivity of the URAS-2 was redetermined each time by passing standard samples of air through $R_1$, $R_s$ and $S_1$ (pathway y in figure 7.2) and $CO_2$-free air through $S_s$ (pathway z in figure 7.2). Knowing the relative length of $S_s$, the sensitivity could be calculated.

The case of the URAS-2 was continually flushed with $CO_2$-free air (figure 7.2).

### 7.2.5 The dew-point hygrometer

A dew-point hygrometer (Cambridge System Inc. model 880) was used to measure the water vapour pressure of the air streams. The instrument was calibrated against air streams of known water vapour pressure, obtained by saturating the air stream at known temperatures.

### 7.2.6 Measurement of leaf area

Projected leaf areas of the plants were determined at the end of the experiment using an LI-3100 area meter (Lambda Instruments Corp.,U.S.A.)

### 7.2.7 Calculations

The following calculations are based on Sesták et al (1971), chapter 16.

#### 7.2.7.1 Transpiration rate and resistances to water flux.

The change in absolute humidity, $\Delta\chi$ , of air passing through the chamber:

$$\Delta\chi = \frac{217(e_i - e_o)}{T_n} g\ m^{-3} \text{ at } T_n\ ^\circ K \qquad (7.1)$$

where $e_i$ is the vapour pressure of the air entering the chamber, mb

$e_o$ is the vapour pressure of the air leaving the chamber, mb

and $T_n$ is the needle temperature, $^\circ K$.

Transpiration rate, E, is:

$$E = \frac{\Delta\chi\ J\ 10^{-3}}{60A\ 10^{-4}} \qquad g\ m^{-2}\ s^{-1} \qquad (7.2)$$

where J is flowrate, 1 $min^{-1}$;

A is leaf area, $cm^2$.

Needle-air vapour pressure deficit, $d_n$ :

$$d_n = \frac{217(e_s(T_n) - e_o)}{T_n} g\ m^{-3} \text{ at } T_n\ ^\circ K \qquad (7.3)$$

where $e_s(T_n)$ is saturation vapour pressure at $T_n\ ^\circ K$.

Total and needle resistances:

$$r_t = d_n/E \quad s\ cm^{-1} \qquad (7.4)$$

$$r_n = d_n/E \quad s\ cm^{-1} \qquad (7.5)$$

7.2.7.2 $CO_2$ flux and resistances to $CO_2$ fluxes

At 15°C, 1 $\mu$l $CO_2$ weights 1.86 $\mu$g at standard pressure.

$CO_2$ flux, F:

$$F = \frac{1.86\ J(C_i - C_o)}{60\ A\ 10^{-4}}\ \mu g\ m^{-2}\ s^{-1} \qquad (7.6)$$

where $C_i$ is $CO_2$ concentration of air entering chamber, ppm( $\mu l\ l^{-1}$)

and $C_o$ is $CO_2$ concentration of air leaving chamber, ppm( $\mu l\ l^{-1}$)

Holmgren et al (1965) show that plant cuticles are effectively impermeable to $CO_2$ flux, so the needle resistance to $CO_2$ flux, calculated from the needle resistance to $H_2O$ flux, is effectively the stomatal resistance to $CO_2$ flux, $r_s'$ :

$$r_s' = r_n D_w/D_c \qquad (7.7)$$

where $D_w$ is the diffusion coefficient of water vapour in air, $m^2\ s^{-1}$

and $D_c$ is the diffusion coefficient of $CO_2$ in air, $m^2\ s^{-1}$

Thom (1968) showed empirically that the boundary layer resistance to $CO_2$ flux is related to the boundary layer resistance to $H_2O$ flux by:

$$r_a' = r_a(D_w/D_c)^{.67} \qquad (7.8)$$

The $CO_2$ gradient from the air in the chamber to the chloroplast is:

$$1.86(C_a - C_c).10^3\ \mu g\ m^{-3} \text{ at } 15°C \qquad (7.9)$$

where $C_a$ is the $CO_2$ concentration of the chamber air, ppm or $\mu l\ l^{-1}$

and $C_c$ is the $CO_2$ concentration at the chloroplast, assumed to be 50 ppm.

Assuming that the total $CO_2$ flux can be estimated by $(F+R)$ g $m^{-2}$ $s^{-1}$, where F is net photosynthesis and R is dark respiration, the residual resistance to $CO_2$ flux, $r_r$ can be estimated from:

$$(F+R)\,\mu g\ m^{-2}\ s^{-1} = \frac{1.86(C_a-C_c).10^3\ \mu g\ m^{-2}\ s^{-1}}{(r_a' + r_s' + r_r).10^2}$$

$$\Rightarrow\ r_r = \frac{18.6(C_a-C_c)}{F+R} - (r_a' + r_s')\ s\ cm^{-1} \qquad (7.10)$$

## 7.3 Results

Results are summarised in figure 7.3, table 7.1 and 7.2. Figure 7.3 shows typical $CO_2$ flux and resistance curves. Differences between wind treatments in photosynthetic fluxes are small and not statistically significant. However, photosynthetic fluxes in the second low windspeed period were consistently lower than values for the first low windspeed period and the high windspeed period, for light intensities above 210 $\mu E\ m^{-2}\ s^{-1}$. Examination of figure 7.3 shows that these slight differences are entirely due to a small increase in stomatal resistance.

Maximum photosynthetic rates and quantum yields listed in table 7.1 are somewhat higher than those reported for conifers by Jarvis et al (1976) and for P. contorta by Dykstra (1974). This may be due to the high reflectivity in the assimilation chamber reducing the unavoidable self-shading of needles to a minimum.

Lopushinsky (1975) reviews earlier literature on P. contorta and reports maximum net photosynthetic fluxes of 7-17 mg $g^{-1}(hr)^{-1}$. The specific leaf area of the plants used in this experiment was about 60 $cm^2\ g^{-1}$, which gives maximum net photosynthetic fluxes of 14.7 mg $g^{-1}(hr)^{-1}$.

Table 7.2 shows that dark respiration rates of the different windspeeds differ significantly from one another. Reference to table 7.1, where the results of Tukey's test (Steel and Torrie 1960) are summarised, shows that the 25% increase in dark respiration during the high windspeed is significant ($P<0.05$).

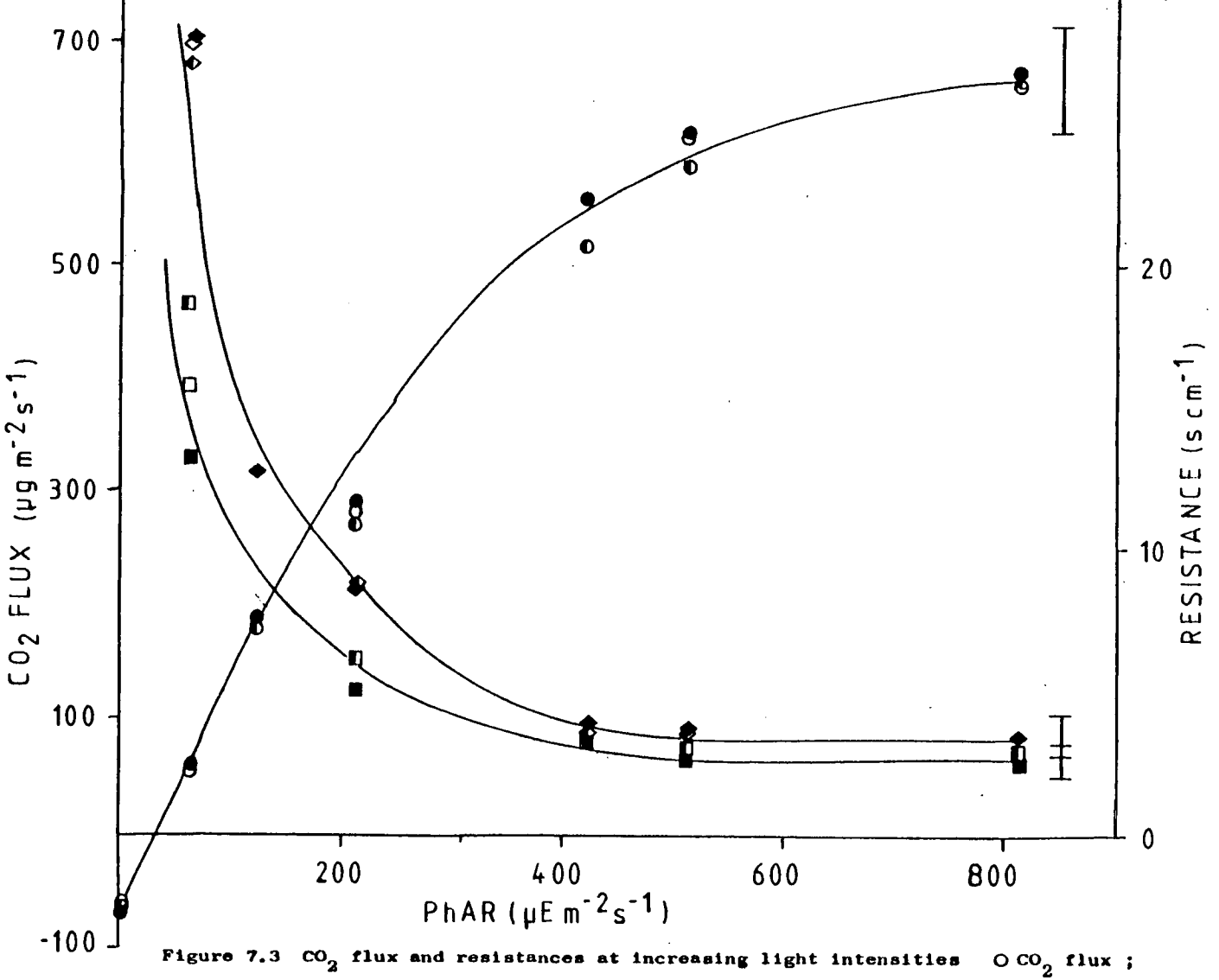


Figure 7.3 $CO_2$ flux and resistances at increasing light intensities ○ $CO_2$ flux ; □ stomatal resistance ; ◇ residual resistance. Open symbols : 1st low wind period ; half-symbols : 2nd low wind period ; solid symbols : high wind period. Bars are 2 standard errors.

Table 7.1 Photosynthetic parameters of P. contorta means and standard errors

| | Dark Respir. $g\ m^{-2}\ s^{-1}$ | Quantum Yield Einsteins $mole^{-1}$ | Fmax $g\ m^{-2}\ s^{-1}$ | $r_s'$ min $s\ cm^{-1}$ | $r_r$ $s\ cm^{-1}$ |
|---|---|---|---|---|---|
| 1st low wind period | $-54.9^b \pm 5.73$ | 21 $\pm$ 1.9 | 677 $\pm$ 23.1 | 2.4 $\pm$ .27 | 3.3 $\pm$ .33 |
| high wind period | $-71.6^a \pm 4.66$ | 20 $\pm$ 1.0 | 678 $\pm$ 19.7 | 2.7 $\pm$ .09 | 3.3 $\pm$ .23 |
| 2nd low wind period | $-59.4^b \pm 3.38$ | 23 $\pm$ 1.3 | 646 $\pm$ 22.2 | 3.1 $\pm$ .09 | 3.3 $\pm$ .48 |
| overall mean | - | 21 | 670 | 2.7 | 3.3 |

a, b: means with different letters differ at $P<0.05$ by Tukey's Test (Steel and Torrie 1960)

Table 7.2 Analysis of variance of dark respiration measurements

| Source | df | SS | MS | F | P |
|---|---|---|---|---|---|
| Among treatments | 2 | 1093.3 | 546.7 | 3.70 | <0.05 |
| Within treatments | 17 | 2509.0 | 147.6 | | |
| Total | 19 | 3602.3 | | | |

## 7.4 Discussion

In chapter 6 it was inferred that net photosynthesis was decreased or dark respiration increased, by shaking. In this chapter it is shown that high wind causes a 25% increase in dark respiration, but has no effect on net photosynthesis. The two experiments together suggest that the reduction in growth caused by continuous motion is due to an increase in dark respiration.

As reviewed in 2.16 and 2.17 there are reports in the literature that shaking increases respiration and contradictory reports of an effect of wind on respiration.

In growth analysis studies respiration is considered as a negative term in the carbon budget (Květ et al 1971; Evans 1972) as it represents a loss of carbon. Yet as Beevers (1970) points out, respiration is a vital plant process as it is the source of ATP, reduced nucleotides and intermediates used in the synthesis of permanent cellular constituents. An increase in respiration rate might be expected to indicate an increased biosynthetic activity in the unstressed plant; a sign of increased, not decreased, growth. Ledig, Drew and Clark (1976) found that increased shoot and root respiration preceded bursts of growth of these organs, in Pinus rigida seedlings.

McCree (1970) divided dark respiration into two components: growth respiration and maintenance respiration. Maintenance respiration has been found experimentally to be proportional to plant dry weight (McCree 1970, 1974, Ledig et al 1976) and from biochemical considerations, Penning de Vries (1972) came to the same conclusion. Semikhatova (1970) suggested that maintenance respiration increases in response to 'stress'. Penning de Vries (1975) discusses the effects of stress on maintenance processes and notes

various ways in which stresses increase the 'cost' of maintenance in plants. Low temperature decreases the P:O ratio (moles of inorganic phosphate converted to organic form per mole of oxygen used) and so should increase respiration rates; high temperatures increases protein turnover and plasmalemma permeability; salinity stress decreases the P:O ratio; and nutrient deficiencies increase protein turnover and respiration. (Penning de Vries 1975). Water stress, on the other hand, generally decreases respiration (Slatyer 1967). Penning de Vries (1975) attributes this to a general reduction in metabolic activity.

Thus the results of the growth analysis and $CO_2$ flux experiments reported here can be explained by postulating that subjecting P. contorta to continuous motion causes an increase in the maintenance 'costs' of the plant, resulting in a reduced amount of respiratory substrate for growth. This must remain a hypothesis until it has been shown that it is indeed the maintenance component of respiration that is affected.

## 7.5 Summary

(1) The effects of wind on the net photsynthesis and dark respiration of P. contorta are described.

(2) High wind significantly increases dark respiration, but has no effect on net photosynthesis.

(3) It is postulated that continuous motion reduces the respiratory substrate available for growth by increasing the maintenance respiration of P. contorta.

# Chapter 8 Effects of wind and shaking on the water relations of *P. contorta*

## 8.1 Introduction

The effects of wind and shaking on plant water relations are reviewed in 2.1.3, 2.1.5 and 2.1.7. Kahl (1951) found that shaking increased transpiration of three plant species, but Beardsell (1977) was unable to detect an effect of handling on transpiration. Increases, decreases and no changes in transpiration rate and stomatal conductance with increasing windspeed have been reported. Cuticular conductances of various grass species and *Acer pseudoplatanus* were increased by high winds due to the abrasive damage caused when leaves collide with one another in the wind (Grace 1974, Wilson 1978). However, only small effects on plant water status have been reported, where this has been measured directly (2.1.5).

There are several ways in which wind and shaking might affect the water relations of *P. contorta*. A reduction of the boundary layer resistance may increase or decrease transpiration rate, depending on specific environmental conditions. Wind-induced needle collisions might affect cuticular and stomatal conductances. Although shaking as applied in these experiments does not cause needle collisions, it may still affect transpiration via an effect of mechanical shock on stomatal conductances. The effect of shaking on the boundary layer resistance is small, as shown by the small temperature differences between shaken and control plants reported in 4.3.2 and further discussed in this chapter.

The work of Milburn and Johnson (1966) and Milburn and McLaughlin (1974) has recently highlighted the role of cavitation in the water relations of plants. It may be possible that wind-induced motion mechanically distorts tracheids and so causes cavitation in the transpiration stream.

If wind and shaking cause water stress in P. contorta, it should be detectable as a decrease in total water potential, $\Psi$. It is presumably possible, that turgor pressure potential, $\Psi_p$, might be affected independantly of $\Psi$. This might occur if the properties of the plasmalemma were altered, changing the solute potential, $\Psi_s$, but not necessarily affecting $\Psi$. Such an effect on the plasmalemma is hypothesised in 2.1.7. In the present work it was therefore decided to determine turgor and solute potentials separately by the method of Scholander et al. (1965). This analysis is discussed in 8.2.

Wind and shaking reduced the growth of P. contorta, as described in 4.3.1, 4.3.2 and 4.3.3. Water potentials of these same plants during the experiments described in 4.3.1, 4.3.2 and 4.3.3 are reported in 8.4.1.

The effect of wind on the cuticular conductance of P. contorta is reported in 8.4.2.

The effects of wind and shaking on the needle conductance, water potentials and components of pressure-volume curves are described in 8.4.3, 8.4.4 and 8.4.5.

Needle conductance, $g_n$, is used in this chapter as it is proportional to transpiration rate, E :

$$g_n = 1/r_c + 1/r_s = E/(\chi_s(T_n) - \chi_a) - 1/r_a \qquad (8.1)$$

where $r_c$ is cuticular resistance;

$r_s$ is stomatal resistance;

$r_a$ is boundary-layer resistance;

$(\chi_s(T_n) - \chi_a)$ is needle-air absolute humidity deficit.

## 8.2 Pressure-volume curves

By measuring the volume of the expressed sap from a shoot in a pressure bomb at given pressures, it is possible to construct 'pressure-volume curves' from which solute and turgor potentials can be deduced (Scholander et al 1965). Tyree and Hammel (1972) provide a theoretical discussion of pressure-volume curves, and conclude that the relation between the pressure on a plant shoot in the pressure bomb and the tissue volume can be written:

$$\frac{1}{P} = \frac{V_o - V_e}{RTN_s F(V_o - V_e)} \qquad (8.2)$$

where $P$ is the total pressure on the cell fluid,

$V_o$ is the original (maximum) volume of all the living cells in the shoot,

$V_e$ is the volume expressed from all the cells,

$R$ is the universal gas constant,

$T$ is the absolute temperature,

$N_s$ is the total number of osmoles of solute in all the living cells

and $F$ is a function relating turgor pressure to volume:

$$\psi_p = F(V) = \varepsilon\left(\frac{V-V_p}{V_p}\right)^n \qquad (8.3)$$

where $\psi_p$ is the turgor pressure potential,

$\varepsilon$ is the bulk modulus of elasticity of the shoot,

$V$ is the volume of the shoot,

$V_p$ is the volume of the shoot, at incipient plasmolysis

and $n$ is a coefficient of non-linearity.

A plot of 1/P against the volume of the shoot or volume expressed from the shoot is curvilinear, becoming linear when $F(V_o-V_e)$ becomes constant, point a on figure 8.1. Tyree and Hammel (1972) assume that at this point, $F(V_o-V_e)$, or $\Psi_p$, is 0. The solute potential at this point is $\Psi_{s,p}$, the solute potential at incipient plasmolysis. The volume or relative water content at this point is referred to as $V_p$ or $RWC_p$ in this chapter. Extrapolation of the linear part of the curve to $V_e$=0(RWC=100%), point b on figure 8.1, gives $\Psi_{s,o}$ the solute potential at full turgor. Extrapolation of the line to 1/P = 0, point c on figure 8.1, gives $V_b$, the volume of the osmotic water. The rate of change of relative symplasmic volume $(V-V_p)/V_p$ with pressure potential gives $\epsilon$, the bulk modulus of elasticity (equation 8.3). $\epsilon$ thus describes the shape of the curved part of the pressure-volume curve, and the linear part can be characterised by $\Psi_{s,o}$, $\Psi_{s,p}$ and either $V_p$ or $RWC_p$. Pressure-volume curves can thus be compared by examination of these parameters.

The solute potential at any water content can be found from the line bac in figure 8.1. Determination of $\Psi$ at that water content allows the calculation of the pressure potential:

$$\Psi = \Psi_p - \Psi_s \qquad (8.4)$$

The above model assumes that the relationship between pressure potential and volume, F(V), for each individual cell can be summed to give a meaningful average. Cheung, Tyree and Dainty (1976) show that variation in $\Psi_{s,o}$ and $\epsilon$ between cells can result in errors in determining $\Psi_{s,p}$ and the exact slope of the extrapolated line. They also point out that $\epsilon$ as defined in equation (8.3) is arbitrary, but still indicates the ability of the shoot to conserve water.

Acock (1975) criticises the model on the following grounds:

(i) it assumes that the matric potential remains constant as total water potential decreases;

(ii) it assumes ideal behaviour of solutes and cell membranes; and

(iii) it assumes that $\Psi_p$ is 0 when the curve becomes linear. He points out that if $\Psi_p$ became increasingly negative as $\Psi$ decreased and the symplasmic volumes becomes smaller, the function $F(V_o-V_e)$ in equation 8.2 will become small and constant, causing linearity in the pressure-volume curve. This would invalidate the assumption that this line describes the relation of solute potential with water content.

Of these criticisms,(iii)is the most serious. However, Tyree (1975) doubts the existence of negative $\Psi_p$ and criticises the methods by which negative $\Psi_p$ have apparently been determined.

The model of Scholander et al (1965) as elaborated by Tyree and Hammel (1972) is accepted in this chapter.

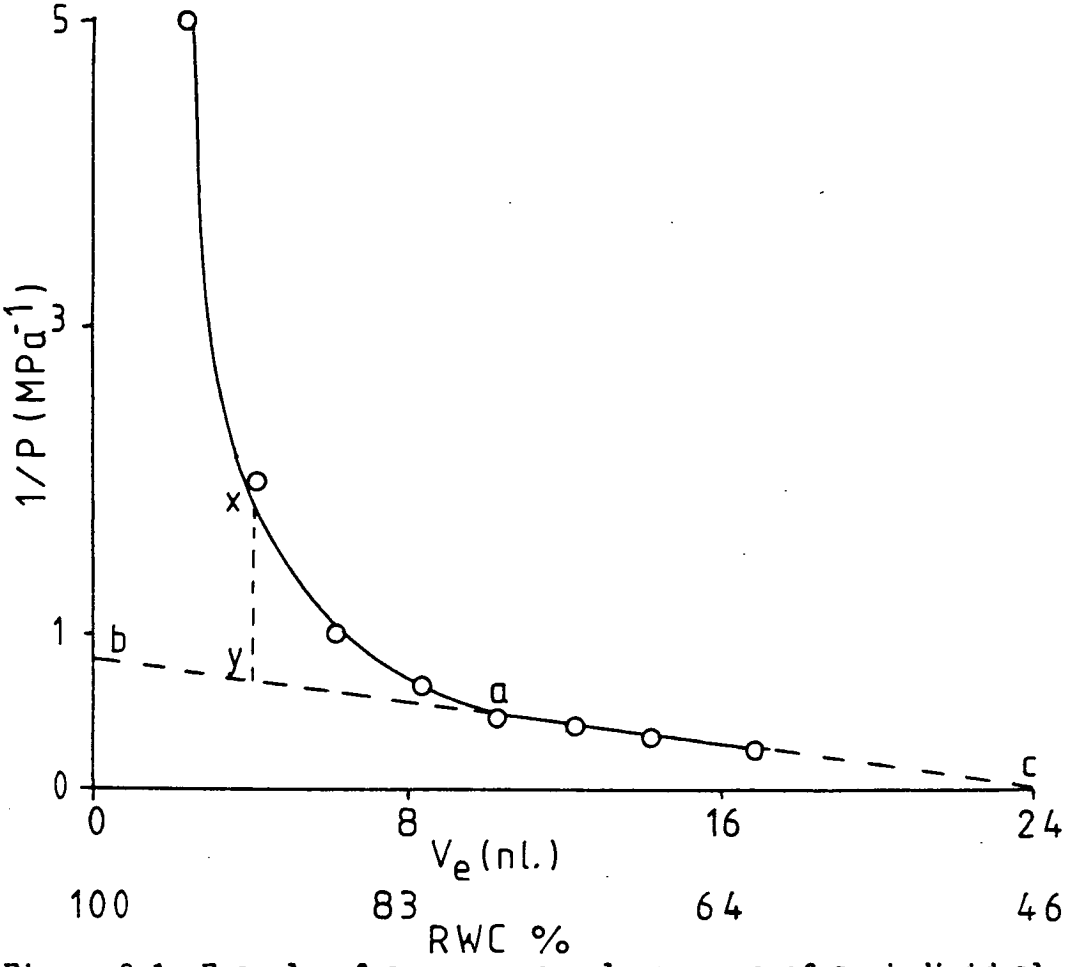


**Figure 8.1** Example of a pressure-volume curve of an individual needle

a point of incipient plasmolysis

b solute potential at full turgor, $\Psi_{s,o}$

c volume of osmotic water, $V_b$

x,y For a given total water potential, x, the solute potential, y, can be found and the pressure potential, $\overline{xy}$, calculated.

## 8.3 Materials and Methods

### 8.3.1 Transpiration rate

Transpiration rates were determined gravimetrically using plants with their pots enclosed in two plastic bags which were sealed separately about the stems. The plastic bags were unsealed each morning for an hour to allow gas exchange to the roots and replenishment of soil water. Weight losses were found to be constant during the light period in the controlled environments, so the rate of water loss was calculated as the regression coefficient of weight loss against time. Projected needle areas were measured using the LI-3100 area meter. Transpiration rate, E, was thus:

$$E = b/A \qquad (8.5)$$

where b is the rate of water loss per second;
and A is the projected needle area of the plant.

### 8.3.2 Boundary layer resistance and needle conductance

To estimate the boundary layer resistances of plants in the controlled environments, the evaporation rate of water from a model plant was measured, using the method of Landsberg and Ludlow (1970). The greater length and flexibility of P. contorta needles than spruce needles made it extremely difficult to apply an even coat of plastic-of-paris to the shoots. Instead, all the needles were removed from a shoot and replaced with as many 6 cm. panel pins as possible. The necessarily reduced 'needle' no. would result in an underestimate of the actual boundary-layer resistance of a real shoot (Landsberg and Thom 1971).

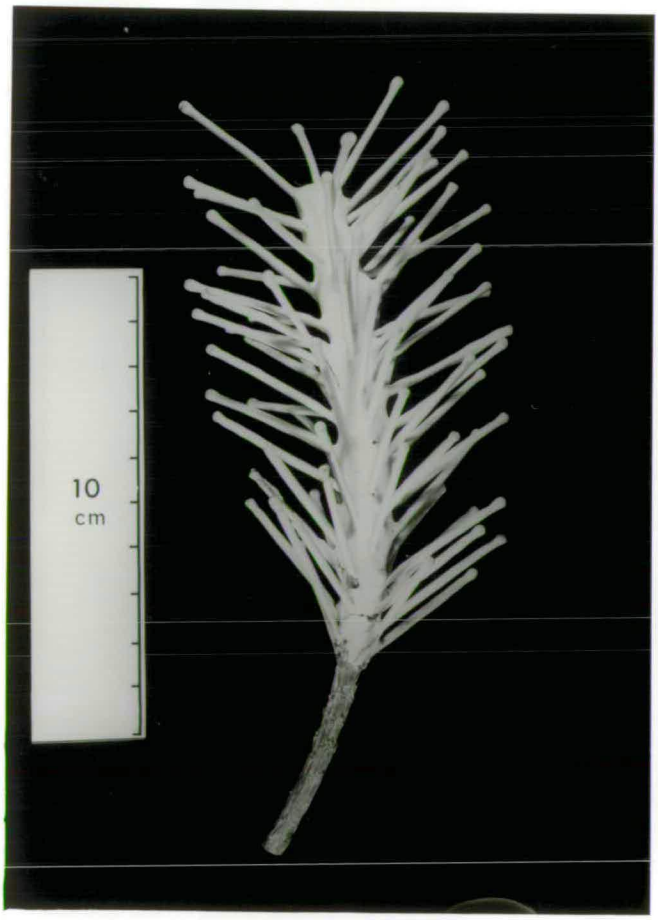


Figure 8.2 This artificial pine shoot was constructed by removing the pine needles and replacing them with as many 6 cm. tacks as possible.

Evaporation from the model was determined with the model standing within the plant canopy in the controlled environments.

A copper/constantan thermocouple (as described in 3.4) embedded in the model showed that the model remained at the wet bulb temperature for at least 15 mins. at the high windspeed.

The projected area of the model was calculated from the mean length and diameter of the 'needles' and stem of the model, assuming that they had cylindrical form.

Boundary-layer resistance, $r_a$, was calculated from the weight loss of the model over 10 min. periods and the projected area of the model.

The needle-air vapour pressure deficit, $e_s(T_n)-e_a$, was calculated from mean needle temperature $T_n$ °K, and air vapour pressure, $e_a$, mb., determined with thermocouples and an Assman psychrometer as described in 3.4.

Needle conductance, $g_n$, was calculated from:

$$g_n = \frac{217E}{T_n(e_s(T_n)-e_a)} - \frac{1}{r_a} \qquad (8.6)$$

### 8.3.3 Cuticular conductance

The method of Hygen (1951) is probably the only satisfactory way of determining cuticular conductances of most plant species. The weight losses of detached needles were monitored over ca. 8 hours. Stomatal closure was taken to have occurred when the weight loss became constant with time and cuticular transpiration rates were determined from the regression coefficient of weight against time, over this period.

Needles were detached and suspended from a horizontal wire below a 250 W Wotan HQ-1 lamp. Light flux density at needle level was 350 $\mu E\ m^{-2}\ s^{-1}$ in the 400-700 nm. waveband. An electric fan provided a windspeed of 2 $m\ s^{-1}$. Assuming the airflow about the needle is similar to that about a cylinder of 1mm. diameter, $r_a$ in these conditions can be calculated from the Reynolds and Sherwood numbers, Re and Sh (Monteith 1973) :

$$RE = du/v \qquad (8.7)$$

$$Sh = .62(K/D_w)^{.33}Re^{.47} \qquad (8.8)$$

$$r_a = d/D_w Sh \qquad (8.9)$$

where d is the cylinder diameter;
v is the kinematic viscosity of air
u is the wind speed

K is the thermal diffusivity of dry air;

and $D_w$ is the diffusion coefficient of water.

At 20°C, $r_a$ is 6.6 $s\ m^{-1}$. As this resistance is very small it was ignored in the calculation of cuticular conductance. Air vapour pressure was continually monitored using an Assman psychrometer (section 3.4). Although air vapour pressure was not regulated, the needle-air absolute humidity deficit varied by less than 10% over the daily measuring period and by less than 6% over the period of cuticular transpiration. The mean of the needle-air absolute humidity deficit over this latter period was considered acceptable for calculation of cuticular conductance.

Needle temperatures were shown, by use of copper/constantan thermocouples, to vary from air temperature by less than .07°C.

Transpiration of individual needles was determined by measuring needle weights to the nearest 10$\mu g$ on a micro-electrobalance

(Cahn Insts/Ventron Corp.,U.S.A., model 4700). The rate of water loss of the needles during the cuticular phase was found by calculating the regression coefficient, b, between needle weight and time over this period. Projected areas of individual needles were found using the LI-3100 area meter. Repeated measurements of projected areas of single needles gave readings varying by less than 5%. Cuticular conductance, $g_c$, was calculated as :

$$g_c = \frac{b}{(\chi_s(T_n) - \chi_a)\ A} \qquad (8.10)$$

where b is the rate of weight loss per second,
$(\chi_s(T_n) - \chi_a)$ is the needle-air absolute humidity deficit,
and A is the needle projected area.

The cut ends of the needles were stood in water in closed vials overnight before determination of weight losses. Knowing the needle turgid weight, tw, and dry weight, dw, (determined by drying the needles for 48 hours at 80°C) the relative water content, RWC, at any given weight, w, could be found.

$$RWC = \frac{(tw-w)}{(tw-dw)} \times 100\% \qquad (8.11)$$

$RWC_s$, the relative water content at stomatal closure, was determined from graphs of needle weight loss against time (Hygen 1951).

8.3.4 Water potentials and pressure-volume curves.

Water potentials of individual needles were determined using a needle pressure bomb similar to that described by Johnson and Nielson (1969).

The bomb was constructed of commercially available standard pipe-fittings (Simplifix Ltd.). Nitrogen gas was used in determinations of water potentials and pressure-volume curves.

Pressure-volume curves were constructed for data collected from individual needles. Twelve needle pressure bombs were connected together in series, and increasing pressures applied to needles within. The expressed sap was collected on filter paper enclosed in aluminium foil 'caps' to prevent evaporation. It was found that the sap so collected was only 50% of the total water lost from the needles during a complete set of measurements. This discrepancy was presumably due to evaporation from the needles in the bombs. The mass (and therefore volume) of water lost from the needles was subsequently determined by removing the needles from the bombs between each pressure increase and weighing them on the Cahn microbalance to the nearest 10 $\mu$g (=10 nl.)

Needles were initially brought to full turgor by standing them in water in closed vials overnight and their dry weights determined by drying in an oven at 80 °C for 48 hours.

The following pressures were applied to the needles for 30 - 40 minute intervals : .2, .5, 1.0, 1.5, 2.0, 2.5, 3.0 and 4.0 MPa. Equilibrium pressures of test needles so treated were found to differ from the applied pressures by not more than .1 MPa.

### 8.3.5 Procedures

#### 8.3.5.1 Cuticular conductance

In the first experiment to be described ten two year old Long Beach and ten two year old Hazelton <u>P. contorta</u> were placed in the wind tunnel

three days before the experiment started. Conditions in the wind tunnel were 14°C, 11 mb vapour pressure, 250 $\mu$E $m^{-2}$ $s^{-1}$, 12 hours day length. During the five day low windspeed period (.8 m $s^{-1}$), one needle per plant was removed each evening, brought to full turgor in water overnight and allowed to transpire freely over an 8 hour period the following day. Cuticular conductances and relative water content at stomatal closure were determined as described in 8.3.3.

The windspeed was increased to 8.5 m $s^{-1}$ average for the subsequent five days. At this windspeed there was considerable stem and needle movement, and collisions of needles with one another.

The second experiment to be reported was performed at the end of the experiment described in 4.3.4. Cuticular conductances of one year old Long Beach P. contorta after 8 and 16 days growth in either the growth room at low windspeed or in the wind tunnel at low or high windspeed were determined. Environmental conditions are described in 4.3.4. At the high windspeed (7 m $s^{-1}$) there were continual needle collisions.

8.3.5.2 Water use and water potentials

The water relations of 6 plants in the wind tunnel were compared with the water relations of 6 control plants in the growth room and 6 plants subjected to shaking in the growth room. Environmental conditions are detailed in table 8.1. The windspeed in the wind tunnel was 'low' for the first 5 days, and the shaking machine in the growth room was switched off. The windspeed was turned up to 'high' for the subsequent 8 days and the shaking machine turned on. Windspeed was returned to 'low' and the shaking machine turned off for the final 3 days.

Table 8.1 Environmental conditions in the growth room and wind tunnel

| | PhAR $\mu E\ m^{-2}\ s^{-1}$ | Net Radn $W\ m^{-2}$ | Temperature °C | | Air vapour pressure mb | Boundary layer resistance $s\ cm^{-1}$ |
|---|---|---|---|---|---|---|
| | | | Air | Needle | | |
| Growth Room | 491 | 225 | 15 | 16.1,16.0* | 12 | .26 |
| Wind tunnel low windspeed | 507 | 205 | 15 | 15.7 | 12 | .31 |
| Wind tunnel high windspeed | 507 | 205 | 15 | 15.0 | 12 | .06 |

* Plants subjected to shaking.

'Day' and 'night' transpiration rates and needle conductances were determined each day. Total water potential of each plant was determined daily (a) before the lights came on, and (b) between 1400 and 1600. One needle of 4 plants per treatment was removed each evening, brought to full turgor overnight and placed in the pressure bombs for pressure-volume determinations the following day. Solute and pressure potentials, $\Psi_s$ and $\Psi_p$ were determined for these plants from the appropriate pressure-volume curves. Parameters describing the pressure-volume curves ($\varepsilon$, $\Psi_{s,o}$, $\Psi_{s,p}$, $RWC_p$) were evaluated as described in 8.2.

## 8.4 Results and Discussion

### 8.4.1 Effects of wind and shaking on total water potential

The total water potentials, $\Psi$, of the plants in experiments 4.3.1, 4.3.2 and 4.3.3 are shown in figure 8.3. $\Psi$ of plants subjected to high winds or shaking are significantly less negative ($P<.01$) than the control plants in (a) and (c). In (b) there are only slight differences in $\Psi$, but again $\Psi$ of shaken plants was consistently less negative than $\Psi$ of controls. Despite their higher water potentials, these plants suffered reduced extension growth (chapter 4), reduced cell division and extension (chapter 5) and reduced dry weight growth (chapter 7). Clearly these effects could not have been caused by a motion-induced water stress.

### 8.4.2 Effects of wind on the cuticular conductance of P. contorta

The cuticular conductance, $g_c$, and relative water content at stomatal closure, $RWC_s$, of plants exposed to high and low windspeeds are shown in figure 8.4. Increasing the windspeed had no effect on $g_c$ or $RWC_s$. A simple t- test of the daily means of $g_c$ showed that the differences between the two provenances were statistically significant ($P < .001$) as were the differences between $RWC_s$ ($P < .05$). The techniques used are sensitive enough to detect differences between provenances, yet no effect of windspeed could be found.

The effects of growing plants for 16 days at low or high windspeeds on cuticular conductance are summarised in table 8.2. The analysis of variance shows that differences between the various environments are not significant, i.e. the different windspeeds had no effect on $g_c$.

The somewhat higher values than in the previous experiment may be due to the fact that these needles had not yet fully expanded (4.3.4.) and so the cuticle had not yet hardened.

Even this 16 day period of high wind had no effect on the cuticular conductance of P. contorta. It must be assumed that needle collisions in P. contorta do not cause cuticular abrasion or epidermal damage, in contrast to the reported results with the broad-leaved species Fragaria x ananassus and Acer pseudoplatanus and with grasses (MacKerron 1976, Wilson 1978, Grace 1974). The light weight of an individual needle may mean that the force one needle can exert upon another is too small to cause cuticular damage.

It must be noted that these conductances actually represent minimum conductances which are not necessarily cuticular conductances. It is possible that when the water loss from a P. contorta needle falls to a constant minimum the stomata are not fully closed. The values reported here are, however, comparable with the cuticular conductances reported by Holmgren et al (1965) for a number of species, and the values for Picea sitchensis reported by Jarvis et al (1976). These values represent a negligible amount of water loss, implying (i) a virtually impermeable barrier to water, and (ii) needle conductances calculated by equation 8.6 are close approximations to stomatal conductances (Jarvis et al 1976).

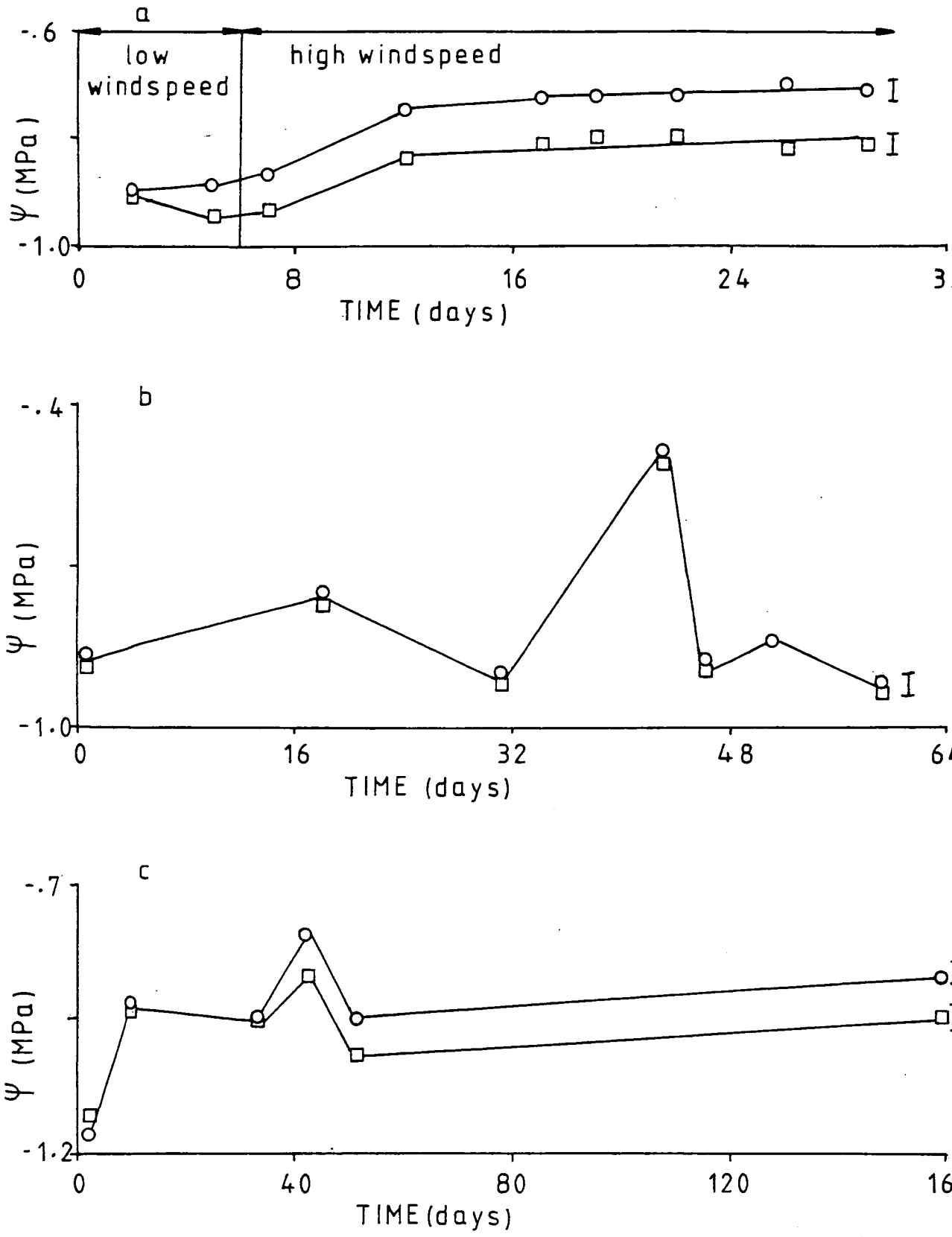


Figure 8.3 Water potentials of plants subjected to high wind or shaking and their controls. a □growth room plants; ○wind tunnel plants at low then high windspeed. b ○shaken plants; □control plants. c ○shaken plants; □control plants. Bars are 2 standard errors.

b. Shaking expt. 4.3.2. c. Shaking expt. 4.3.3

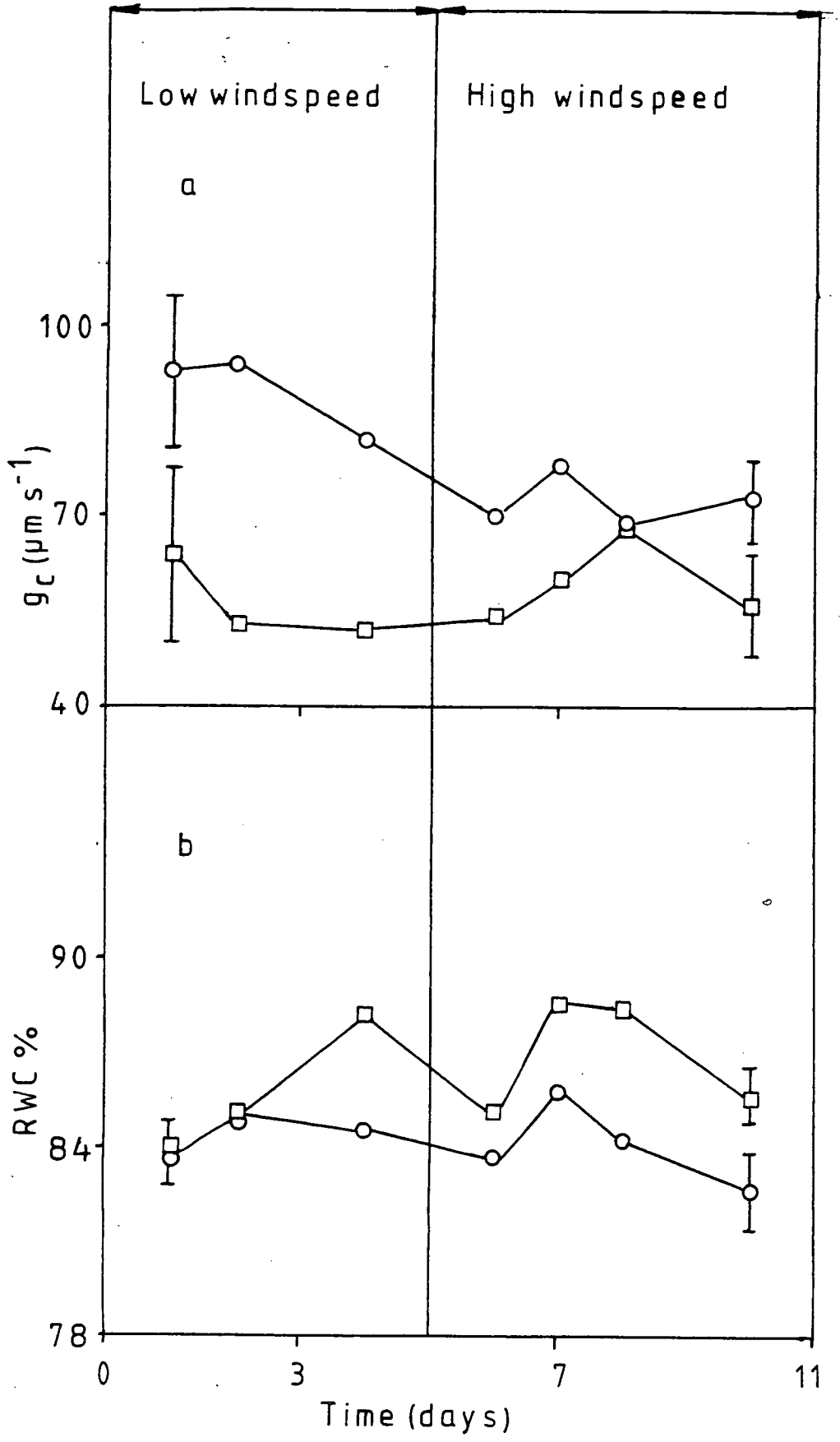


Figure 8.4 a Cuticular conductance of needles of P. contorta subjected low and high windspeed. b RWC at stomatal closure.

○ Long Beach provenance; □ Hazelton provenance. Bars are 2 standard errors.

Table 8.2a Mean (and standard errors) of cuticular conductance of needles of *P. contorta* grown in high or low windspeed environments, $\mu m\ s^{-1}$.
Other environmental parameters were similar (see sections 8.3.5.1 and 4.3.4)

| | Day 8 | Day 16 |
|---|---|---|
| High windspeed | | |
| Wind tunnel | 200 ± 9.2 | 187 ± 7.6 |
| Growth room | 162 ± 8.8 | 144 ± 10.4 |
| Low windspeed | | |
| Wind tunnel | 172 ± 7.6 | 239 ± 13.0 |
| Growth room | 229 ± 14.4 | 228 ± 16.5 |

Table 8.2b Analysis of variance with subgroups of table 8.2a

| Source | df | SS | MS | F | P |
|---|---|---|---|---|---|
| Among days | 7 | 134,518 | | | |
| Among environment | 3 | 95,423 | 31,808 | 325 | NS |
| Among days within envs. | 4 | 39,095 | 9,774 | 489 | .001 |
| Among plants within days | 118 | 236,630 | 2,005 | | |
| Total | 125 | 371,148 | | | |

### 8.4.3 Effects of wind and shaking on the needle conductance of *P. contorta*

Needle conductances of control, shaken and wind-tunnel plants are presented in figure 8.5. Day to day variations in needle conductance and transpiration rate were apparent, but no effects of wind or shaking could be detected. Tranquillini (1969), Caldwell (1970), Davies et al (1974) and Grace et al (1975) also found that needle conductances of various species of spruce and pine were unresponsive to windspeed; this may be a general characteristic of conifers.

The very low values of conductance during the dark period are camparable with cuticular values, suggesting complete stomatal closure in the dark. This has also been noted by Lopushinsky (1975).

The shaking treatment caused a decrease in needle temperature of the order of .05 C, suggesting a very small effect of shaking on $r_a$. Needle conductance was unaffected by shaking, so assuming a value of 4 mm $s^{-1}$ for $g_n$ (i.e. a needle resistance of 2.5 s $cm^{-1}$) and inserting appropriate values into equation 2.25, this temperature difference implies a decrease in $r_a$ of about 2 s $m^{-1}$. The effect of shaking on $r_a$ thus appears to be negligable.

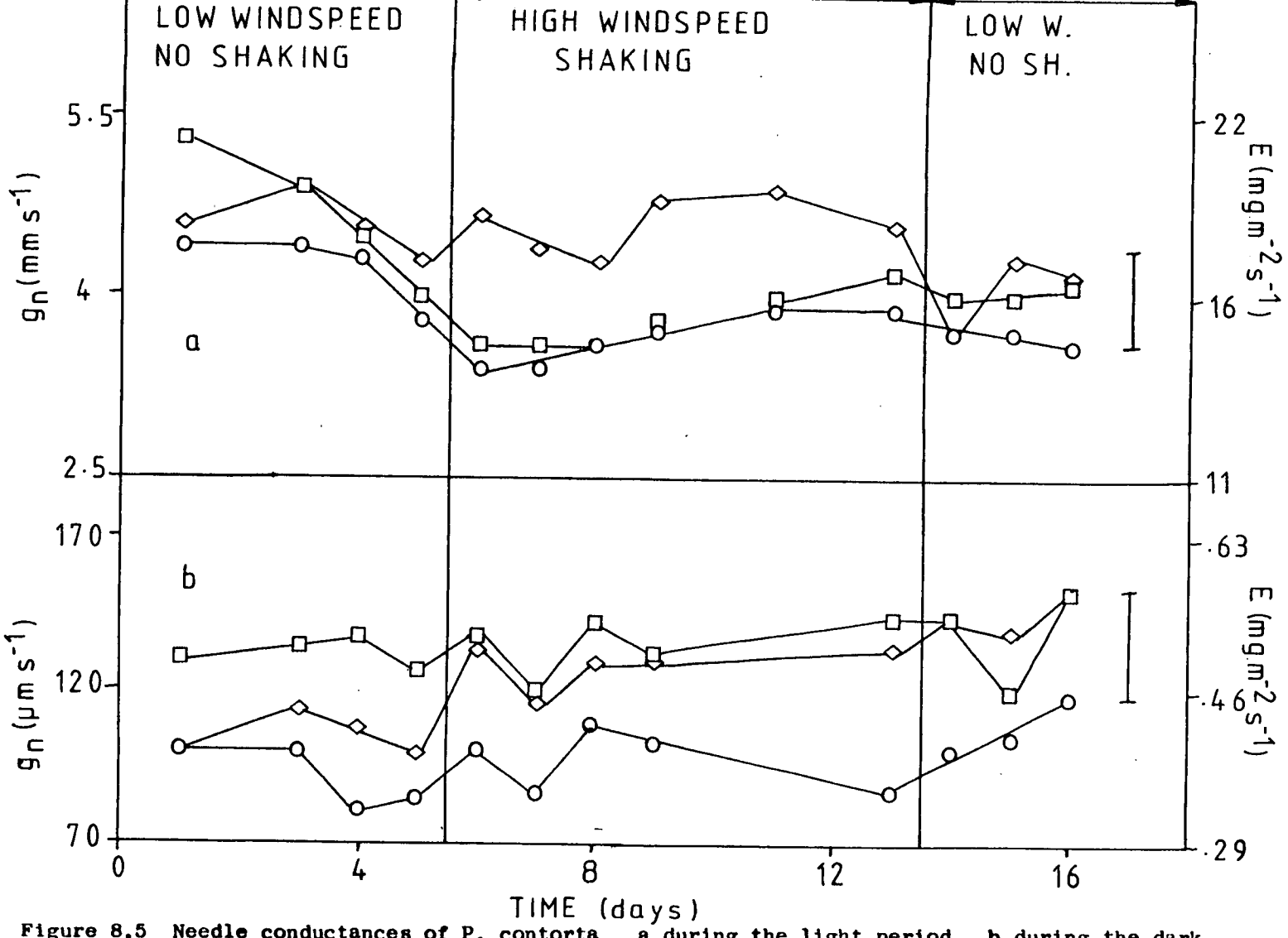


**Figure 8.5** Needle conductances of *P. contorta* a during the light period. b during the dark period. ○ control plants □ shaken plants ◇ wind tunnel plants. Bars are 2 standard errors.

### 8.4.4 Pressure-volume curves of individual needles

Table 8.3 and figure 8.6 summarise data extracted from pressure-volume curves of 11 needles taken at random from the same plant. Figure 8.7 shows that the relation between pressure potential $\Psi_p$ and relative symplasmic volume, $(V-V_p)/V_p$, is linear for these needles. The bulk modulus of elasticity, $\epsilon$, was calculated as the regression coefficient of the relationship between $\Psi_p$ and $(V-V_p)/V_p$, i.e. a value of n=1 in equation 8.3 was assumed.

The small variation between needles suggests that single needles can provide adequate representation of the water relations of the needles of the whole shoot. The values for $\epsilon$, $\Psi_p$ etc. may well differ between tissues of different types and ages, however, (Hsiao 1974). The values derived from individual, fully extended needles such as these may differ from those of extending needles or of the extending shoot, but it seems unlikely that the response to a given stress might differ between tissues and age classes. It is assumed in this chapter that the effects of wind and shaking on the water relations parameters of mature needles will be reflected in growing tissues although actual values may differ.

Parameters of the pressure-volume curves are plotted against time in figure 8.8. The considerable day to day variation in the data is at least partly due to the small number of replicates per 'treatment' (4). The occasional breakage of a needle in the pressure-bomb had a large effect on the mean values of these parameters.

There is no indication of an effect of wind on any of these water relations parameters.

Table 8.3 Means and standard errors of pressure-volume curve parameters of 11 needles picked at random from 1 plant

| | $\psi_{s,o}$ MPa | $\psi_{s,p}$ MPa | $RWC_p$ % | $\varepsilon$ MPa | $V_b/(fw-dw)$ |
|---|---|---|---|---|---|
| Mean | 1.15 | 2.0 | 75.4 | 7.01 | .557 |
| Standard error | .0169 | 0 | .702 | .223 | .0122 |
| Coefficient of variation | 4.9% | 0 | 3.1% | 10.6% | 7.2% |

$\psi_{s,o}$ solute potential at full turgor

$\psi_{s,p}$ " " " incipient plasmolysis

$RWC_p$ relative water content at incipient plasmolysis

bulk modulus of elasticity

$V_b/fw-dw)$ Volume of osmotic water/(fresh weight-dry weight)

= volume of osmotic water/total water

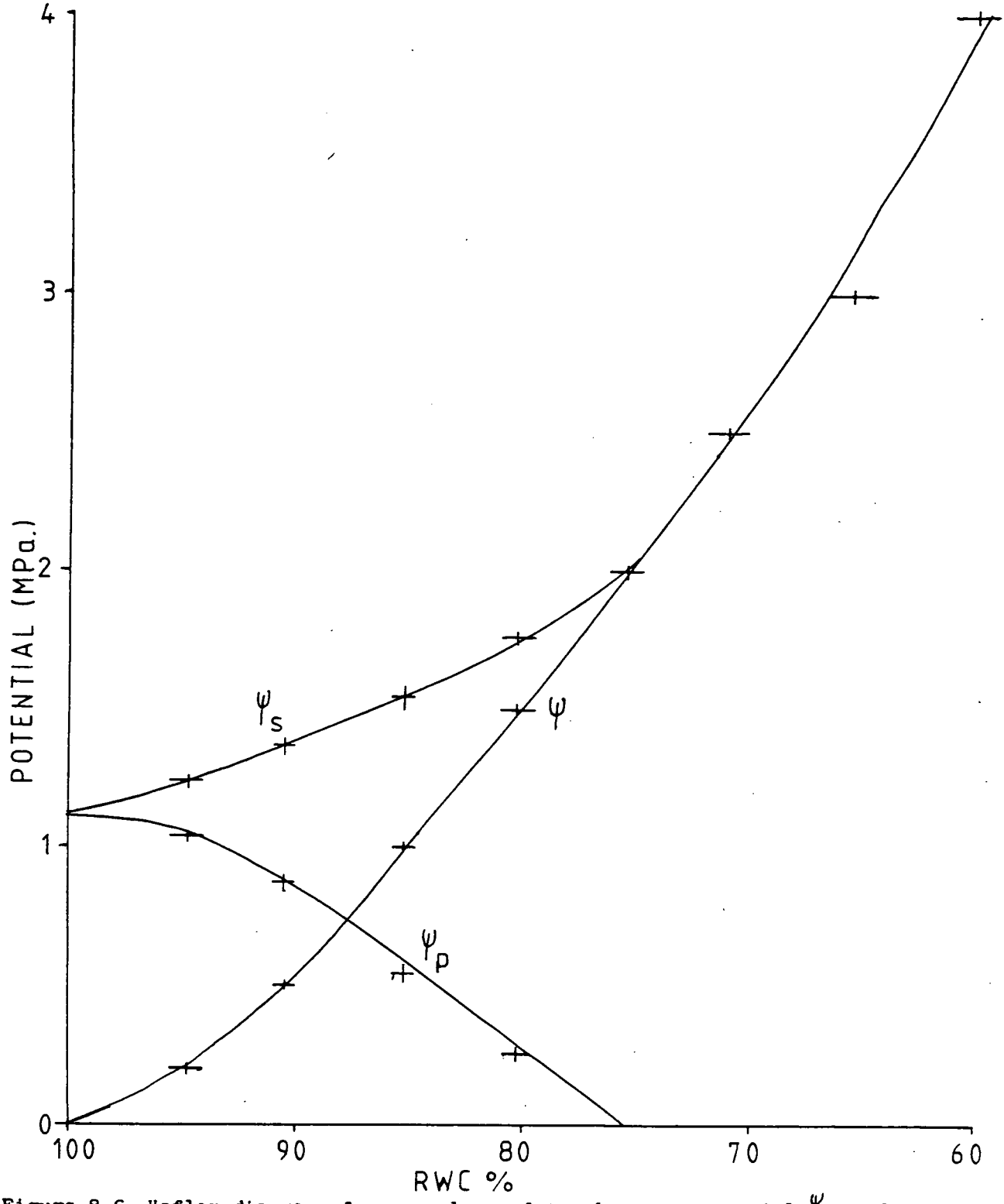


Figure 8.6 Hofler diagram of mean values of total water potential, $\psi$, solute potential, $\psi_s$, and pressure potential, $\psi_p$, plotted against mean values of RWC. Vertical bars are 95% confidence limits of potential, horizontal lines are 95% confidence limits of RWC.

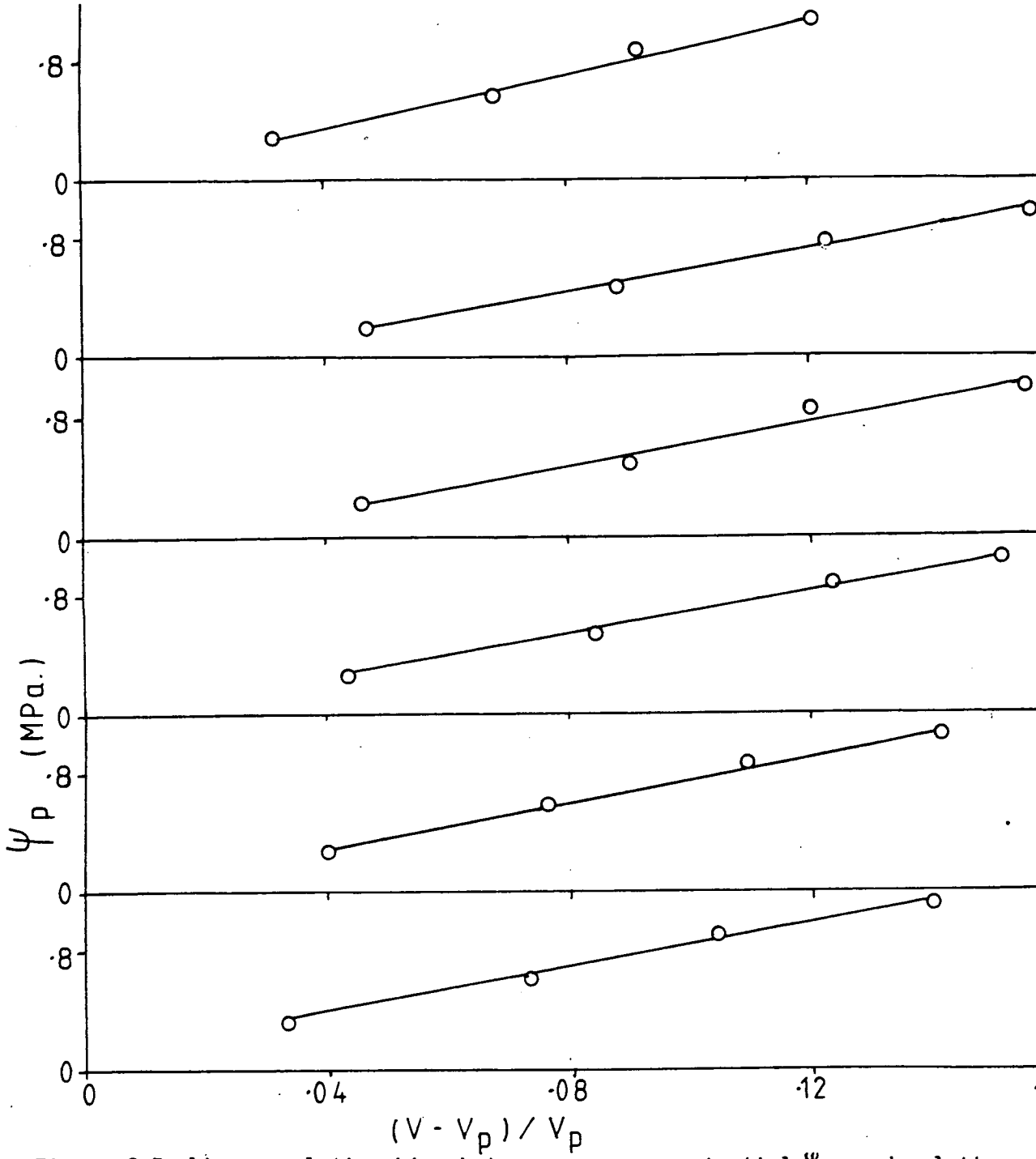


Figure 8.7 Linear relationships between pressure potential, $\psi_p$, and relative symplasmic volume, $(V-V_p)/V$ , for 6 needles taken at random.

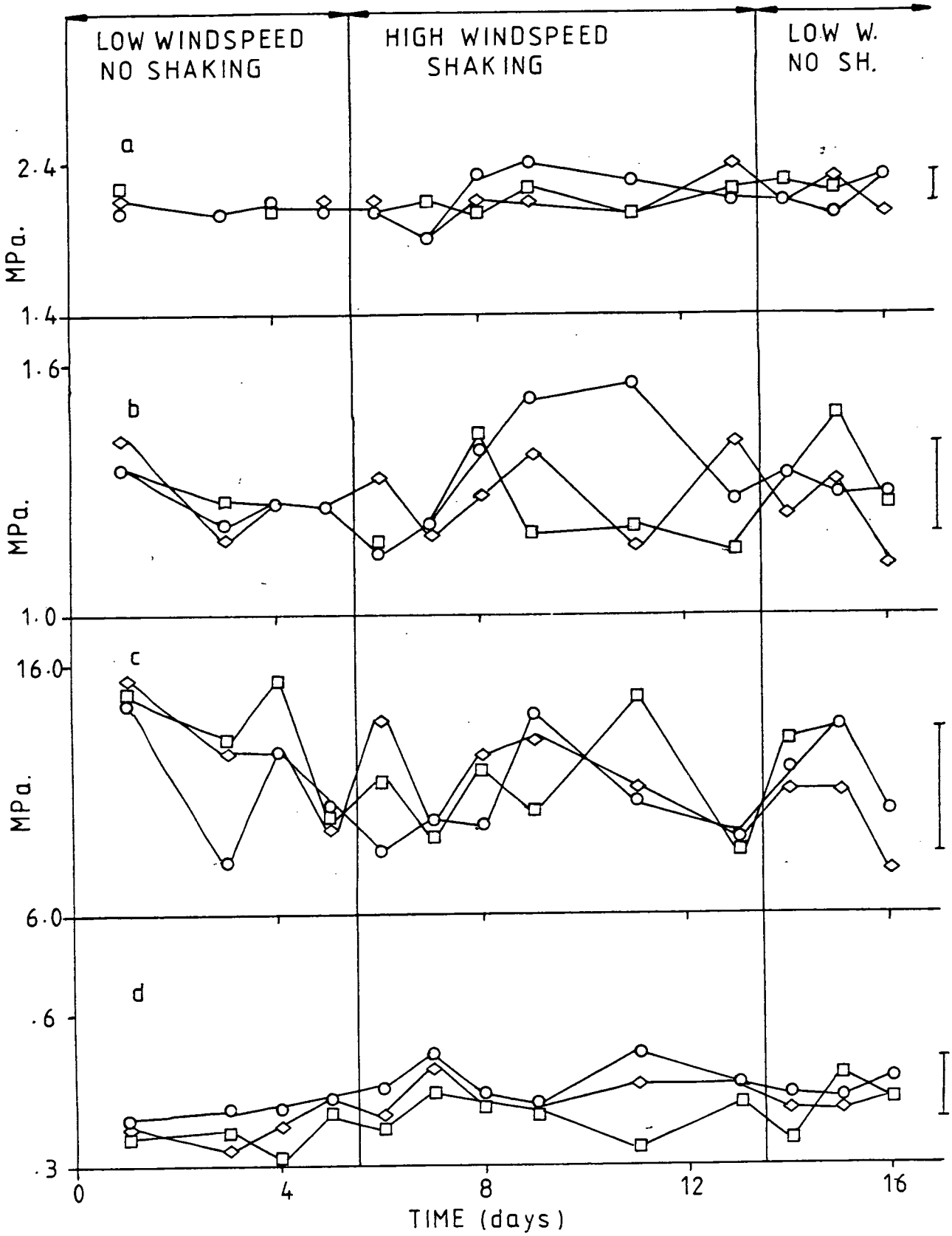


Figure 8.8 Variation in parameters of pressure-volume curves with time. a solute potential at full turgor, $\psi_{s,o}$; b solute potential at incipient plasmolysis, $\psi_{s,p}$; c bulk modulus of elasticity, $\varepsilon$ ; d ratio of osmotic water to total water, $V_b/(tw-dw)$ ○ control; □ shaken; ◇ wind tunnel plants. Bars are 2 standard errors.

### 8.4.5 Effects of wind and shaking on the components of water potential of *P. contorta*

Total, solute and pressure potentials for the dark and the light periods are plotted in figures 8.9 and 8.10.

Total water potential was unaffected by wind and shaking as might be expected, as transpiration rate was unaffected. The hypothesis that water stress might be caused by motion-induced cavitation seems unlikely, in the light of these results. Turgor potentials and solute potentials also appear unaffected by wind and shaking, confirming that motion does not cause a water stress in *P. contorta*. As discussed in 8.4.4, although these results were obtained when the plants bore mature needles, it seems unlikely that motion affects the water-relations of expanding tissues differently.

### 8.4.6 Wind, shaking and water relations.

The results of this chapter show that wind and shaking have no effect on the water relations of *P. contorta*. Despite this, wind and shaking reduced the extension growth, cell growth and dry weight growth of *P. contorta*. Russell and Grace (1978b) also found that the water potential of *F. arundinacea* and *L. perenne* was unaffected by wind, yet leaf area growth was reduced. These results suggest that motion affects plant growth by some mechanism(s) not involving the water relations of plants.

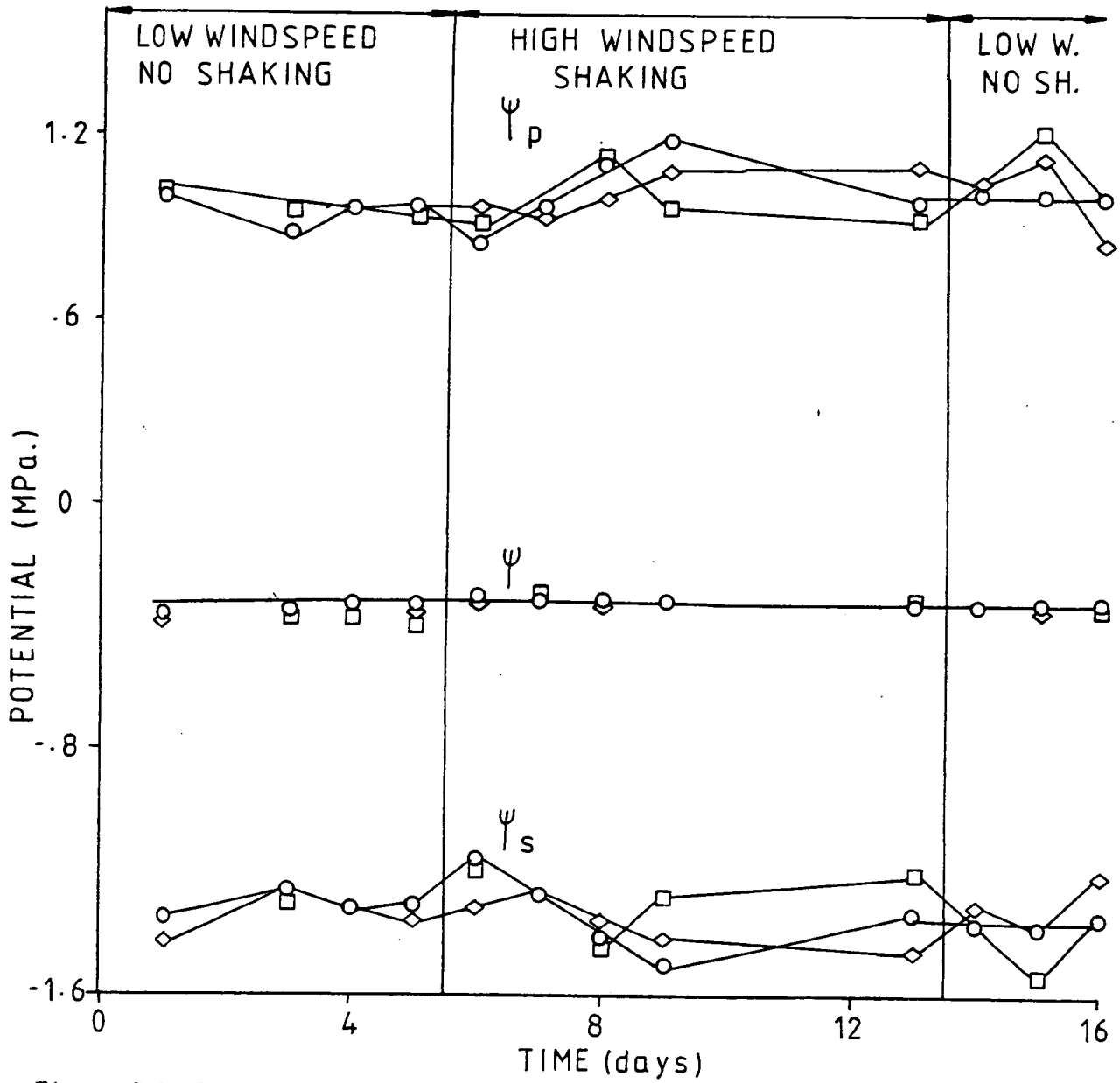


Figure 8.9 Components of water potential of P. contorta during the dark period. $\psi_p$ pressure potential; $\psi$ total water potential; $\psi_s$ solute potential. ○ control; □ shaken; ◇ wind tunnel plants. Bars are 2 standard errors.

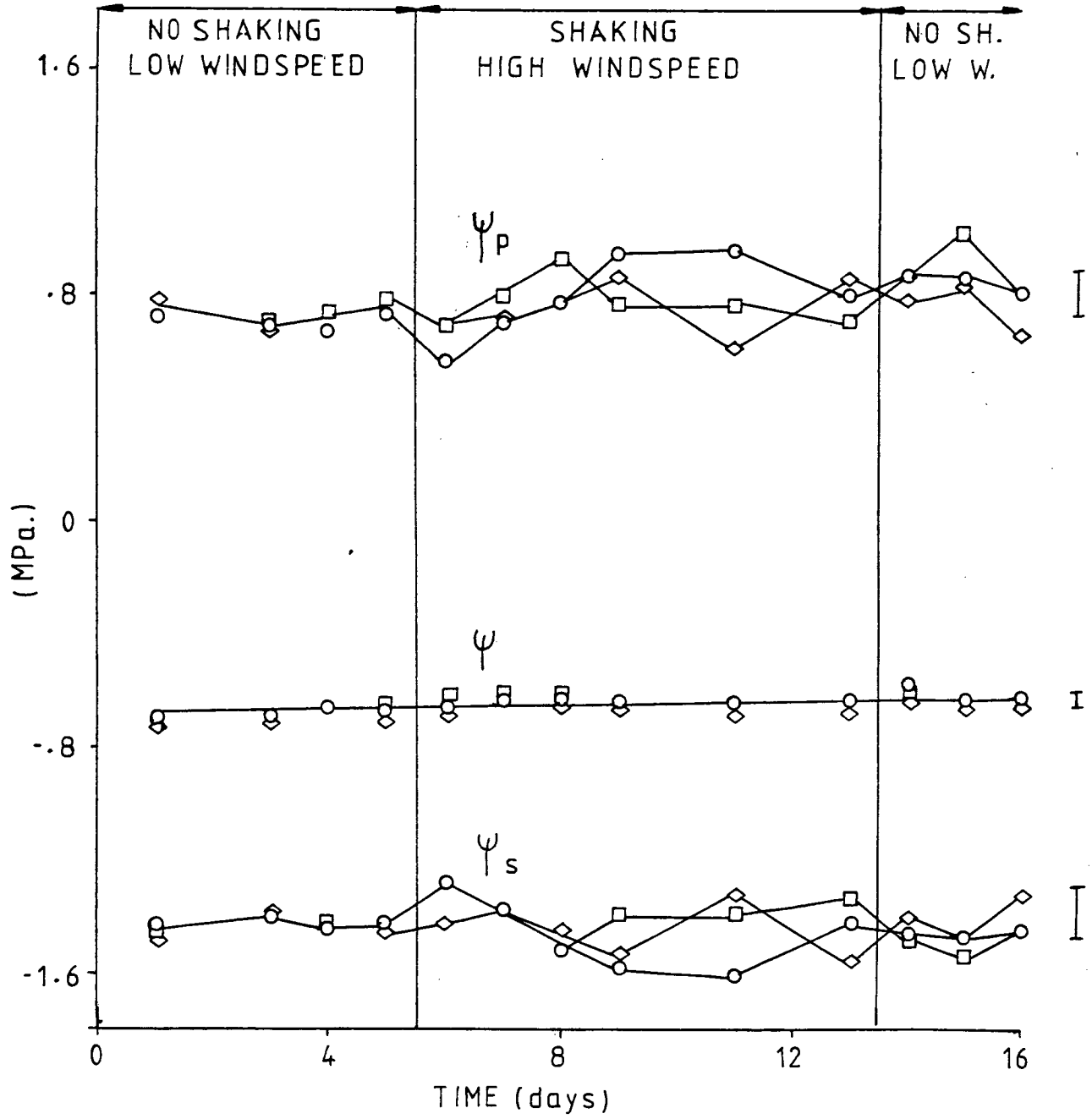


Figure 8.10 Components of water potential of P. contorta during the light period. $\psi_p$ pressure potential; $\psi$ total water potential; $\psi_s$ solute potential. ○ control; □ shaken; ◇ wind tunnel plants. Bars are 2 standard errors.

## 8.5 Summary

(i) High winds had no effect on cuticular conductance of P. contorta despite wind-induced needle collisions. Differences in cuticular conductance and relative water content at stomatal closure between two provenances of P. contorta were observed.

(ii) Wind and shaking had no effect on the needle conductance of P. contorta.

(iii) Pressure-volume curves for individual needles were constructed. The bulk modulus of elasticity, solute potentials at full turgor and at incipient plasmolysis, relative water content at incipient plasmolysis and ratio of osmotic water to total water were used to compare these curves. No effects of wind or shaking on any of these parameters could be detected.

(iv) No effects on total, solute or turgor pressure potentials due to wind or shaking could be detected.

(v) Water potentials (total) of plants which showed reduced extension, cell and dry weight growth were either not different from, or slightly less negative than control plants.

(vi) It is concluded that the effects of wind and shaking on plant growth are not mediated via a water stress effect.

# Chapter 9 The effects of shaking on the growth of *P. contorta* in year n + 1.

## 9.1 Introduction

In chapter 4 it was shown that wind and shaking reduced the extension growth of *P. contorta*. The number of stem units (sensu Doak 1935) present in the bud also influences extension growth (Kozlowski 1962, 1971, Garrett and Zahner 1973, Cannell et al 1976) as discussed in detail in 2.2.2. If wind and shaking affect the production of primordia in the bud, there will be a carry-over effect into next year's growth. This is examined in this chapter.

The size of the bud appears to be a good indicator of potential shoot growth (Kozlowski et al 1973, chapter 4) and so bud sizes of control and shaken plants may anticipate the effects of shaking on the subsequent year's extension. The buds of the control and shaken plants harvested at the end of the 1978 growing season (chapter 7) were measured prior to the harvest; results are briefly reported in this chapter. An experiment comparing the extension during 1979 of *P. contorta* subjected to shaking in 1978 with plants not shaken in 1978 is also described.

## 9.2 Materials and Methods

Eighteen Long Beach P. contorta in their second year of growth were subjected to shaking (as described in 3.3) from 15/7/78 to 30/11/78. Eighteen control plants stood nearby in the cold frames. In April 1979 the plants were divided into four groups: half of the shaken plants were again shaken in 1979 (SS) and the other half stood nearby as controls (SC), half of the control plants were shaken in 1979 (CS) and the other half stood nearby as controls (CC).

Final measurements of stem lengths and widths, and fascicle numbers on the leader stems were made on 1/7/79 as described in 4.2.

## 9.3 Results and Discussion

The plants whose extension growth and dry weight production are described in 4.3.3 and chapter 7 also showed reduced bud growth (table 9.1). The number of lateral buds produced was not affected. This data suggests that the extension of the shaken plants and the number of fascicles would be reduced in the following year.

Initial and final measurements of the plants shaken in 1978 are presented in tables 9.2 and 9.3. Bud growth also seems to be somewhat reduced; the difference between this and the above experiment is probably due to the fact that this experiment did not start until 15 July. The data of Cannell and Willett (1975) indicate that one third of the primordia would already have been produced by this date. The 9% difference in fascicle number between shaken and control plants is not statistically significant.

In contrast to the results reported in chapter 4, shaking appears to have stimulated an increase in stem width and to have had no effect on needle extension. It appears that shaking might affect stem radial growth of P. contorta, but further experiments must be performed to ascertain this. Considering all three experiments on the effects of shaking on radial growth of P. contorta (4.3.2, 4.3.3 and chapter 9), the weight of the evidence suggests that radial growth is not affected by shaking. Table 9.4 shows the measurements of the plants after they had been split into four groups. The plants were divided so that SS and SC (i.e. plants that were shaken in 1978) had similar mean stem and leader bud lengths; and likewise for CS and CC. An inevitable

consequence of this division is that the standard errors of these smaller groups are larger than those of the initial groups (compare tables 9.3 and 9.4).

Basal widths and leader lengths were significantly affected by the various treatments (table 9.5). Comparing each group with the control group (CC) by Dunnet's test (Steel and Torrie 1960) shows that only groups SS and SC differ significantly in leader length from CC, i.e. shaking in the current year only affects extension. The reduction due to current year shaking is ca. 24%.

This experiment shows that shaking plants from July to September in year n has no effect on extension in year n + 1. Presumably, if the plants had been shaken from the beginning of the growing season, there would have been a larger effect on bud growth and fascicle production. However, the results of this experiment suggest that there would still have been at most a small effect on extension in year n + 1.

## 9.4 Summary

(i) Shaking P. contorta significantly reduced bud growth.

(ii) The reduction in fascicle numbers caused by shaking was not statistically significant.

(iii) Shaking in year n had no effect on extension in year n + 1.

Table 9.1 Bud dimensions of control and shaken *P. contorta* at the end of the 1978 growing season. Means and standard errors. Extension growth and dry weight production of these plants are described in 4.3.3 and chapter 7.

| Group | Leader bud | | No. lateral buds |
|---|---|---|---|
| | width mms. | length mms. | |
| Control | 5.6 ± .13 | 24 ± 1.14 | 6.7 ± .26 |
| Shaken | 5.2 ± .12 | 20 ± .69 | 6.4 ± .30 |
| level of statistical significance | 0.002 | 0.05 | NS |
| % change | -7% | -17% | - |

Table 9.2 Year n initial measurements. Means and standard errors 15/7/78

| Group | Stem width mms. | Stem length mms. | Needle length mms. |
|---|---|---|---|
| Shaken | 3.04 ± .107 | 113 ± 2.2 | 50 ± 1.8 |
| Control | 2.96 ± .071 | 110 ± 1.5 | 49 ± 2.3 |

Table 9.3 Year n final measurements. Means and standard errors 18/9/78

| Group | Stem | | Leader bud | | No. Lat. buds | Needle length mms. | Fascicle no. on leader * |
|---|---|---|---|---|---|---|---|
| | width mms. | length mms. | width mms. | length mms. | | | |
| Shaken | 4.7 ± .15 | 139 ± 5.6 | 4.0 ± .11 | 12.1 ± .63 | 5.3 ± .73 | 86 ± 2.4 | 201 ± 9.1 |
| Control | 4.3 ± .09 | 149 ± 5.0 | 4.1 ± .09 | 13.5 ± .45 | 5.4 ± .61 | 87 ± 3.0 | 221 ± 9.0 |
| level of statistical significance | 0.05 | NS | NS | 0.1 | NS | NS | NS |
| % change | +9% | - | - | -10% | - | - | - |

* determined 1/7/79

Table 9.4 Year n + 1 initial measurements. Means and standard errors 4/4/79.

| Group | Stem | | Leader bud | | No. | No. |
|---|---|---|---|---|---|---|
| | length mms. | width mms. | length mms. | width mms. | laterals | plants |
| SS* | 149 ± 9.3 | 5.2 ± .17 | 13.0 ± .71 | 4.5 ± .71 | 6.4 ±1.26 | 9 |
| CS* | 159 ±10.2 | 4.6 ± .16 | 14.7 ± .87 | 4.3 ± .09 | 5.1 ±1.16 | 7** |
| SC* | 151 ± 8.3 | 4.7 ± .25 | 13.4 ± 1.40 | 4.0 ± .17 | 4.2 ± .64 | 9 |
| CC* | 158 ± 6.5 | 4.3 ± .21 | 15.0 ± .69 | 4.2 ± .17 | 6.0 ± .78 | 9 |

* SS : shaken in year n, shaken in year n + 1

CS : control in year n, shaken in year n + 1

SC : shaken in year n, control in year n + 1

CC : control in year n, control in year n + 1

** Two plants damaged by shaking.

Table 9.5 Year n + 1 final measurements. Means and standard errors.

1/7/79

| Group | Basal width mms. | Leader width mms. | Leader length mms. | Mean lateral length mms. | Apical Control % | Fascicle no. on leader |
|---|---|---|---|---|---|---|
| SS* | 7.2 ± .26 | 5.9 ± .28 | 184 ± 14.2 | 84 ±10.4 | 48 ± 4.6 | 191 ± 11.2 |
| CS* | 6.5 ± .22 | 5.5 ± .22 | 202 ± 9.9 | 96 ±12.5 | 48 ± 5.8 | 217 ± 9.8 |
| SC* | 6.4 ± .29 | 5.6 ± .23 | 251 ± 15.6 | 106 ± 9.8 | 44 ± 5.7 | 210 ± 14.3 |
| CC* | 6.2 ± .14 | 5.2 ± .28 | 255 ± 15.3 | 101 ± 6.8 | 40 ± 3.1 | 224 ± 15.7 |
| level of statistical significance** | 0.025 | NS | 0.01 | NS | NS | - |

* shaken in year n, shaken in year n + 1 )SS)
control in year n, shaken in year n + 1 (CS)
shaken in year n, control in year n + 1 (SC)
control in year n, control in year n + 1 (CC)

** one way analysis of variance (Steel and Torrie 1960)

# Chapter 10 The effect of a brief period of shake on the growth of *P. contorta*

## 10.1 Introduction

Most of the recent experiments on the effects of shaking on plant growth have examined the effects of thirty seconds shake per day on indoor plants (2.1.7). In this thesis, continual shaking has been used, as the experiments were performed out-of-doors in the cold frames, where stationary conditions for the control plants could not be provided. Plants outdoors are rarely shaken continually by the wind, so in this chapter, the effects of a brief period of shake per day on the extension growth of *P. contorta* were determined.

## 10.2 Materials and Methods

The growth of ten two year old Long Beach *P. contorta* subjected to shaking for twenty-four minutes per day was compared with that of nearby control plants in the cold frames. The shaking frame, described in 3.3 was turned on and off each morning by an electronic timer (Sangama Weston Ltd.). It proved impossible to achieve a shorter period of shake with this timer. Measurement of the plants were made as described in chapter 4.

Final measurements of the plants were made on 1/7/79, when stem extension growth should have finished (Thompson 1974, Cannell and Willett 1976, chapter 4).

## 10.3 Results and Discussion

Initial and final measurements are detailed in tables 10.1 and 10.2. Extension growth of leader stems was reduced by 11%. Lateral extension, radial stem growth and apical control were not affected by shaking.

The reduction in extension caused by twenty-four minutes shaking is approximately half that caused by continual shaking. Bearing in mind that the control plants were rarely completely stationary, it appears that shaking is a potent inhibitor of extension. In chapter 4 it was observed that little extension occurred during the day, so the shaking of these plants each morning must have had some carryover effect into the night.

Most authors have suggested that an effect of shaking on plant hormones is responsible for this carryover effect on growth (2.1.7). However, a short period of shake could also conceivably affect plant growth by inducing cavitation or by increasing respiration. It was shown in chapter 8 that shaking apparently does not cause cavitation (or at least, does not cause a water stress). The work of Audus (1935), Barker (1935), Godwin (1935) and Audus (1939) showed that the effects of bending and flexing detached leaves on respiration rate were sustained over several tens of hours. Thus, the effects of short periods of shake on plant growth could be explained by the hypothesis presented in chapter 7; that shaking increases the maintenance component of respiration, with a resultant decrease in respiratory substrate for growth.

Table 10.1 Initial measurements. Means and standard errors 8/4/79

| Group | Stem | | Leader bud | | No. lateral | No. |
|---|---|---|---|---|---|---|
| | length mms. | width mms | length mms | width mms | buds | plants |
| Shaken | 161 ± 7.3 | 4.7 ± .13 | 18 ± 2.4 | 4.2 ± .10 | 5.2 ± .90 | 10 |
| Control | 163 ± 6.1 | 4.6 ± .25 | 18 ± 1.7 | 4.1 ± .19 | 5.7 ± .79 | 10 |

Table 10.2 Final measurements. Means and standard errors 1/7/79

| Group | Basal | Leader | | Lateral | Apical | Fascicle no. |
|---|---|---|---|---|---|---|
| | width mms. | width mms. | length mms. | extension mms. | control % | on leader |
| Shaken | 6.5 ± .16 | 5.7 ± .21 | 221 ± 8.3 | 108 ± 11.9 | 48 ± 4.5 | 240 ± 7.3 |
| Control | 6.4 ± .29 | 5.6 ± .37 | 248 ± 6.2 | 100 ± 4.8 | 40 ± 2.3 | 238 ± 12.0 |
| level of statistical significance | NS | NS | 0.02 | NS | NS | NS |
| % change | - | - | -11% | | | |

## 10.4 Summary

A twenty-four minute daily shake significantly reduced the leader extension of P. contorta by 11%. Lateral extension, radial growth and apical control were not affected by this daily short period of shake.

# Chapter 11 Discussion

## 11.1 Summary of results

The main findings of this thesis are summarised below:

(i) Exposure to a high windspeed or to continuous shaking reduced the extension growth of leader and lateral stems of P. contorta by 20%. Rates of needle elongation were reduced by 11% by shaking and by 30% by wind in a short-term experiment. Stem radial growth and 'apical control' were not affected by wind or shaking (chapter 4).

(ii) The reduction in leader extension caused by wind and shaking was shown to be due to reduced cell division and cell extension. The reduction in cell division was greater than the reduction in cell extension (chapter 5).

(iii) The reduced extension growth caused by shaking was accompanied by a reduction in dry weight. Relative growth rate and unit leaf rate were reduced, but leaf area ratio was unaffected. This suggested that either net photosynthesis was reduced by shaking, or dark respiration was increased (chapter 6).

(iv) Subjecting P. contorta to a high windspeed had no effect on net photosynthesis, but significantly increased dark respiration (chapter 7).

(v) The growth reduction of P. contorta subjected to high wind or shaking was not associated with a reduction in total water potential. No effects of wind on cuticular conductance could be detected, suggesting that wind-induced surface abrasion does not occur in P. contorta. No effects of wind or shaking on stomatal conductance, solute and pressure potentials or parameters of the pressure-volume curves could be detected (chapter 8).

(vi) Continuous shaking in year n did not significantly affect the fascicle production of P. contorta and had no effect on extension growth in year n + 1.

(vii) Subjecting P. contorta to shaking for just twenty-four minutes per day significantly reduced extension growth of leader stems by 11%.

## 11.2 A unified hypothesis

The effects of wind and shaking on the growth of P. contorta are remarkably similar, both qualitatively and quantitatively. This suggests that the effect of wind on plant growth is primarily due to the shaking caused by wind.

The reduced extension growth and cell growth of P. contorta caused by shaking was accompanied by reduced dry weight production. The reduced dry weight production was shown to be due to an effect of shaking on unit leaf rate. Either the carbon-harvesting system (photosynthesis) or the carbon-utilisation system (respiration) must be affected by shaking. High wind had no effect on net photosynthesis but increased dark respiration. It is postulated that continuous motion of either type increases the maintenance respiration of P. contorta, reducing the amount of respiratory substrate available for growth. As a result of this, cell division and extension are reduced, with a consequent reduction in extension growth.

The division of respiration into 'maintenance' and 'growth' components is somewhat arbitrary (e.g. Penning de Vries 1972). 'Growth respiration' is considered to be the respiration associated with the synthesis and transport of components necessary for active growth, whereas 'maintenance respiration' is that respiration associated with the processes compensating for the degradation of existing structures and organisation (Penning de Vries 1972).

Perhaps wind-induced shaking interferes with some aspect of the various maintenance processes, such as decreasing the lifetime of structural protein. However, the precise relationships between the varied and

complex processes of respiration and plant growth are only poorly known and presumably any disruption of the processes of respiration might be expected to reduce plant growth.

Audus (1935, 1939), Barker (1935) and Godwin (1935) all found that the increases in respiration caused by handling was sustained over several tens of hours. If shaking also has a persistent effect on the respiration of P. contorta, the above hypothesis can also account for the reduction in extension growth caused by just twenty-four minutes shaking per day.

## 11.3 The role of water relations in the effects of motion on plant growth

As discussed in 2.1.3, the effect of wind on plant growth has long been thought to be due to it's 'drying effect'. A consideration of the effects of wind on plant transpiration via the boundary layer resistance indicates that an increase in windspeed may often reduce transpiration (2.1.3). Increasing windspeed may increase transpiration by a direct effect on stomatal and cuticular conductances in some species, but the stomata of other species, particularly conifers, seem unresponsive to wind (2.1.5). In situations of restricted water supply, the effects of wind-induced surface damage might be important to the water relations of broad-leaved plants. In P. contorta however, and probably other conifers, the results of this thesis indicate that wind-induced surface damage does not occur. Wind has been shown to have considerable effects on the growth of grasses, but to have little effect on total water potential (Grace and Russell 1978b). This thesis reports similar results for P. contorta.

It seems reasonable to conclude that although wind may in some circumstances cause a water stress, this is a secondary effect and not important to the effect of wind on plant growth. This is further confirmed by the similarity of the effects of shaking on the growth of P. contorta, as shaking also had little effect on water relations.

## 11.4 The effects of wind on *P. contorta* in the field

Lines and Howell (1963) found a significant negative correlation between height growth of *P. contorta* and rates of tatter of standard flags. Lines (1976) found that artificial shelter improved the stem extension growth of *P. contorta* by up to 56%. These results imply that high winds have an adverse effect on the growth of *P. contorta* in the field.

In this thesis, it is shown that increasing windspeed, while maintaining other environmental parameters constant, does indeed reduce the growth of *P. contorta*. The growth reductions reported by Lines and Howell (1963) and Lines (1976) thus could have been due to wind. The results of these researchers, together with the results described here, strongly suggest that wind is an important factor affecting the growth of *P. contorta*. The growth reduction caused by short daily periods of shake imply that occasional periods of high wind might be detrimental to the growth of *P. contorta*.

It is proposed in this thesis that it is the shaking caused by wind that is responsible for the effects of wind on plant growth. The results of the controlled experiments reported here, and of the field experiments noted above strongly suggest that wind-induced shaking is an important environmental stress restricting the growth of *P. contorta*.

## 11.5 Addendum - the light spectra in the wind tunnel and growth room

In June 1979, light spectra in the wind tunnel and growth room were determined with a recently purchased Quanta Spectrometer QSM-2500 (Techtrum Insts., Sweden) and the ratio of red: far red photon flux densities, measured at 660 nm. and 730 nm., $\zeta$ , were compared. $\zeta$ can have considerable effects on plant growth and development (Smith 1976, McClaren and Smith 1978).

The ratio of 60 W tungsten bulbs to 400 W metal-halide lamps was 1:1 in both of the controlled environments. Despite this, values of $\zeta$ were 1.5 and 3.4 in the growth room and wind tunnel respectively.

Holmes and McCartney (1976) and Holmes and Smith (1977) demonstrated that $\zeta$ in the natural environment does not exceed 1.2 in full sunlight and falls to as low as 0.2 in dense shade. There is little data on the effects of $\zeta$ above 1.2 on plant growth. However, Holmes and McCartney (1977) determined the effects of $\zeta$ on the phytochrome photoequilibrium over a wide range of $\zeta$ , using etiolated Phaseolus vulgaris seedlings. The ratio of far-red phytochrome to total phytochrome, $\phi$ , increased rapidly as $\zeta$ increased from 0 to 1, but changed very little as it increased above 1. The values of $\phi$ corresponding to the $\zeta$ values of the growth room and wind tunnel, read from their figure 29.6,are .62 and .67 respectively (compared to .4 when $\zeta$ = .5). This suggests that the differences in $\zeta$ between the growth room and wind tunnel may not be physiologically important. McClaren and Smith (1978) accepted $\zeta$ of 4.2 as being representative of full daylight in their experiments, presumably because of the small change in $\phi$ between $\zeta$ values of 1.2 and 4.2.

Reference to figure 4.1 shows that during the first nine days of experiment 4.3.1, when the windspeed in the wind tunnel matched that in the growth room, the wind tunnel plants were growing at a greater rate than the growth room plants. The wind tunnel plants' extension did not decrease relative to the growth room plants' until a few days after the windspeed was increased, suggesting that it was indeed the change in windspeed that was responsible for the growth reduction.

The similar effects of high wind and shaking on the growth of P. contorta further supports the contention that it was the wind-induced shaking that affected the growth of P. contorta in the wind tunnel, rather than $\zeta$ or $\phi$. However, the possibility that the differences between the growth room 'control' and wind tunnel might have influenced the results cannot be completely disregarded.

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