

STRESS RESISTANCE AND QUALITY CRITERIA FOR
TREE SEEDLINGS:
ANALYSIS, MEASUREMENT AND USE

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ABSTRACT

Stress resistance and seedling quality are considered to be fully defined by the curve of future shoot growth. The factors controlling this curve's starting level, slope, and upper asymptote are analysed in terms of four major subsystems: substrate utilisation, photosynthesis, water, and information.

Published equations describing the first three of these subsystems are used to define a necessary and sufficient set of quality criteria. These include functional capabilities such as specific maintenance rate and photochemical efficiency, material properties such as elasticity and hydraulic conductances, environmental coefficients such as the temperature range for root growth, and lethal doses such as frost hardiness. In addition, they include variables describing the current state of the plant, such as leaf area, and water content.

The informational subsystem is considered to control the seasonal change, or "acclimation", in parameters of the other three subsystems, but is still too poorly understood for mechanistic description. Quality criteria arising from it include the extent to which chilling requirement has been fulfilled.

Applying such analyses to the business of reforestation consists of choosing a subset of the quality criteria according to past and future conditions in the crop and measuring them by methods such as those outlined here. Important methods include carbohydrate and infra-red gas analysis, porometry, the pressure-volume technique, and short-cut procedures derivable from these. Measurements of field-proven quality criteria can be compared with seasonal norms, or with values calculated from mechanistic models to be suitable for given site conditions. Practical decisions can then be made about nursery treatments, site preparation, planting, and genetic selections.

INTRODUCTION

Seedlings that flourish in spite of the relatively harsh environment into which they are normally transplanted from the nursery, are variously said to be "stress resistant", "hardy", "vigorous", or of "high quality". Producing them consistently and economically

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is the nurseryman's prime objective. It is an objective made difficult, however, by the absence of definition of these terms, the complexity of plant-environment interactions embraced by them, and the lack of a rational framework in which to view these relationships.

In this paper I show how mechanistic models of various aspects of plant growth can provide such a framework and definition. If the models are sound and operate at the right level of detail, their parameters can be adopted as precisely defined quality criteria. I show how appropriate criteria can then be selected, measured, and interpreted for use in reforestation programmes, and discuss the extent to which each is of proven *versus* still-hypothetical value.

Scope and Definition of Stress Resistance

Stress can be an excess or deficiency of any factor needed for growth — light, heat, water, CO₂, etc. — as well as the presence of such unneeded factors as browsing animals, disease-causing organisms, or toxic chemicals. Depending on its intensity, rapidity of onset, total duration, and frequency of occurrence, stress may be injurious or merely inhibitory. Or it may act by leading to secondary stresses (Levitt, 1972), as in the case of low temperature, which injures through desiccation by intercellular ice; or flooding, which causes an oxygen deficiency in the roots. One or many growth processes may be directly or indirectly affected, for example in cold storage. Here, the dark and chilly environment has an apparently direct effect on the membranes and/or proteins of early-lifted seedlings (which although still well-hydrated will quickly die), and indirect effects on late-lifted seedlings through desiccation, or respiratory consumption of needed food reserves over a long period.

Mechanisms of "resistance" to any one of these stresses are equally diverse, and again have been extensively reviewed by Levitt (1972). They consist of the plant's ability (1) to avoid coming to equilibrium with the stressful component of its environment, e.g., by conserving water through stomatal closure and rapid root extension, or (2) to tolerate the stress within the plant itself. Tolerance can in turn be rigid, plastic, or repairable in nature. In the case of a drought in which the plant has attained a low value of xylem water potential, these would correspond respectively with (1) retention of water by the surrounding tissues due to high solute content of the cell sap, or stiffness of the cell wall, (2) loss of water from the tissue which, due to other cell characteristics, was not harmful, (3) an injurious loss of water, following which the cells could nevertheless be repaired. Two or more of the mechanisms of avoidance and/or tolerance may contribute quantitatively to the plant's total resistance to a particular environmental factor.

The effectiveness of any one resistance mechanism may also change (reversibly) under non-injurious levels of stress, such that the plant becomes "acclimated". This may take place over time scales of days, weeks, or even years as exemplified respectively by shade-adaptation of leaves, frost hardening, and changes in tree form following canopy closure. The acclimated or "hardened" seedling is then less adversely affected by further or more severe exposures.

In general, there are three types of physiological process relevant to any discussion of stress resistance, which operate over different regions of a particular environmental factor's range. These are shown schematically with respect to temperature in Fig. 1,

together with Levitt's limited analogy of the elastic and plastic strains in a stretched spring. The progresses are: (1) growth, which includes optimal and two non-optimal or inhibitory (elastic strain) regions; (2) injury (plastic strain), from heat or cold in this case, which may be repairable or not; and (3) acclimation, which can lead to a change in (1) and/or (2). The environmental ranges over which any two processes occur may overlap considerably, and the cumulative effects increase with exposure time.

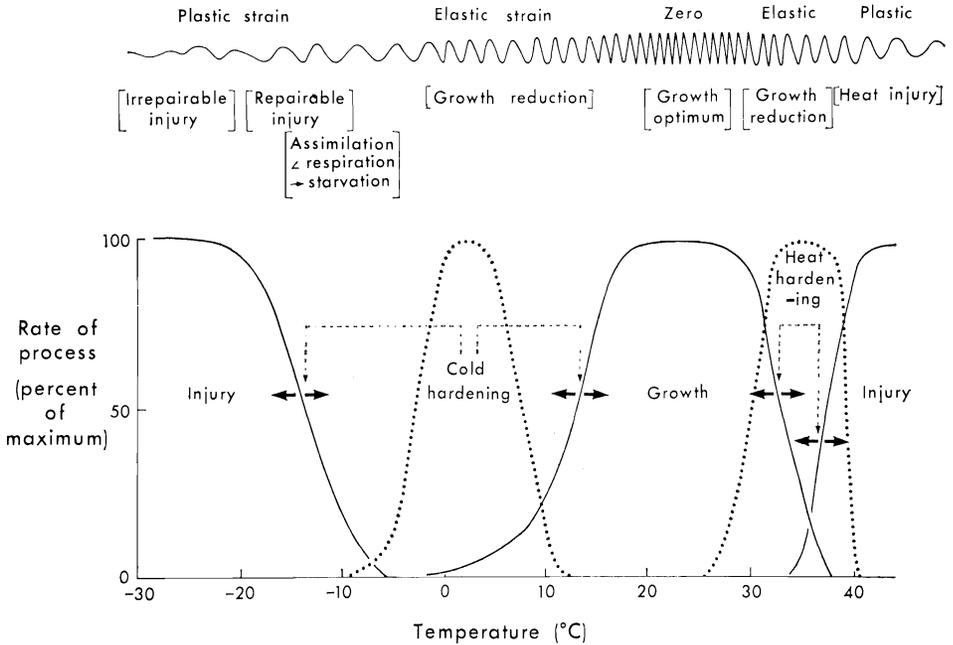


FIG. 1—Schematic relationship of growth inhibition and injury (strains) to temperature (stress) in tree seedlings. The analogy of strains in a stretched spring is shown at the top. Dotted curves represent acclimation processes, which lead to shifts in the (solid) curves for growth and injury.

When it is considered that similar diagrams can be constructed for the other environmental factors, and that the climate and soils in forest nurseries and plantations are such that the various environmental optima for growth almost never coincide in time, then one thing becomes clear. Tree seedlings are *always* under stress, and are designed by nature to grow that way. Some stress is needed to drive water through the plant and provide the cues for essential developmental change. The narrower view of stress, that conditions must be extreme enough for there to be a potential for direct injury, fails to recognise the dominant effect that non-injurious stresses can have on seedling establishment and plantation growth. If persistent, even these stresses will eventually be injurious through their negative effect on the seedling's competitive and recuperative vigour. Adopting instead the definition that stress resistance is the plant's ability to continue growing, or retain its ability to grow, in non-optimal environments, properly emphasises the integral role of stress in plant growth and development, and equates resistance to it with seedling quality.

ANALYSIS OF STRESS RESISTANCE AND STOCK QUALITY COMPONENTS

The ideal criterion of seedling quality is the shape that would be taken by the shoot growth curve under the sequence of soil and weather conditions likely to prevail in the first two years after lifting from the nursery. This information is already "written" within the plant in the form of more rapidly measurable quantities describing (1) its *current state* with respect to biomass, chemical composition, etc.; and (2) its *material and functional properties* such as photosynthetic efficiency and root resistance to water flow. An analysis of the processes of growth and degeneration or injury represented in Fig. 1, enables us to identify a comprehensive set of these quantities.

The Growth Curve

Consider first the curve describing growth. The cumulate result of this extending over several years will often appear similar to that in Fig. 2a. This consists of a sequence of periods of rapid and slow growth which correspond with variations in weather such that the rapid phase occurs during favourable conditions, e.g., springtime in temperate regions. A single period of cumulative growth in shoot's structural dry matter W_{GS} , can be described by a logistic equation (Kozlowski, 1971; Cannell and Willett, 1975; Landsberg, 1974; Denne, 1974; Emmingham, 1977).

$$W_{GS} = \frac{a}{1 + e^{-b-ct}} \quad (1)$$

in which t is time, e is the base of the natural logarithm, and a , b , and c are constants defining upper and lower asymptotes and maximum slope respectively. Such a curve has the characteristic (Richards, 1969) that its slope, the rate of growth at any point in time, is proportional to both the present weight and the fraction of total growth still to be made before a maximum (a) is reached, i.e.,

$$\frac{dW_{GS}}{dt} = \frac{cW_{GS}(a - W_{GS})}{a} \quad (2)$$

the parameters a , b , and c have a physiological meaning for tree seedlings because the cyclic growth pattern of the shoot is the result of the separate processes of leaf initiation, and the subsequent expansion of these leaves and associated internodes (stem units of Doak, 1935). Parameter " a " represents the maximum size that j stem units can attain; b is related to j , the number of units present in the bud before growth starts in spring ($t = 0$), by

$$j = \frac{a}{1 + e^{-b}} \quad (3)$$

and c is the rate of structural growth during the "central" part of the shoot expansion phase, i.e., when $W_{GS} \cong a/2$.

From the view point of seedling quality, the maximum shoot weight per initiated stem unit $\frac{a}{j}$, will for the moment be considered a fixed characteristic of the species.

The parameter c , mid-point growth rate in a symmetrical curve, depends on the biosynthetic capacity of the sub-apical growth centre, the amount of substrate in the plant (needed for both energy and carbon skeletons), turgor pressure, temperature, and

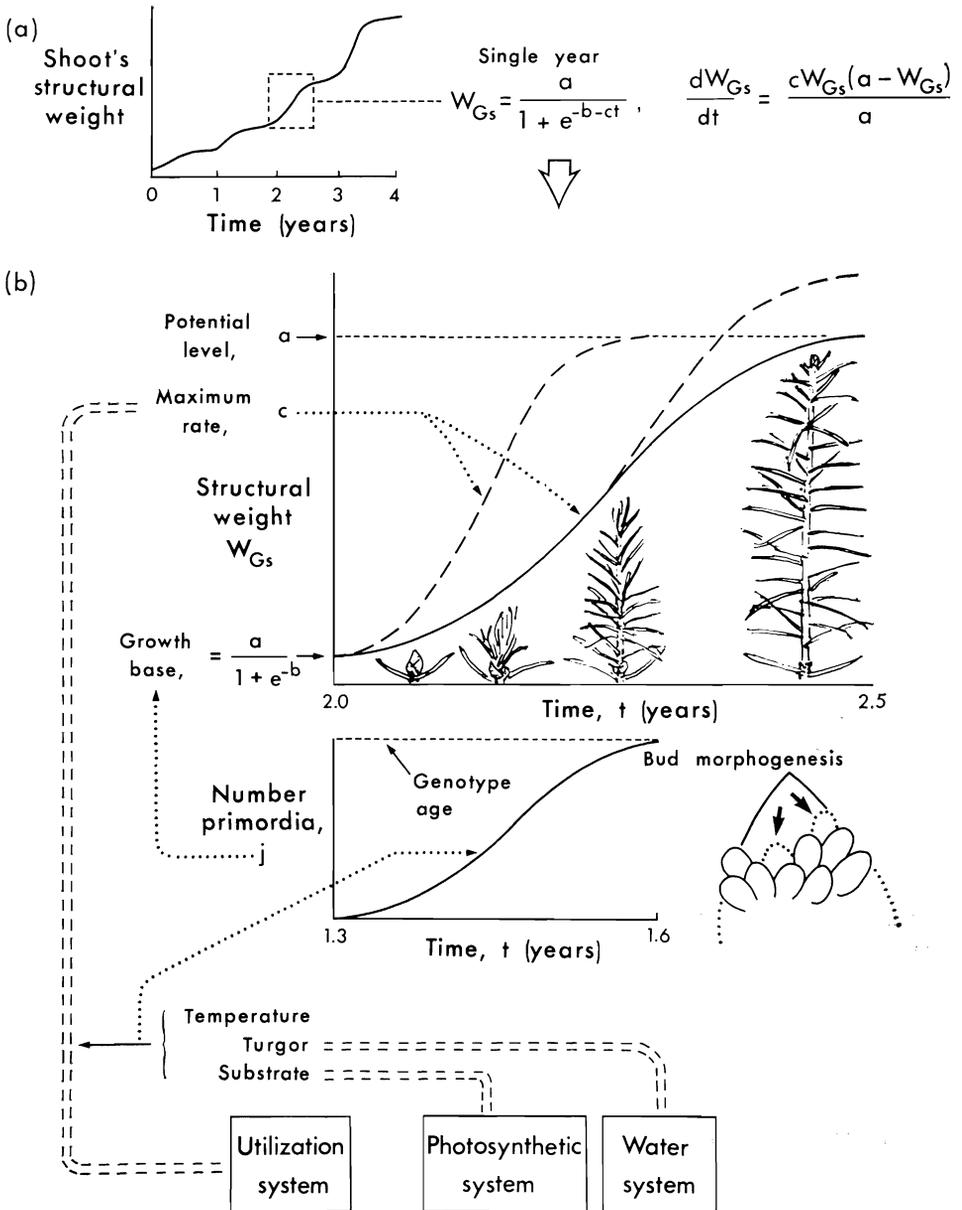


FIG. 2—Shoot growth in relation to major physiological systems. Changes (dashed curves) in the shoot's structural weight can result from changes in the logistic curve parameters a , b , or c . The last two are controlled through temperature, turgor, and substrate level by the functioning of three major subsystems. Parameter a represents the potential mass of j stem units, and reflects in part the degree of dormancy. e is the base of the natural logarithm.

the extent to which other processes are competing for the substrate. The rather complex subject of mineral nutrition, on which c also depends, will be avoided here by confining discussion to mineral-rich conditions. Collectively, these interrelationships will be considered to constitute the major plant subsystem of utilisation.

Amount of substrate, in turn, depends upon the past and present activity of the photosynthetic subsystem. Through this, the effect of environmental variables, such as CO_2 concentration and light intensity, will make themselves felt upon parameter c . Both utilisation and photosynthesis are strongly dependent on turgor pressure, which provides the driving force for cell expansion and stomatal movement. The shoot's turgor pressure is the result of water potentials, fluxes and conductances in the soil, the vascular system, and the cells. Together these constitute a third major subsystem to be considered in analysing stress resistance and seedling quality, the water system.

Parameter j (related to b by Equation 3), which determines the base for expansion growth in the same sense that the invested principle determines amount of interest earned, is the end result of the process of bud morphogenesis at the shoot apex. For most occasions when seedling quality needs judging, the bud will be fully formed and the number of leaf primordia it contains will provide the value of j . Where bud morphogenesis is in progress, the rate will again be dependent on substrate, temperature, and turgor (Pollard and Logan, 1977; 1979; Clements, 1970; Garrett and Zahner, 1973). Parameters b and c in the shoot growth equation are both therefore dependent on the health of the utilisation, photosynthetic, and water subsystems, as illustrated schematically in Fig. 2. It is from the structure of these subsystems that logical candidates for quality and stress resistance criteria relating to growth under field conditions can be identified.

Utilisation System

Five concepts will be introduced to describe the structure of the utilisation system. The first is due to Thornley (1972), and states that the plant can be considered as consisting of only two chemical species: structural material and substrate. Growth of the whole plant occurs by the conversion of substrate to structure, with a portion of the substrate being broken down to provide energy for the synthesis, and released from the plant as CO_2 . The process can be described by the equation

$$\frac{dW_G}{dt} = Y_G U, \quad (4)$$

where dW_G/dt is the rate of structural growth and U is the rate at which substrate is used up in this process. Y_G is the conversion efficiency, assumed to be the same throughout the plant. For each gram of substrate so used, Y_G grams of structure are formed, and $1 - Y_G$ grams respired. Thus the rate of respiration associated with growth, R_G , is given by

$$R_G = (1 - Y_G)U, \quad (5)$$

The second concept, which has come through the work of several investigators (McCree, 1970; Thornley, 1970; de Wit *et al.*, 1970; Penning de Vries, 1972; 1975) is that a portion of respiration not associated with growth, but involving the maintenance and/or resynthesis of inherently unstable cell structures and tissues, can be added to

R_G to give total respiration, R . This portion is proportional to total structural weight, W_G . Hence,

$$R = (1 - Y_G)U + mW_G, \quad (6)$$

where m is the specific maintenance rate.

The third concept, also introduced by Thornley (1972), is that, if the plant is regarded as having two physical compartments, the root and the shoot, then the relationship between supply and use of substrate in the plant is given by two conservation-of-matter equations:

$$\frac{dW_{Ss}}{dt} = P_g - T_{sr} - U_s - mW_{Gs}, \quad (7)$$

i.e.,

rate of change of substrate in shoot and for roots = gross photo-synthesis (inflow) — transport to root (outflow) — utilisation — maintenance

$$\frac{dW_{Sr}}{dt} = T_{sr} - U_r - mW_{Gr}, \quad (8)$$

where subscripts s and r denote shoot and root respectively. By re-arrangement, substitution for T_{sr} in Equation 7, and putting $W_{Gr} + W_{Gs} = W_G$, and $dW_{Sr}/dt + dW_{Ss}/dt = dW_S/dt$, these become

$$U_s = P_g - U_r - \frac{dW_S}{dt} - mW_G, \quad (9)$$

As a fourth concept, Thornley considered utilisation itself to be the result of enzyme action, and that its rate in response to substrate level would be described by a Michaelis-Menten equation (Fig. 3):

$$U = \frac{kVS}{K + S}, \quad (10)$$

where V is the fresh tissue volume, S the weight of substrate per unit volume (concentration) and k and K are parameters describing the capacity of the growth centre for structural synthesis. Specifically, k is the maximum possible rate, i.e., when the enzyme systems are saturated with substrate, the asymptote in Fig. 3. Parameter K is the substrate level at which U is half-maximum, and controls steepness of slope.

The fifth concept is to include temperature and turgor pressure effects as modifiers of the utilisation terms (U_s and U_r), taking a value between 0 and 1. The example given by Landsberg (1977) to illustrate this was that, if the temperature effect could be described by a normal curve, then the temperature modifier of utilisation in the shoot $f(T_s)$ would be given by

$$f(T_s) = e^{-(T - T_{s \text{ opt}})^2 / \sigma_s^2}, \quad (11)$$

where $T_{s \text{ opt}}$ is the optimum temperature, and the parameter σ_s , also in degrees Celsius, controls the width or spread of the curve. Assuming as a simplification, that the effects of turgor and temperature are independent and non-interacting, and

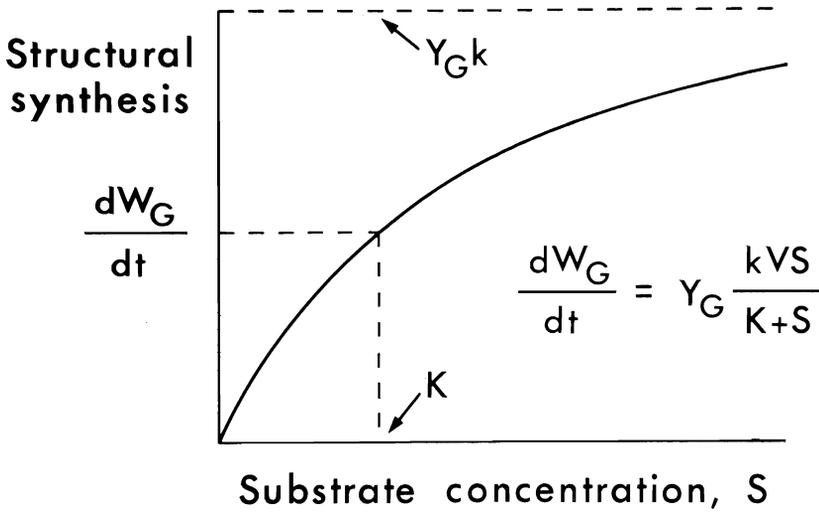


FIG. 3—Michaelis-Menten curve presumed to describe structural growth rate dW_G/dt (after Thornley, 1976). Y_G is the substrate \rightarrow structure conversion efficiency, k the maximum utilisation rate under substrate-saturating conditions, and K the substrate concentration at half this rate.

expressing Equation 10 in terms of volume and substrate weight, rather than concentration, then utilisation under non-optimal conditions, i.e., under stress, is given by

$$U = \frac{kW_S}{K + W_S/V} \cdot f(T) \cdot f(\psi_p) \tag{12}$$

where $f(\psi_p)$ is the turgor pressure modifier.

These five concepts can now be put together to show exactly how the shoot's structural growth is dependent on those factors, listed in the preceding section, that directly determine it. This is done by placing the growth-respiration part of U_s (i.e., $[1 - Y_G]U_s$) on the right hand side of Equation 9, leaving the structural-growth part as the subject of the equation. Then Equation 12, subscripted for roots and shoots, is used to substitute for U_s and U_r to give:

$$\begin{aligned} \frac{dW_{Gs}}{dt} = P_g - (1 - Y_G) \frac{k_s W_{Ss}}{K_s + W_{Ss}/V_s} \cdot f(T_s) \cdot f(\psi_{ps}) - \frac{k_r W_{Sr}}{K_r + W_{Sr}/V_r} \\ \cdot f(T_r) \cdot f(\psi_{pr}) - \frac{dW_S}{dt} - mW_G \end{aligned} \tag{13}$$

The right hand side of this equation contains six state variables, which change continuously as the plant grows, and 10 parameters which stay relatively constant. These correspond to the two types of "measurable quantities" written into the seedling, as mentioned earlier. The state variables are structural weight and volume of the shoot and roots, and the amount of substrate, or food reserves, in each. The parameters are of three groups: (1) the conversion efficiency and specific maintenance rate, which relate to respiration; (2) the maximum rate and substrate-sensitivity constants (k_s , k_r , K_s , K_r), which describe the biosynthetic capability of the growth centres; and (3) the

temperature and turgor modifiers of growth centre activity, which comprise parameters for optima, thresholds, and slopes of empirical response curves. Together these constitute the necessary and sufficient criteria for health of the utilisation subsystem, and thus a significant part of the potential growth curve slope, c.

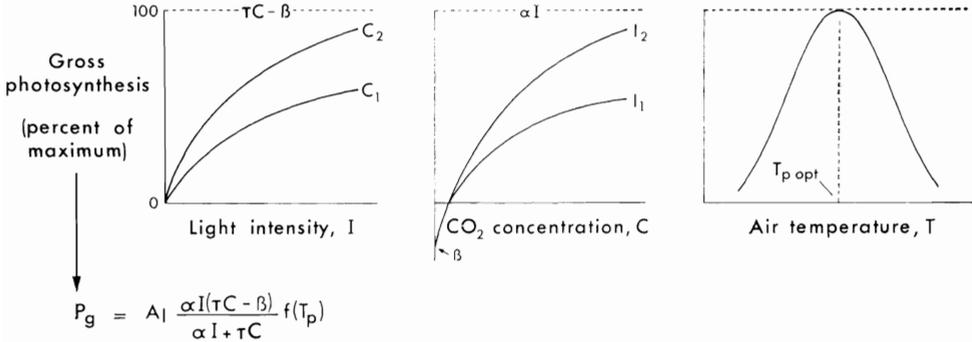


FIG. 4—Essential behaviour of the photosynthetic system according to the simplified model of Charles-Edward and Ludwig (1974). The parameters are photochemical efficiency α , photorespiration constant β , leaf conductance to CO_2 τ , and a temperature function, $f(T_p)$. Gross photosynthesis is here taken to include the negative effect of photorespiration.

Photosynthetic System

Production of substrate by photosynthesis, P_g in Equation 13 (taken to include the negative effect of photorespiration), is directly related to the environmental variables light intensity I , CO_2 concentration C , and temperature T (Fig. 4). The effect of the first two may be most usefully summarised from the point of view of seedling quality by a semi-empirical three-parameter equation due to Charles-Edwards and Ludwig (1974):

$$P_g' = \frac{\alpha I (\tau C - \beta)}{\alpha I - \tau C} \tag{14}$$

The parameters are photochemical efficiency α , CO_2 conductance of the leaves τ , and a photorespiration constant (β) which represents the amount of substrate photo-respired in 21% oxygen. Equation 4 is on a unit leaf basis, and to make it consistent with Equation 13, must be multiplied by A_1 , the leaf area.

Temperature has a complex relationship through CO_2 diffusion, light reactions, and biochemical processes, and again is best added as a modifier having empirical parameters for optimum and spread. Hence, on a whole-seedling basis

$$P_g = A_1 \cdot \frac{\alpha I (\tau C - \beta)}{\alpha I + \tau C} \cdot f(T_p) \tag{15}$$

where $f(T_p)$ is the temperature effect. The three parameters can be determined by infra-red gas analysis as indicated later. A portion of τ due to stomata τ_c , bears a constant relation to stomatal water vapour conductance τ_1 ($\tau_c = 0.63 \tau_1$, (Andrussow, 1969)). The latter can be measured directly by porometry, and is affected by turgor in a way that will be further examined below. This enables the other portion, mesophyll conductance, to be determined separately, if desired.

More interesting, however, is a recent finding by Wong *et al.* (1979) for several species, including young trees. Stomatal conductance to CO_2 is closely related to net photosynthesis under conditions known to directly affect photosynthetic reactions (expressed in α and β) rather than stomata. This implies a control of τ by P_g rather than the reverse, and a single-parameter definition of the health of the photosynthetic subsystem. Otherwise the five parameters and one state variable of Equation 15 can be taken to describe this subsystem, and account for a second major part of the variation in potential growth curve slope, *c.*

Water System

The structure of the water system will be examined in two parts in order to arrive at a set of tentative quality criteria for root and shoot turgor. These concern (1) the flow of water through the apoplast (comprising xylem, cell walls, and intercellular spaces) and (2) the relatively small but critical amount that is exchanged between the apoplast and the symplast (comprising material enclosed by the outer cell membranes). Again, several generalisations and simplifying assumptions must be made in the interest of identifying criteria likely to be of practical value. The reader can learn of these through the cited literature.

Water flow through the soil-plant-atmosphere continuum can be described in terms of a chain of resistances, in which the two predominant ones, from soil to root xylem, and through the stomata, are variable (Fig. 5). Powell and Thorpe (1977) cite the classic works leading to this view, and with a mathematical model based upon it, Farnum (1977) obtained good predictions of water stress in outplanted conifer seedlings. The flow through any resistance conforms to D'Arcy's law, and equals water potential difference times reciprocal resistance, or conductance. Under steady-state conditions, *i.e.*, when water uptake equals water loss

$$A_r \tau_r (\psi_e - \psi_r) = A_x \tau_s (\psi_r - \psi_l) = A_l \tau_l (D_l - D_o), \quad (16)$$

favouring low boundary layer
resistance)

where the environmental variables are soil water potential ψ_e , and the drop in water vapour concentrations between the sub-stomatal cavities and the atmosphere, $D_l - D_o$. The latter is a function of atmospheric vapour pressure deficit, radiation load, air temperature, and windspeed (Farnum, 1977). The state variables are root and leaf surface areas A_r and A_l , xylem cross-sectional area in the stem A_x , and water potential in the xylem of the roots ψ_r , and leaves ψ_l . The parameters are hydraulic conductances per unit area of root surface τ_r , and per unit stem cross-section τ_s , and leaf diffusive conductance to water vapour τ_l . Parameter τ_l itself has a dependence on vapour pressure deficit, leaf water potential, and light intensity, which can be described by empirical curves (Emmingham and Waring, 1977; Running, 1976; Watts *et al.*, 1976). The other important conductance τ_r , varies with uptake rate and soil temperature. Both variable conductances quantify aspects of drought avoidance, and are further examined below.

Under non-steady state conditions water exchanged between the apoplast and symplast at a rate dV_w/dt , proportional to the water potential difference between them, *i.e.*,

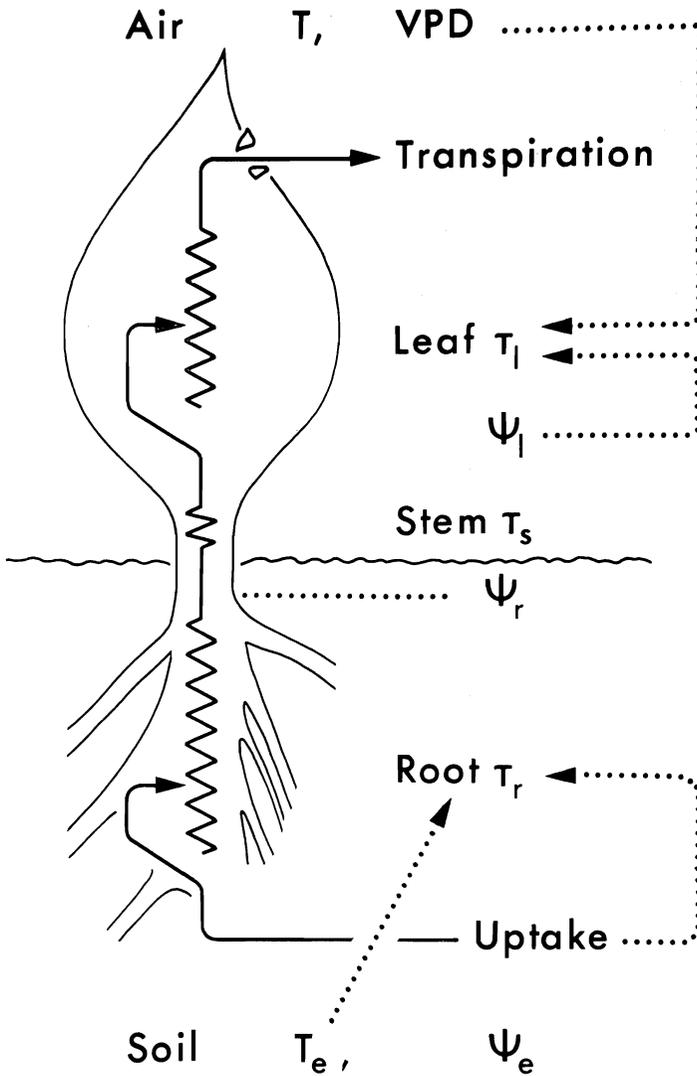


FIG. 5—Conductances (τ) to steady-state flow of water and vapour in the soil-plant-atmosphere continuum. ψ represents water potential outside the root (subscript e), in the root xylem r , and at the evaporation sites within the leaf l . Conductance through the stomata τ_l , is controlled by vapour pressure deficit VPD, and ψ_l , while τ_r is a function of uptake rate and soil temperature T_e .

$$\frac{dV_w}{dt} = \tau_{xc}(\psi_l - \psi_e), \tag{17}$$

where τ_{xc} is the parameter denoting hydraulic conductance of the apoplast-symplast pathway and V_w is intracellular water volume. The leaf xylem water potential ψ_l , is a state variable dependent on flows and conductances through the soil-plant-atmosphere system, as described above. Cell water potential ψ_e , however, depends on the bulk

elastic and osmotic properties of the cells, which have recently been analysed in detail (Tyree and Hammel, 1972; Hellkvist *et al.*, 1974; Powell and Blanchard, 1976), and are illustrated in Fig. 6. Cell water potential is the sum of osmotic (π) and hydrostatic (p) components:

$$\psi_c = \psi_\pi + \psi_p, \tag{18}$$

The osmotic component is related to the number of osmols of solute N , by

$$\psi_\pi = \frac{-\delta R'(T + 273)N}{V_w}, \tag{19}$$

where R' is the gas constant, T the temperature, and V_w the intracellular water volume. The parameter δ is the "bulk" reflection coefficient of the cell membranes and will almost equal 1 in healthy tissue, less if the membranes are injured and leaky.

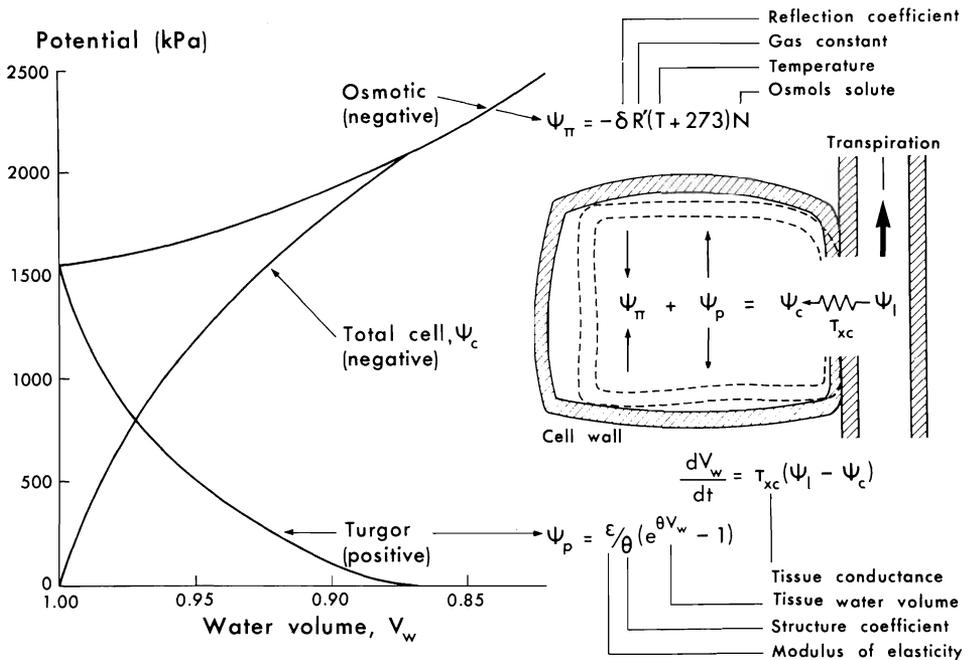


FIG. 6—Components of sympastic water potential. The curves representing behaviour of osmotic and turgor components as water is withdrawn from the cell into the transpiration stream are for shoot of western hemlock seedlings (*Tsuga heterophylla* (Raf.) Sarg.) (Kandiko *et al.*, in press).

The turgor component is related to intracellular volume by parameters describing the bulk modulus of elasticity of the tissue ϵ , at full turgor, and the slope θ , relating ϵ to turgor pressure. The empirical equation given by Powell and Blanchard (1976) is

$$\psi_p = \frac{\epsilon/\theta}{\theta} (e^{\theta V_w} - 1), \tag{20}$$

Equations 16-20 show how turgor pressure can be related to environment by (1) eight state variables comprising surface areas, water potentials, solute contents, and intracellular water volumes of root and shoot, and (2) 15 parameters comprising four

conductances, five empirical coefficients relating (a) root conductance to uptake rate and soil temperature and (b) stomatal conductance to leaf water potential, vapour pressure deficit and light intensity, two root- and two shoot-elasticity parameters, and root and shoot tissue reflection coefficients. Together these uniquely define the health of the water subsystem, and thus account for the third major part of the variation in c , the slope of the curve for potential growth.

Degenerative Processes and Injury

The foregoing analysis has concerned the process of growth in Fig. 1, but growth can be negative if carbohydrate reserves and current photosynthesis are insufficient to maintain existing structures. Under these circumstances, which may pertain, e.g., in competitive situations and cold stores, there will be a loss of biochemical machinery, and eventual death. Thornley (1977) has shown how a model that includes a degradable fraction of structure and no maintenance term can account for "death by starvation" more explicitly. McMurtrie (pers. comm.¹) extended this to examine adaptations that favour survival in droughty situations. This three-chemical model is reconcilable with the traditional approach used here (Barnes and Hole, 1978), and no additional parameters are needed to account for a seedling's resistance to slow degeneration.

However, accounting for resistance to injury, represented with respect to low temperature by the curve on the left of Fig. 1, does require additional parameters. While negative growth may be likened to the orderly disassembly of machinery, injury is more like an act of sabotage. Resistance to it is best described empirically as the degree of environmental² abuse needed to break a critical part. Though there is merit in considering a *rate* of injury, as in Fig. 1, in order to account for the interplay of environmental severity and exposure time, it is probably an unnessecary refinement for identifying practical criteria of quality. All that must be known for each major subsystem is what level of the factor in question will permanently destroy its capability to function. Implied is an exposure time long enough to permit the relatively rapid injury process to be substantially completed. Experience with several conifer species (e.g., Timmis, 1976) has shown that it is necessary only to distinguish lethal values for shoot meristems collectively (cambium and buds) and roots, in order to have a survival prediction for a given extreme site. A lethal value for the leaves is also desirable. Their loss is replaceable in the absence of meristem damage (other factors being favourable), but will nonetheless affect growth potential by reducing substrate availability.

Thus seedling quality criteria that relate to injurious processes rather than processes of growth, comprise mainly lethal high or lethal freezing temperatures, and critical low water contents, of roots, shoot meristems, and leaves. Resistance to extremes of other factors such as sunshine, physical abrasion or compression, toxic chemicals, etc., could also be described in terms of lethal doses in circumstances where these factors were a feature of the seedling's future environment.

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² This refers to environment **within** the plant such as shoot temperature, not air temperature and tissue water content, not soil or atmospheric water content.

SELECTION AND VALUE OF QUALITY CRITERIA IN PRACTICE

Summary of Criteria

The criteria of quality and stress resistance derived in the preceding section are by no means the only possible set, but result from the particular models cited, and their associated assumptions. They are summarised in Table 1 with respect to the three subsystems, two compartments (root and shoot), and two types of information (state variables and parameters). For many of these variables, or ones closely related to them, there is experimental evidence to support the theoretical likelihood of their correlation with field performance. Table 1 offers a list that is precisely defined, relevant to laboratory-supported reforestation practices as will be shown later, and complete except for mineral nutrition and some biotic effects. In principle it is possible to simulate the essential growth behaviour of a seedling in any environment with this information in numerical form.

TABLE 1. Summary of stress resistance and stock quality criteria (Numbers in parenthesis represent circumstances in Table 2 where the criterion is likely to be important)

| | PHOTOSYNTHETIC SYSTEM | | WATER SYSTEM | | UTILISATION SYSTEM | |
|--|---|-------|--|------|---|------|
| | Shoot | Shoot | Shoot | Root | Shoot | Root |
| | | | | | | |
| EQUATION PARAMETERS (Physiological and Material Properties) | Stomatal conductance - Water potential coefficient(s) [1,4,5,8,13] | | Hydraulic conductance - Uptake rate coefficient(s) [2-5,13] | | Specific maintenance rate [1,4,5,8] [2,3,4,5,7] | |
| | Stomatal conductance - Light intensity coefficient(s) | | | | | |
| | Stomatal conductance - VPD coefficient(s) [1,4,5,8,13] | | Conductance - Root temperature coefficient(s) [12] | | Conversion efficiency [1,5] [2,3,5] Michaelis-Menten constant [1,4,5,9,14] [2,3,4,9] | |
| | Photochemical efficiency [1,4,5,8,14] | | Reflection coefficient [1,4,5,7] [2,4,5,7] | | Maximum utilisation rate [1,4,5,7,9,14] [2,3,4,9] | |
| | Photorespiration constant [8] | | Tissue-to-xylem hydraulic conductance | | Temperature coefficient(s) utilisation [10] [11] | |
| | Temperature coefficient(s) of photosynthesis [10] | | Elasticity-volume coefficient(s) [13] | | Turgor coefficient(s) of utilisation [13] [13] | |
| | | | Water volume [4,5,13] [1,5,15] | | Structural dry weight [6,7,11,14] [6,7] | |
| | | | Xylem water potential [4,5,7,13] [4,5,7,13] | | Substrate concentration [5,11] [5] | |
| | | | Leaf surface area [6,7,11,13,14] | | Root area [6,7,13] [1,7,11,14] | |
| | | | Cell sap osmolality [13] | | Number of primordia [13,17] | |
| STATE VARIABLES (Morphological and Chemical) | Lethal low temperature [10] | | | | Lethal low temperature [10] [5] | |
| | Lethal high temperature [16] | | | | Lethal high temperature [16] [16] | |
| | Lethal low water content [13] | | | | Lethal low water content [13,16] [13,16] | |
| INJURY POTENTIAL | | | | | | |
| | | | | | | |
| | | | | | | |

Selection and Case Histories

It is not suggested, however, that the many items in Table 1 be used to estimate seedling quality; only that these form the basis for selecting a smaller number appropriate to the situation. Such selection requires dialogue between nurserymen, district foresters, and plant scientists because it is dependent on familiarity with two aspects of the local reforestation process: (1) the history of the seedling crop, hence its possible weaknesses and injuries, and (2) the main stresses likely to be experienced in its next year usually, but not always, as an outplanted seedling.

As examples of environmental and cultural situations that have afflicted Weyerhaeuser's crops in these two categories one can cite in the first, mid-winter freezing of shoots, freezing and flooding of root systems, mechanical injury from equipment, debilitation in cold stores, desiccation in frozen soil or after lifting, and improperly timed or foreshortened periods for growth or chilling. The second category includes out-of-season frosts, browsing animals, cold early-drying soils, vegetative competition, and drought. A more complete list of nursery and planting site problems, together with appropriate quality criteria, appears in Table 2. For most items in this list only a relatively small number of quality criteria are needed to define their impact on survival and growth, as discussed in the following examples.

In the case of a crop that has had frozen or flooded root systems in the nursery before lifting, one would concentrate attention on the maintenance and maximum utilisation rates, the hydraulic conductance, and the bulk reflection coefficient of the root system by the methods outlined below. Low values of the last two may in fact provide a clear enough indication of the general condition of the roots if this is poor. The inverse correlation of membrane leakiness as measured by electrical impedance and electrolytic methods, with survival following frost injury, is well established (Timmis, 1976). The first two criteria will give specific information on the potential of the roots' meristematic centres for growth (k_r) or the amount of repair in progress (m). On theoretical grounds one would expect a greater sustained value for specific maintenance rate where injury was being successfully repaired, although this has not been tested experimentally. Parameters K_r (and K_r , which is determined in conjunction with it) will assume greater importance when damage to the root system is light and roots need to grow quickly, e.g., on an early-drying site. Several studies demonstrating a strong correlation between root growth potential (related to k_r) and field performance, are cited by Ritchie and Dunlop in this volume.

In cases where injury to shoots has been a problem, as with frost or physical damage, the values of photochemical efficiency, leaf conductance to CO_2 , and the maintenance and maximum utilisation rates of buds and cambium are likely to be of most importance. Survival of early and late winter frost injury is predicted well by the reduction in photosynthesis, and by slight discolourations of the cambial zone (Timmis, 1976). The latter presumably indicates a loss of function that would show up better in parameters such as k_r , Y_G , and m . Leaf area, and substrate content of both shoot and roots will be important state variables. It must be borne in mind in these and other examples of previously stressed nursery crops that localised injuries, to leaves or root tips, for example, will eventually be reflected in worse-than-normal values of many quality criteria throughout the plant, or simply in repaired but rather stunted

TABLE 2, Conditions determining selection of quality criteria

| PAST INJURIES | Criteria of likely importance | FUTURE STRESSES | Criteria of likely importance |
|--|---|--|---|
| 1. Freezing of tops | $\tau_l \alpha \delta_s m_s Y_{Gs} k_s K_s j$ | 10. Freezing tops | $LT_s f(T_p) f(T_s) T_c \text{ opt}$ |
| 2. Freezing of soil, especially containerised stock | $\tau_r \delta_r Y_{Gr} k_r K_r m_r$ | 11. Browsing or insect defoliation | $W_{Gs} S_s j A_l$ |
| 3. Flooding of soil, or root diseases | as above | 12. Cold soil | $k_r \text{ as } f(T_e) \tau_r \text{ as } f(T_e)$ |
| 4. Drought or excessive exposure during lifting | $\tau_l \alpha \tau_r \delta_s \delta_r m_s m_r k_s$ $k_r K_s K_r V_{ws} V_{wr} \psi_l \psi_r$ | 13. Drought, or excessive exposure during transport and planting | $\tau_l \text{ as } f(\text{VPD}, \psi_l) \epsilon \theta$ $k_s \text{ as } f(\psi_{ps}) LV_w N$ $k_r \text{ as } f(\psi_{pr}) A_l A_r V_w$ |
| 5. Cold or freezer storage | as above plus $Y_{Gs} Y_{Gr} S_s S_r$ | 14. Vegetative competition | $W_{Gs} A_l \alpha j k_s K_s$ |
| 6. Stunting of size or root/shoot imbalance | $A_l A_r W_{Gs} W_{Gr}$ | 15. Hot bare soil surface | $W_{Gs} LH_s$ |
| 7. Physical damage by lifter, pruning, etc. | $m_s m_r A_r A_l j \psi_s \psi_r$ $W_{Gs} W_{Gr} \delta_s k_r \text{ etc.}$ depending on location | 16. Excessive heating during transport or on-site | $LH S_s S_r V_{ws} V_{wr}$ |
| 8. Excess sunshine | $\alpha A_l \beta m_s \tau_l$ | 17. Improper planting: - soil compaction around roots | $k_r \psi_{pr} N_r \epsilon_r W_{Gr} A_r$ |
| 9. Growth or dormancy out of synchrony with intended environment | $k_s K_s k_r K_r \psi_r Ch$ | - vapor gaps between soil and root | as in 13 above |

plants. Selection of quality criteria must then be based mainly on the conditions likely in the second half of Table 2, rather than on both past and future conditions.

As an example of future limiting conditions, we can consider planting sites that are generally cold. These should focus our attention on lethal low temperatures and the temperature coefficients of photosynthesis and utilisation as criteria of stock quality. The importance of temperature coefficients for utilisation requires testing. The shift of the optimum temperature for photosynthesis from 22° to 10°C in spring (Neilson *et al.*, 1972) is evidence of the importance of $T_{p \text{ opt}}$.

In particular, some sites high on the Cascade mountain slopes, are characterised by cold soils which can dry out rapidly in early summer. For these places, seedlings with relatively high k_r , and relatively low temperature thresholds for k_r and the root's hydraulic conductance, would be of high quality. So, too, would seedlings capable of root growth in relatively dry soil, i.e., with a higher than average value for $f(\psi_{pr})$. At present, evidence in support of these criteria is limited to the demonstration of the importance of root growth potential in general (see above), coupled with field observations of the absence of root growth on such sites when seedlings had been initially healthy in other respects. Current experiments at Weyerhaeuser should clarify the role of temperature and turgor coefficients.

Where planting is to be done in relatively dry places to begin with, criteria describing short term drought avoidance are of first importance. These include the vapour pressure deficit and ψ_1 modifiers of stomatal conductance, cell sap osmolality N , the bulk modulus of elasticity ϵ , and its relationship θ , to turgor pressure, especially of roots. There is good evidence for the relevance of all these criteria to field performance. This appears in studies by Rook (1969), Zavitkovski and Ferrell (1970), and Keller and Tregunna (1976) in the case of stomatal water vapour conductance. Tyree *et al.* (1978), Kandiko *et al.* (in press) and current (unpublished) studies at Weyerhaeuser provide evidence for the importance of osmotic and elasticity parameters. Quality criteria for droughty situations must also include the surface areas (or related measure) of the root system and foliage (see, e.g., Farnum's modelling study, 1977) and the xylem water potentials and water contents of each (e.g., Cleary and Zaerr, this volume).

As a last example of expected situations that govern our selection of quality criteria, we may note that many low-lying forest sites that are climatically very favourable for tree growth are also very favourable for weeds and browsing animals. The state variables describing shoot dry weight, food reserve content, foliage area and number of leaf primordia, and the parameters for utilisation in the shoot k_s and K_s , and photochemical efficiency α , will then be the predominant criteria of seedling quality. These will determine the seedling's ability to compete for light and recover from browsing when water is abundant, and are characteristics of the large 2+1 transplants sought by foresters for such sites.

Fuller information on the significant quality criteria for various field situations is provided in Tables 1 and 2. For the most generalised forms of stress, such as occur in cold stores or droughts, a fairly large number may be indicated. But only a few need be measured in order to conclude that the stock is definitely in very poor shape. The measured number of criteria (and individuals) can be increased with healthier stock, with increasing economic importance of the end decision, and with increasing

ease and economy of measurement. The last factor may dominate in urgent situations, and will now be discussed.

MEASUREMENT OF STRESS RESISTANCE AND STOCK QUALITY

The intent of this section is to outline briefly how some of the more important and less familiar criteria in Table 1 can be measured. While this is in some cases simpler than their names would suggest, there is still much scope for development both of better basic analytical techniques and reliable short-cuts for the field.

Growth and Maintenance Parameters

Estimating the conversion efficiency Y_G , maintenance rate m , maximum utilisation rate k , and substrate-sensitivity of utilisation (Michaelis-Menten constant) K , is simple enough in principle. It requires that we determine the relationship between the seedling's respiration rate and its rate of growth in structure when the rate at which substrate is added to the system by photosynthesis, is known. Graphical solutions to equations for the simplest case of a large substrate pool being used up in the dark, are shown in Fig. 7. When no further structural growth is detectable the respiration rate represents maintenance. The residual respiration (after 48 hours in darkness) has been used as a

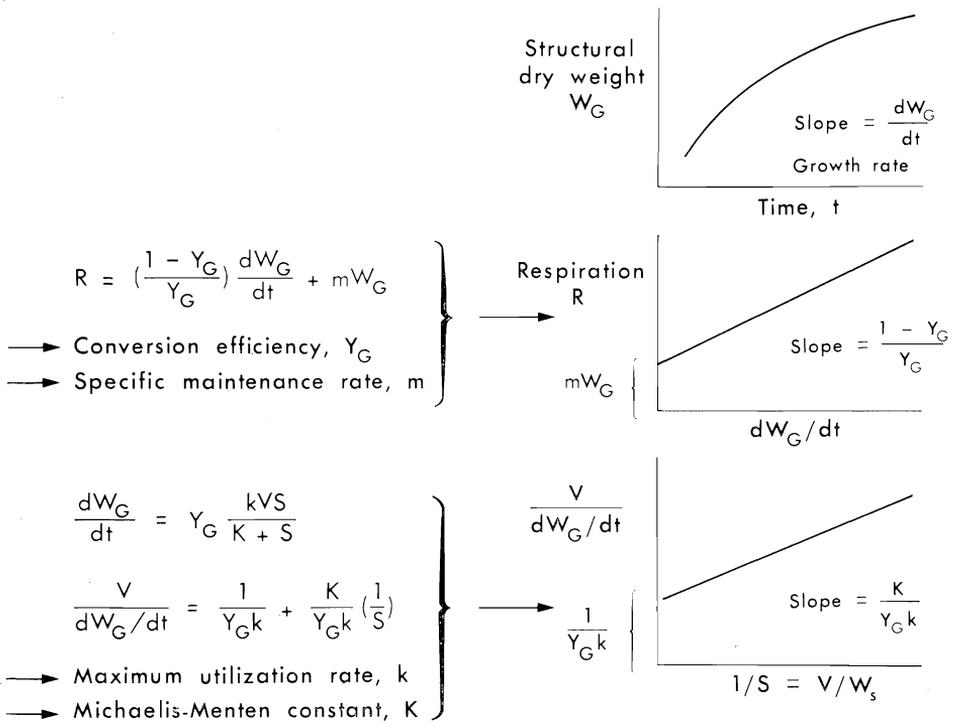


FIG. 7—Theory for estimation of four parameters of the utilisation system. The graphs show how measurements of fresh tissue volume V , structural dry weight W_G , substrate weight W_s , and respiration of seedlings in darkness, can in principle be used to estimate parameters in the equations at left (which are explained in the text).

measure of m without prior measurements of structural growth (Moldau and Karolin, 1977). For determining Y_G , k , and K , however, the amount of structure and substrate must be determined by chemical analysis. This is a laborious procedure (Smith, 1969) when done to the $\pm 1\%$ accuracy needed to measure changes occurring in a single dark period. It would be facilitated by use of clonal material and better analytical methods. Substrate-structure changes can be measured more accurately over longer periods, but this requires a knowledge of contributions by photosynthesis. When separate estimates are required for shoots and roots, the transport of substrate between these must be determined, or prevented (in short-term studies) by girdling. Nevertheless, estimates of Y_G and m have been obtained in a variety of ways (Lambers, 1979), and plant growth does conform to a Michaelis-Menten substrate dependency in the simple callus system so far investigated in this regard (Hunt and Loomis, 1976). Research is underway to adapt the approach shown in Fig. 7 to tree seedlings, and thereby improve upon the present time-consuming utilisation criteria: root growth potential and speed of bud break.

The temperature and turgor modifiers of utilisation, comprising, for example, the threshold temperature for root growth or the relation of turgor to leaf expansion, can be estimated fairly quickly from measurements or respiration at various temperature and turgor levels (Fig. 8). Controlling temperatures in the cuvette or culture solution, and recording the stable respiration rate is a routine matter. Simply leaving several shoots or root systems to dry out on a darkened laboratory bench and periodically

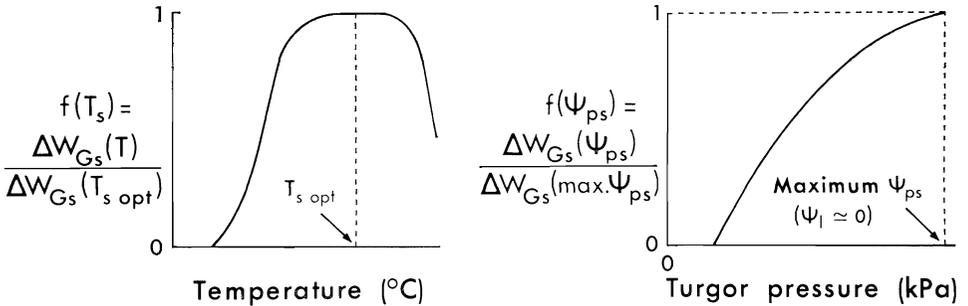


FIG. 8—Hypothetical curves describing temperature and turgor pressure dependence of the parameter for maximum utilisation in the shoot k_s . These modifiers, $f(T_s)$ and $f(\psi_{ps})$ respectively, are given a value between 0 and 1 by dividing the shoot's observed structural dry weight increment ΔW_{G_s} , by its maximum increment.

measuring their water potential (by pressure chamber) and respiration rate, will provide the necessary data for the water stress effect. The recurrent respiration measurements can be done on the same sample provided that a concurrent time series sampling is run on seedlings kept fully moist, so that the effects of substrate depletion can be adjusted for. The estimates will contain some error due to the contribution by maintenance respiration if this has different temperature or turgor coefficients, but the error is unlikely to be important, and could in any case be separately determined. A water-potential modifier can substitute for turgor in practice, if parameters of the hydraulic system that would relate water potential to turgor pressure, are not to be determined.

Hydraulic and Vapour Conductances

The variable conductances of the foliage (stomatal) and roots tell us much about the degree of control a plant has over its absorption and transpiration of water. These, together with the less important (Farnum, 1977) stem conductance τ_s , can both be estimated by the following procedure, due largely to Farnum, whose thesis provides fuller details. Some actual and hypothetical data are shown in Fig. 9.

The seedlings are transplanted into pots for purposes of the test and allowed to stabilise for several days. They are then re-watered to field capacity and, after standing overnight, are placed in environments known from preliminary measurements to result in high, medium, and low rates of transpiration. The soil surface is covered; the transpiration rate is recorded by periodic weighing, and when steady the plant is severed at the root collar. The whole pot is placed in a pressure chamber, with stump protruding, to get a measurement of root water potential *in situ* ψ_r , and the stomatal resistance of a portion of the shoot τ_1 is measured directly, at ambient humidity using a null balance diffusion porometer of published design (Beardsell *et al.*, 1972). Then water potential of the shoot ψ_1 , is also determined. The severed shoots are allowed to dry out over several days under controlled conditions, and are remeasured for ψ_1 and τ_1 periodically. Finally, the (one-sided) leaf areas and root lengths or areas, of the seedlings are determined by standard gravimetric and photometric means.

By assuming that soil water potential ψ_e , in the pots is zero, root conductance τ_r , is obtained as the steady state transpiration rate divided by ψ_r . A curve fitting procedure will then provide the parameters of its relationship to uptake rate as in the example of Fig. 9b. Also, stem conductance can be obtained by dividing transpiration rate by $\psi_r - \psi_1$. The parameters for hydroactive stomatal closure are obtained by fitting a curve to the τ_1/ψ_1 data (Fig. 9a). In principle, at least, the relationship between leaf conductance and vapour pressure deficit should be obtainable as a bonus by making several determinations of τ_1 with the null-point humidity set at a different level each time. This will be a very small addition to the work load when a self-nulling porometer is developed, but is otherwise a modest extra effort yielding valuable information on drought avoidance and economy of water use.

Turgor, Osmotic, and Elasticity Parameters

For measuring the parameters governing exchange of water between tissue and xylem, the pressure-volume technique has been developed (Scholander *et al.*, 1966; Tyree and Hammel, 1972). This is an extension of the pressure chamber technique in which additional increments of pressure, beyond the initial balance point, are given. The corresponding increments of water expelled from the cut end, and weighed after absorption on to filter paper, are taken to represent what would be lost from the tissue in response to an equivalent negative pressure in the xylem under natural conditions. With a pair of pressure chambers, each equipped with three insertion holes, data for up to 12 pressure-volume curves can be obtained in one day, with the yield of much information in seedling quality.

When the reciprocal of the applied pressure is plotted against expelled volume a steeply downward sloping curve with a straight line tail results (Fig. 10). The straight line portion represents osmotic behaviour in accordance with Vant Hoff's law (osmotic pressure inversely proportional to volume). Extrapolation of this to the vertical axis

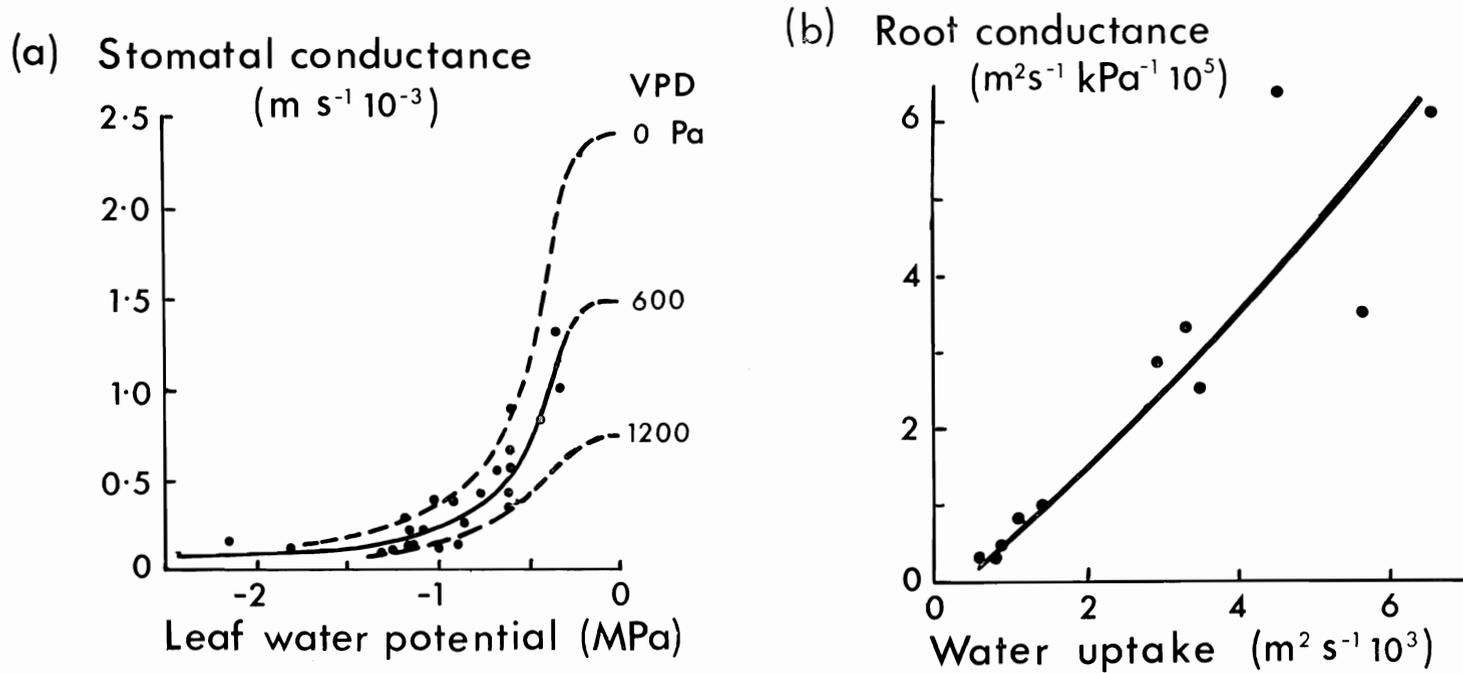


FIG. 9—Curves describing the control of stomatal and root conductances by seedling water status and environment. Data points in (a), from Emmingham and Waring (1977) and Running (1976), are for a vapour pressure deficit (VPD) of ~ 600 Pa (= 6 mb), and relate to pre-dawn water potentials of Douglas fir. The dashed curves for higher and lower VPD's are based on the relationships given by Watts *et al.* (1976) for Sitka spruce (*Picea sitchensis* (Bong.) Carr.). Data points in (b) are from are: 1. Tyree *et al.* (1978) eastern hemlock (*Tsuga canadensis* (L.) Carr.), 2750 kPa, 0.56 day^{-1} . 5. McKenzie *et al.* (1974) red osier dogwood (*Cornus stolonifera*

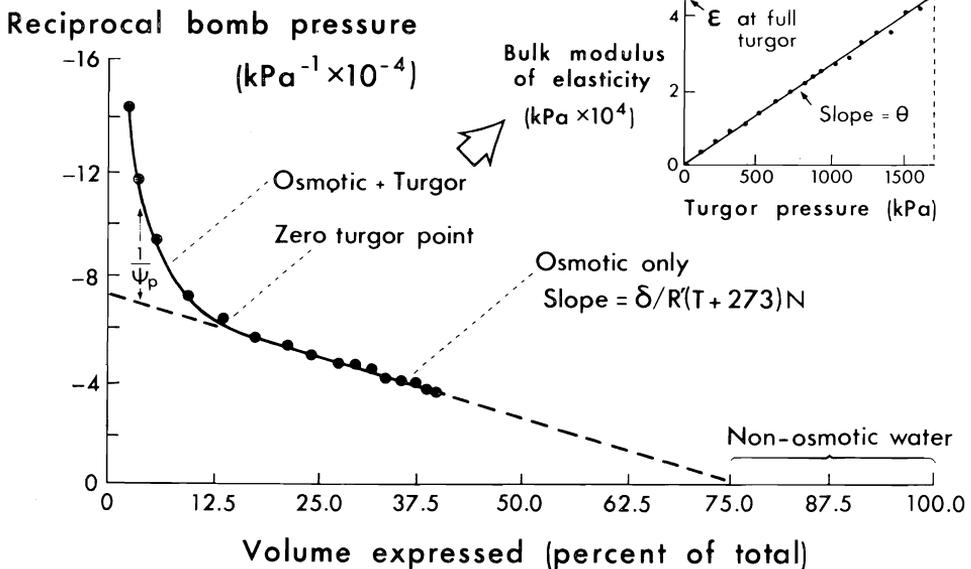
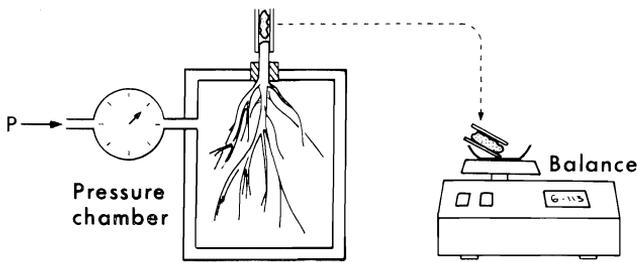


FIG. 10—Estimation of parameters relating to turgor pressure (ψ_p) (parameters ϵ and θ), and osmotic potential (cell sap osmolality N , reflection coefficient δ) by the pressure-volume technique. R is the gas constant and T the Celsius temperature. Data are from Kandiko *et al.* (in press) for western hemlock seedlings.

gives an estimate of the osmotic component ψ_π of cell water potential ψ_c at full hydration. Extrapolation to the volume axis (infinite pressure) gives an estimate of the initial volume of osmotically active water, which can be taken to approximate the intracellular water volume V_w initially present. The slope of the straight line in tissues with perfect semi-permeable membranes, and where V_w is expressed in millilitres, will be equal to $1/R'(T+273)N$, from which N , the osmolality of cell sap, can be calculated. If an independent estimate of N is available, for example from a vapour pressure osmometer reading of a freeze-killed and crushed tissue sample of known weight, then the value of reflection coefficient δ (substituting for unity in the numerator of the expression for slope) can be calculated.

The difference between the curved portion in Fig. 10 and the extrapolated straight line, after inversion of the reciprocal, represents the turgor pressure ψ_p . From the slope of the turgor pressure-volume curve, we can obtain the elasticity parameters ϵ and θ (Fig. 10). The value of tissue-to-xylem hydraulic conductance τ_{xc} , can also be estimated from the time required for each increment to be expelled. But this does not appear to be a very important parameter and further details can be obtained elsewhere (Tyree and Dainty, 1973).

Significant on the pressure-volume curve and so-called Höffler diagram (Fig. 6) prepared from it, is the zero turgor point. Beyond this point no expansion growth can occur, and the cell walls either collapse inward, leading eventually to the attainment of a lethal minimum cell volume, or remain rigid and support water under negative pressure ("negative turgor") within. Rigid walls (high ϵ) will be an advantage for the non-meristematic portion or roots, by conserving root volume and delaying the formation of rhizospheric air spaces.

Photosynthetic Parameters

Leaf conductance to CO_2 , and the photorespiration constant, can be obtained by measuring net photosynthesis P_n' , and then dark respiration R , at high light intensity and a series of low ambient CO_2 concentration when temperature is optimum ($f(T_p) = 1$). Substitution of $C = 0$ into Equation 14 shows that the curve of P_g' ($= P_n' + R$) against ambient CO_2 concentration will intercept the vertical axis at a point equal to $-\beta$ (Fig. 4). At its intersection with the horizontal axis, i.e., at $P_g' (= 0)$, the slope will be equal to τ . From Equation 14, the photochemical efficiency α , can then be calculated. The temperature coefficients of photosynthesis can be obtained from measurements of P_g' at various temperatures, followed by appropriate curve fitting.

If the findings of Wong *et al.* (1979) are confirmed for tree seedlings under a range of conditions that includes foliar injury, then there will be no reason to measure these individual photosynthetic parameters — which Luukanen and Kozlowski point out, have not been very successful in predicting growth. The parameters of leaf conductance to water vapour already described will then contain this information.

Lethal Doses

Ideally, the degree of heat, cold, or water loss that will destroy the functioning of a subsystem is measured by the methods already described, *after* exposing that subsystem to various degrees of the extreme condition. Each exposure-and-recovery test must be made on a different group of individuals, and one will therefore end up with a sigmoid dose-response curve for the population. From this can be obtained a 50% kill value LD_{50} , or LD_{10} , etc., and associated standard deviation, by probit analysis (Finney, 1971).

In practice, care must be taken to see that the stress is applied in such a way as to be reproducible and resemble its occurrence in nature. The paper by Warrington and Rook in this issue reviews this subject with respect to freezing tests. I have encountered no equivalent review for critical water content determination; many so-called drought tolerance tests fail to even include this variable. A specific test of heat injury to the basal shoot tissue of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings,

simulating natural soil surface temperatures, has been described by Keijzer and Hermann (1966), and its relevance to seedling performance under exposed conditions has been demonstrated by Silen (1960).

Care must also be taken to determine whether or not the post-exposure lowering of function is permanent. This involves either (1) making subsequent measurements (of photosynthesis, respiration, reflection coefficient, or whatever) to determine whether the system is deteriorating or being repaired, or (2) using previously established correlations between the post-exposure values of function, or more easily measurable properties related to function, and long-term survival of the housing organ or whole plant. The numerous ways in which people have attempted to do this for freezing injury, and the underlying principles, have been reviewed by Timmis (1976). Many of these can be applied to assess other types of injury. Such short-cut methods have applications through the entire range of quality criteria, provided either that their relation to basic processes or properties is understood, or that their use is confined to the particular circumstances under which the empirical correlations were developed.

Short-cut and Field Methods

Many common-sense criteria of seedling condition, such as the colour, firmness, degree of succulence, and abundance of foliage, excised bud centres, inner bark and roots, are directly and obviously related to the state variables in Table 1. The root system's "fibrosity" (Burdett, 1979), for example, which has to do with A_r/W_{Gr} , is correlated with field performance. The period of assessment for bud break (emphasised by Lavender and Zaerr in this volume) and root growth potential, can probably be shortened to a few days with more detailed observation. Among physiological indicators, electrical impedance of tissue to a small electric current passed between inserted electrodes is an accepted technique. It is based on the fact that cell membranes are good electrical insulators (Olien, 1961; Fensom, 1966) and when damaged, impede current flow much less. This reduction is probably a measure of reflection coefficient and has been used effectively to determine LD_{50} 's for low temperature (Timmis, 1976). In the long run, however, the most effective and widely applicable short-cut procedures are likely to be those developed from the more elaborate ones already described. Curves describing stomatal conductance characteristics can probably be substituted by ratios of values at two humidities or water potentials. A "field" version of the pressure-volume technique involving a single overpressure application has shown good discrimination at Weyerhaeuser, between healthy seedlings and ones of dubious quality. The use of an oxygen electrode to estimate k_r in culture solution is currently being explored. Coupled with efficient sampling procedures and new techniques, such short-cuts should render the measurement of most quality criteria a routine matter.

INTERPRETATION AND USE OF STOCK QUALITY CRITERIA (OR HOW MUCH IS ENOUGH?)

The purpose of this final section is to address two related questions that have so far been avoided: (1) how, having estimated the numerical value of a quality component, we can say whether it is good or bad and act accordingly; (2) how phenological variables (dormancy, photoperiod, acclimation, etc.) are expressed in the growth curve (Fig. 2) and subsequent analytical framework.

Establishing Quality Standards

It is first necessary to recall the point that, although parameters are fairly constant relative to state variables, most of them do in fact exhibit considerable seasonal change (Fig. 11). The most extreme example is that of the maximum utilisation rate parameter for shoot growth, which in species of temperate regions is maximum in spring and almost zero in early winter until a chilling requirement has been met. With few exceptions at present, a quality measurement can be interpreted for reforestation decisions only if we know what value it normally takes in healthy seedlings (i.e., good performers for the site in question), at that time of year. Some of this information is already available for some species under some conditions (Fig. 11). Where it is not, the important parts of it (Table 2) should be accumulated through research.

Parameter value
(% of maximum)

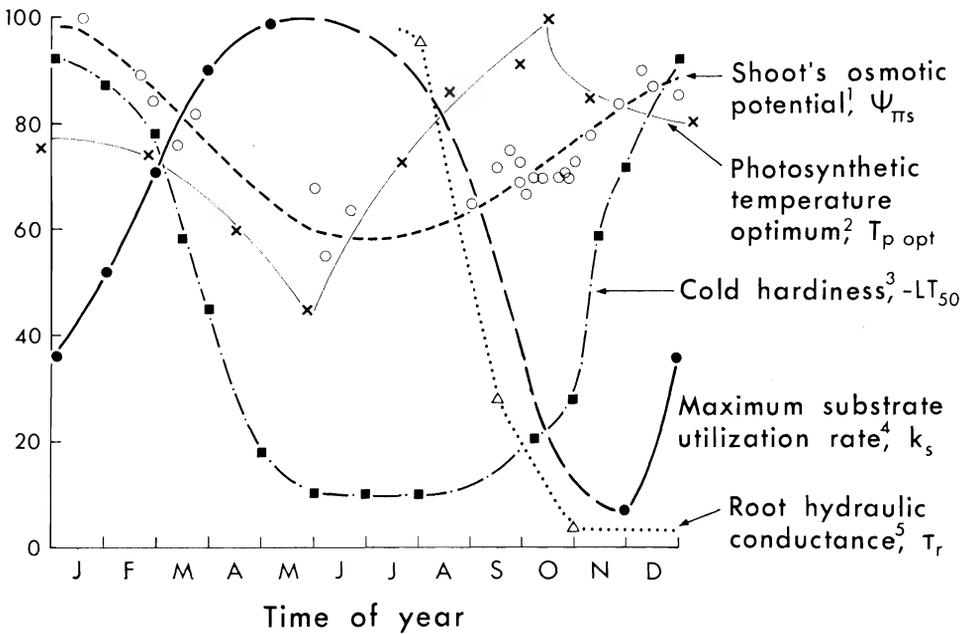


FIG. 11—Seasonal trends of various quality criteria. Sources, species, and maximum values are: 1. Tyree *et al.* (1978) eastern hemlock (*Tsuga canadensis* (L.) Carr.), 2750 kPa. 2. Neilson *et al.* (1972) Sitka spruce, 22°C. 3. Timmis (unpubl.) Douglas fir, -27.5°C. 4. Several Weyerhaeuser studies, Douglas fir, 18 days to bud break = 0.56 day⁻¹. 5. McKenzie *et al.* (1974) red osier dogwood (*Cornus stolonifera* Michx.), arbitrary units.

A better way to interpret measurements of quality is to know what values they must take based directly on a knowledge of the soil and weather conditions to be experienced. One of the few cases where this approach has been used is for the shoot's lethal freezing temperature. A graphical comparison of LT₁₀ under various cultural

treatments, and remote-site frost probabilities for two sites, revealed that in one case, efforts to acclimate seedlings crops, or select one with $LT_{10} \leq -6^\circ$ for mid-October planting would be justified, and in the other case would not (Fig. 12). The use of planting weather guidelines in conjunction with pressure chamber measurements of ψ_1 (see Clearly and Zaerr in this volume) represents a similar approach.

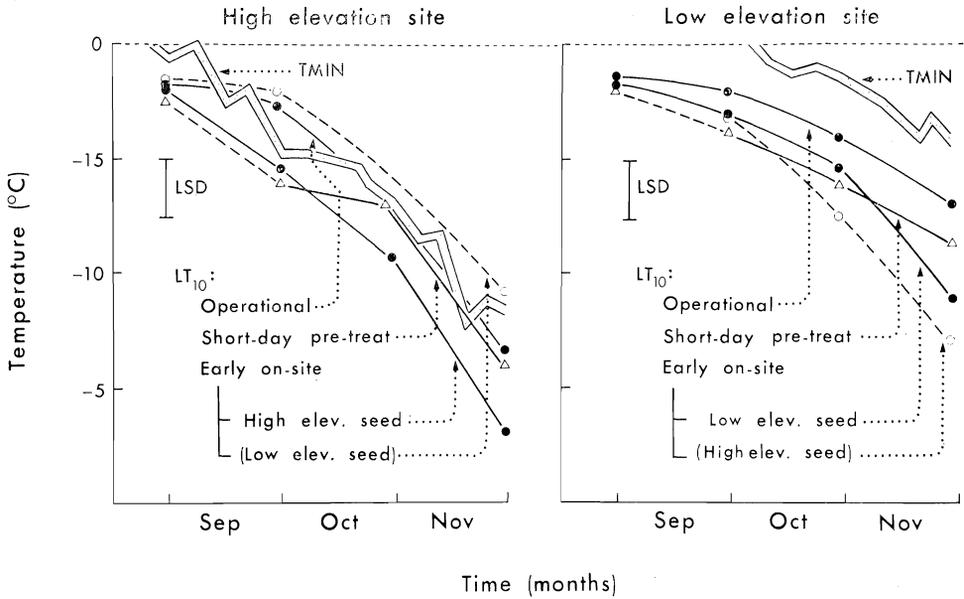


FIG. 12—Lethal low temperatures (10% population kill) under various management options on two sites compared with 20-year minimum temperatures (TMIN) for those sites. Data are for containerised western hemlock seedlings from unpublished studies by the author. LSD = least significant difference (5% level) for LT_{10} curves.

For most quality criteria, however, defining a value that is just sufficient to guarantee good performance under given conditions is more difficult. It requires years of empirical trials, or a simulation model of growth based on the equations given earlier or, preferably, some economical combination of the two with laboratory studies.

The Information System

Consideration of long-term growth models, i.e., seedling models that would simulate response for a whole growing season, brings us to the question of accommodating phenological parameters. Seasonal models must include the processes of acquisition and release of dormancy (expressed by k_g), and the seasonal or culturally-induced acclimation of other parameters. Some of these changes occur in response to photoperiod and chilling, which have been considered to act mainly as information (Campbell, 1978). A number of factors in addition to photoperiod, such as temperature, mineral nutrition, and water stress affect dormancy induction. It is thus likely that the response in these cases occurs indirectly through a general slowing of height growth which, like photoperiod and chilling, affects a balance between growth promoting and inhibiting hormones

in an informational master system. Some evidence (e.g., Dormling *et al.*, 1968) indicates that photoperiodic effects on utilisation can be modelled as causing a raising or lowering of the maximum shoot weight parameter a , the asymptote in Fig. 2, rather than k_s . Relevant parameters would include the photoperiodic modifier of " a " (or k_s , as the case may be), optimum chilling requirement in hours, and the optimum and spread of the effective chilling temperature curve (Sarvas, 1974). Short-cut measurement techniques might involve the determination of hormone levels in various organs and would indicate the extent to which a seedling had been or could be culturally "misinformed", with regard to the timing of its growth-centre activities *vis-à-vis* the intentions of the forester. In general, the information system is poorly understood, and is a profitable area for basic study.

Summary of Applications

In the foregoing attempt to show how stock quality in all its various aspects can be combined within a mathematical framework of practical value, I have omitted to mention several aspects of that value. Our increasing capability to quantify the everyday concepts of health and vigour should be used, not only for particular plant/no-plant decisions, but as a basis for scientific management throughout the life of nursery crops. Quality can be tracked and steered (see Räsänen in this volume) toward desired standards, using our increasing knowledge of how various cultural practices affect it.

Our ability to model and simulate the growth process, or even limited parts of it, is being increased by the efforts, e.g., on hormone analysis, of many researchers. Model parameters should commend themselves to us as quality criteria because, as our increased understanding of the growth process becomes expressed in such models, these criteria acquire direct meaning in terms of future plantation growth. It will then be possible to set quality standards for untested situations, evaluate the progeny of tree breeding programmes earlier, and weigh the benefits of specific cultural treatments against the cost of achieving them.

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APPENDIX - Definition of symbols

| Symbol | Description | Units ¹ |
|---|--|-------------------------|
| A_l, A_r, A_x | areas of leaf surface (one-sided), root surface, and stem cross-section respectively | m^2 |
| a | maximum value taken by the structural dry weight of a determinate shoot in its first season. Upper asymptote of the logistic growth curve | kg |
| b | lower asymptote of the logistic shoot-growth curve | kg |
| C | CO ₂ concentration | $kg\ m^{-3}$ |
| c | maximum slope of the logistic shoot-growth curve | $kg\ s^{-1}$ |
| Ch | fraction of chilling requirement already met | dimensionless, 0-1 |
| D_i, D_o | water vapor concentration in the substomatal cavities and the atmosphere, respectively | $kg\ vapor\ m^{-3}$ |
| e | base of natural logarithm (2.718) | |
| $f(T), f(T_s), f(T_r)$ | some function of temperature controlling structural growth in the whole plant, the shoot, and root respectively | 0-1 |
| $f(T_p)$ | function of temperature controlling gross photosynthesis | 0-1 |
| $f(\Psi_p), f(\Psi_{ps}), f(\Psi_{pr})$ | function of turgor pressure controlling structural growth in the whole plant, the shoot, and root respectively | 0-1 |
| I | light intensity | $\mu E\ m^{-2}\ s^{-1}$ |
| j | number of primordia in bud | dimensionless |
| K, K_s, K_r | Michaelis-Menten constants for substrate utilisation for structural growth in whole plant, shoot, and root respectively | $kg\ m^{-3}$ |
| k, k_s, k_r | maximum rate of substrate utilisation for structural growth (asymptote of Michaelis-Menten curve), in whole plant, shoot, and in root respectively | $kg\ m^{-3}\ s^{-1}$ |

| | | |
|-----------------------|---|---------------------------------|
| LT_s | lethal low temperature for the shoot | $^{\circ}C$ |
| LH | lethal high temperature | $^{\circ}C$ |
| LV_w | lethal minimum volume of intracellular water, as percentage of volume at full hydration | % |
| m_s, m_r | specific maintenance rate for whole plant, shoot, and root respectively | s^{-1} |
| N | osmolality of cell sap | dimensionless |
| P_g', P_n' | whole-plant gross and net photosynthesis respectively | $kg\ s^{-1}$ |
| P_g | gross photosynthesis per unit leaf area | $kg\ m^{-2}\ s^{-1}$ |
| R | respiration | $kg\ s^{-1}$ |
| R_G | respiration associated with structural growth | $kg\ s^{-1}$ |
| R' | gas constant divided by molecular weight of water (4.619×10^6) | $L\ Pa\ kg^{-1}\ O_K^{-1}$ |
| r | subscript denoting root | |
| S_s, S_g, S_r | concentration of substrate in the plant, the shoot, and root respectively | $kg\ (m^3\ fresh\ tissue)^{-1}$ |
| s | subscript denoting shoot | |
| T, T_e | air and soil temperature, respectively | $^{\circ}C$ |
| $T_{s\ opt}$ | optimum temperature for structural growth of shoot | $^{\circ}C$ |
| $T_{c\ opt}$ | optimum temperature for chilling to break dormancy | $^{\circ}C$ |
| T_{sr} | rate of transport of substrate from shoot to root | $kg\ s^{-1}$ |
| t | time | s |
| U_s, U_r | utilisation of substrate for structural growth by whole plant, shoot, and root respectively | $kg\ s^{-1}$ |
| V_s, V_r | fresh tissue volumes (full hydration of whole plant, shoot, and root respectively) | m^3 |
| V_w, V_{ws}, V_{wr} | intracellular water volume of whole plant, shoot and root respectively | m^3 |

| | | |
|------------------------------|---|--|
| VPD | vapor pressure deficit | kPa |
| W_G, W_{GS}, W_{Gr} | structural dry weight of whole plant, shoot, and root respectively | kg |
| W_S, W_{SS}, W_{Sr} | weight of substrate in whole plant, shoot, and root respectively | kg |
| Y_G, Y_{GS}, Y_{Gr} | substrate \rightarrow structure conversion efficiency for whole plant, shoot, and root respectively | 0-1 |
| α | Photochemical efficiency | $\text{kg } \mu\text{E}^{-1} \text{ s}^{-1}$ |
| β | photorespiration constant | $\text{kg m}^{-2} \text{ s}^{-1}$ |
| $\delta, \delta_s, \delta_r$ | reflection coefficient for whole plant, shoot, and root respectively | 0-1 |
| ϵ | bulk elastic modulus of fully hydrated tissue | kPa |
| θ | slope of elastic modulus - turgor pressure regression | dimensionless |
| σ_s | parameter controlling width of structural-growth-versus-temperature curve | $^{\circ}\text{C}$ |
| τ | leaf conductance to CO_2 | m s^{-1} |
| τ_c | stomatal conductance to CO_2 | m s^{-1} |
| τ_l | stomatal conductance to water vapor | m s^{-1} |
| τ_s, τ_r | hydraulic conductance of stem and root respectively | $\text{m s}^{-1} \text{ kPa}^{-1}$ |
| τ_{xc} | hydraulic conductance of symplast-to-apoplast pathway | $\text{m}^3 \text{ s}^{-1} \text{ kPa}^{-1}$ |
| ψ_e, ψ_l, ψ_r | water potential of soil, leaf, and root respectively | kPa |
| $\psi_c, \psi_{\pi}, \psi_p$ | cell water potential, cell sap osmotic potential, and cell turgor pressure respectively | kPa |

¹ masses refer to glucose unit equivalents