Modelling Stem Height and Diameter Growth in Plants

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A model of stem height and diameter growth in plants is developed. This is formulated and implemented within the framework of an existing tree plantation growth model: the ITE Edinburgh Forest Model. It is proposed that the height:diameter growth rate ratio is a function of a within-plant allocation ratio determined by the transport-resistance model of partitioning, multiplied by a foliage turgor pressure modifier. First it is demonstrated that the method leads to a stable long-term growth trajectory. Diurnal and seasonal dynamics are also examined. Predicted time courses over 20 years of stem mass, stem height, height:diameter ratio, and height:diameter growth rate ratio are presented for six treatments: control, high nitrogen, increased atmospheric carbon dioxide concentration, increased planting density, increased temperature and decreased rainfall. High nitrogen and increased temperature give initially higher stem height:diameter ratios, whereas high CO₂ gives an initially lower stem height:diameter ratio. However, the responses are complex, reflecting interactions between factors which often have opposing influences on height:diameter ratios, for example: stem density, competition for light and for nitrogen; carbon dioxide and decreased water stress; rainfall, leaching and nitrogen nutrition. The approach relates stem height and diameter growth variables via internal plant variables to environmental and management variables. Potentially, a coherent view of many observations which are sometimes in apparent conflict is provided. These aspects of plant growth can be considered more mechanistically than has hitherto been the case, providing an alternative to the empirical or teleonomic methods which have usually been employed.

Key words: Plant, stem, height, diameter, growth, model, forest, plantation, trees.

INTRODUCTION

The height and diameter growth of plant stems are of wide concern to agronomists, foresters and agro-foresters who are pursuing practical and economic problems, to ecologists and ecophysicists interested in climate and environment, and to evolutionary theorists and ecosystem modellers who are constructing mathematical representations for general and specific applications. Many studies of stem height and diameter growth have focused strongly on trees and forests, where these relationships are economically important, rather than on plants of agricultural importance, although in the latter area breeding plants which retain short stems under well-fertilized conditions has been a very significant and highly successful activity.

My principal objective here is to construct a mechanistic submodel of stem height and diameter growth in plants based on internal plant variables, rather than depending directly on environment and management variables. This should give a unified view of what sometimes appears dauntingly complex—the responses of height and diameter growth to nitrogen, CO₂ concentration, temperature, rainfall and planting density. Moreover, the submodel must be suitable for use in what is perhaps the most common type of crop and plant growth simulator: these simulators use aggregated biochemical categories where plant dry mass is divided into structure and substrates/storage, and where organs are similarly grouped into ‘foliage’, ‘stem’, ‘coarse roots’ etc. The plant stem height:diameter growth submodel can only be constructed and evaluated within the context of a plant simulator: for this purpose I use the ITE Edinburgh Forest Model (henceforth, EFM). The EFM takes account of all pools and fluxes of C, N and water in a fully coupled soil-plant-atmosphere system; it uses a within-day time-step, and various management options, such as fertilizer application and thinning, can be applied. The EFM provides a suitable framework which has been documented, applied and validated over some years (Thornley, 1991; Thornley and Cannell, 1992, 1996). This account of the problem is therefore centred on trees and forest plantations, although the method is equally applicable to grassland or other plants.

Three principal modelling approaches to quantifying and predicting height and diameter growth have been employed, which may be described as empirical, teleonomic, and mechanistic. Empirical allometric equations for tree height-diameter-mass relationships have been widely used (Ogawa and Kira, 1977; Cannell, 1984; West et al., 1991; Sumida, Ito and Isagi, 1997; see Causton, 1985, for a review). Typical examples are

\[ M_{SN} = c_l d_{stem}^3, \quad M_{SH} = c_g (h_{stem} d_{stem}^2)^{1/3} \]

(1)

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where $M_s$ (kg structural dry matter per stem), $h_{stem}$ (m) and $d_{stem}$ (m) are stem dry mass, height and diameter; $c_1$, $c_2$, $q_1$ and $q_2$ are constants that are specific to each species and situation. These models often give a good description of a limited range of experimental data, but they usually fail to account for the complexity of the observed responses to environment and management when a wider range of treatments and conditions is applied.

The second category of investigations of tree height, diameter and dry mass relationships is based on concepts of teleonomy or purpose. In the teleonomic approach the capacity to perform some function is optimized. An early paper by Patridge (1973) considered the photosynthesis per unit ground area averaged over the lifetime of the trees. McMahon (1973), Mattheck, Bethge and Erb (1993) and many others have studied mechanical criteria. The pipe-model theory of tree form proposed by Shinozaki et al. (1964) has been applied by e.g. Valentine (1985) and Maäkäli and Sievänen (1992) have examined a strategy which balances self shading with structural costs in determining height growth. Ludlow, Randle and Grace (1990) give a useful discussion of the determinants and benefits of height growth.

A teleonomic model requires three layers of contingent assumptions: first, an optimum function (goal) whose choice may appear plausible but which is often rather subjective; second, evolutionary pressures exist to fulfill the goal; and third, there are mechanisms which can fulfill the teleonomic goal and are accessible by adaptation. Doubt has been expressed as to whether teleonomic thinking is sound scientific methodology (Monod, 1974). When a teleonomic submodel fails, as all models do eventually, there seems no logical way forward other than by ad hoc adjustment. In some areas mechanistic (non-goal-seeking) models appear to give optimized responses without being constrained to do so [e.g. allocation (Makela and Sievänen, 1987); phyllotaxis (Thornley and Johnson, 1990)]. This may also be true for height and diameter growth in trees. Finally, because goals can only be achieved by means of mechanisms, and because a mechanistic model permits step-by-step elaboration and refinement as theory and experiment improve, it seems preferable to proceed mechanistically. A mechanistic model.
can sometimes be simplified and approximately interpreted in goal-seeking terms.

I am not aware of any mechanistic models of height growth in trees. Ludlow (pers. comm.), in an unpublished review of C and N allocation in Sitka spruce, outlined an approach comparable to that used here when he suggested that: ‘The rate of shoot extension and xylem formation… be made to depend on carbohydrate availability…’. More recently, and closely related to our approach, Deleuze and Houllier (1997) have proposed a very interesting model of tree ring width growth which is substrate-driven with transport resistances along the stem. Their model predicts a strong relationship between morphology and foliage: root allocation, which is similar to the basis of the present model. However, in their model, stem height is assumed to be constant, and also, the treatment of the stem profile, using partial differential equations, is too detailed for our purpose, which focuses on the relation between stem height and mean stem diameter. Nevertheless, Deleuze and Houllier’s (1997) approach, using internal tree variables, with ‘free’ or objective equations, offers a promising route for further development. We explore here the extent to which some simple assumptions, along the lines of Ludlow’s suggestions (see above) and Deleuze and Houllier’s work (1997), can ‘explain’ observed responses. Since the submodel is to be part of a plant ecosystem simulator, simplicity is important; but equally, the submodel must have one of the prime virtues of a mechanistic submodel—that of being open to rational modification and extension when it is found to fail.

The responses of interest concern the dynamics of stem height, diameter and mass, and how these are affected by environmental and management variables such as nitrogen fertilization, atmospheric CO$_2$, planting density, temperature, and water. The version of the EFM used here is not thinned during the 20-year growth period examined. Only the relations and equations pertinent to the current investigation are described. These equations, suitably adapted, could be incorporated into other mechanistic plant growth models of the same genre.

The traditional view of plant morphogenesis is that plant form results from cellular activities, such as cell shape and planes of cell division, and these may be controlled by plant morphogens, possibly mediated by factors such as phytochrome. However, there is evidence to support the idea that plant form is a result of the differential growth of parts of the plant, and that this constrains cellular activities (Adler, 1974; Kaplan and Hagemann, 1991; Cooke and Lu, 1992). It is easier to represent the latter view in a plant growth model, and arguably the differential-growth approach may account for many interesting morphological responses. We therefore make no attempt to represent plant morphogens or their possible effects on cellular-level activities. Such considerations could be added to the currently proposed framework if and when it is found to be inadequate.

Shoot extension has been widely researched, and it is known that relevant factors can be nutrient status (Mooby and Bestord, 1983), turgor pressure (Van Volkenburgh, Hunt and Davies, 1983), hormones (Thomas et al., 1981), light quality and quantity (e.g. Lesgrove and Green, 1981; Jones, 1992) and temperature. These factors can interact in a complex manner which is not fully understood—for instance, temperature affects nutrient status, turgor pressure and usually all rate constants in the system; light may influence nutrient status but may also change hormone levels. Smith, Casal and Jackson (1990) suggested that phytochrome can enable plants to detect the proximity of neighbouring vegetation, a mechanism which could be important in forest plantations but which is ignored here.

We use internal plant variables taken from within the tree submodel of Fig. 1, supplemented by a water submodel for the soil-plant-atmosphere system (see for example Fig 6.1 of Thornley, 1998b) which calculates water potential and its components in the tissue boxes of Fig. 1. These internal variables are assumed to determine the stem height:diameter growth rate ratio. The effects of the environment only operate through the internal variables, and not directly. While this restricts the scope of the height:diameter submodel which can be constructed, it provides a valuable focus and constraint, ensuring that the submodel can be incorporated into, and evaluated within, a common type of plant growth simulator.

THE MODEL

The tree submodel of the EFM is shown in Fig. 1. The core plant submodel is described in Thornley (1991). One extra foliage pool (‘photosynthetic N’) has been added to the plant submodel to give photosynthetic acclimation to light, nitrogen, CO$_2$ and temperature (Thornley, 1998c). More important to the present application is the addition of soil and water submodels (Thornley, 1998b). The soil submodel describes C and N cycles in the plant-litter-soil system, including mineral N pools, a soluble C pool, biomass and soil organic matter (SOM) pools. The processes represented are competing N uptake by roots and biomass, C and N exudation, C and N leaching, volatilization, nitrification, denitrification, respiration, mineralization, immobilization, and SOM transformations. The water submodel considers water pools and fluxes in the soil-plant-atmosphere system; it is driven by the Penman-Monteith equation with water flow down gradients of water potential. It is similar to the model of Williams et al. (1996), but uses a variable capacitance with elastic cell walls. Within the plant, the osmotic and pressure components of water potential, with relative water content, are calculated for the root and the shoot. The two submodels for soil and water are important in modulating the responses of the plant submodel in Fig. 1.

The representation of Fig. 1 gives good predictions of allocation between the different tree compartments, based on the variables shown for aggregated biochemical categories. Deleuze and Houllier (1997) found ‘a strong relationship between morphology and foliage: root allocation’, and we use this same level of description to construct a model of stem height and diameter growth. That is, those factors which determine differential mass growth (i.e. allocation) also determine the relationship between stem height and diameter growth, with a modifier for turgor pressure. Here just the equations relevant to the growth of stem dry mass (DM), height and diameter are given.
Stem growth

The differential equation determining growth of stem structural DM \([M_{sx}] (kg \text{ structural } DM \text{ per stem})\) is given approximately by:

\[
\frac{dM_{sx}}{dt} = f_{\text{full}} k_{GM,s,20} A_{stem}(C_sN_s)^2
\]

Here \( t \) is the time variable (d). \( f_{\text{full}} \) is a dimensionless function of air temperature with value unity at 20 °C (figure 3.6, cubic, T. Thornley, 1998b). \( C_s \) and \( N_s \) are the C and N substrate concentrations in the stem meristem, with units of kg C, kg N substrate (kg stem meristem structural dry matter)^{-1} [see eqn (9a) of T. Thornley, 1991]. \( C \) and \( N \) denote units of substrate concentration, e.g. kg substrate C, N (kg structural dry matter)^{-1}. \( k_{GM,s,20} \) is a stem meristem growth rate constant at 20 °C. \( A_{stem} \) is a constant describing the dependence of meristem dry mass on stem surface area \((A_{stem})\) and stem nutrient status \((C_sN_s)\).

Equation (2) has been simplified for presentation here, in order that an explicit equation for the rate of growth of stem structural DM can be written down. The details of this simplification are unimportant; the important relationships define how the stem structural DM growth is partitioned between height growth and diameter growth.

Obligate relationships between stem growth and height and diameter growth

Some equations must be satisfied to meet the requirements of geometry and conservation. Variable stem shape factors are ignored (but see Dewar, 1993; Deleuze and Houllier, 1997). Assuming that the stem is cylindrical with height \(h_{stem}(m)\) and a constant diameter \(d_{stem}(m)\), stem volume \(V_{stem}(m^3)\) is given by

\[
V_{stem} = \frac{\pi}{4} d_{stem}^2 h_{stem} = \frac{M_{sx}}{\rho_{stem}}
\]

Where \( \rho_{stem} \) is the stem structural dry mass density. Taking logarithms of each side of \( M_{sx} = \varphi_{stem} h_{stem} d_{stem}^2 \) and differentiating with respect to time \( t \) gives:

\[
\frac{1}{M_{sx}} \frac{dM_{sx}}{dt} = \frac{1}{h_{stem}} \frac{dh_{stem}}{dt} + \frac{2}{d_{stem}} \frac{dd_{stem}}{dt}
\]

The ratio of the instantaneous height and diameter growth rates is denoted by:

\[
\lambda_{h/d} = \frac{\frac{dh_{stem}}{dt}}{\frac{dd_{stem}}{dt}}
\]

Stem height and diameter growth

I assume that there are two factors determining the height:diameter increment ratio of eqn (5): (1) relative ‘nutrient’ status, for which meristem specific growth rates are a surrogate; and (2) water status at the top of the stem, for which foliage pressure (turgor) potential is used. The gross specific growth rates of the meristems of foliage \((l)\) and stem \((s)\) are \(\mu_{M,l}, \mu_{M,s} (d^{-1})\), with [T. Thornley 1991, eqns (3a), (9b)]

\[
\mu_{M,l} = k_{GM,l,20} C_l N_l
\]

\[
\mu_{M,s} = k_{GM,s,20} C_s N_s
\]

\( k_{GM,l,20} \) and \( k_{GM,s,20} \) are 200 [(C) (N) d]^{-1} \( k \) is a rate parameter at 20 °C for growth of meristem in foliage and stem. Temperature and water-status modifiers are omitted from eqn (8) for simplicity (T. Thornley, 1998b).

The gross specific growth rate of a meristem depends on its nutrient status \((= \text{ the product of } C \text{ and } N \text{ substrate concentrations})\), and this determines plant form.

The ratio of these two gross specific growth rate constants is:

\[
r_{M,l/s} = \frac{\mu_{M,l}}{\mu_{M,s}}
\]

This ratio depends [eqn (8)] on the relative nutrient status in the foliage \((C,N_l)\) and the stem \((C,N_s)\). The local nutrient status is an important factor in the transport-resistance model of allocation (T. Thornley, 1998a), and here the concept...
is extended by assuming that a nutrient status ratio also determines the ratio between height growth and diameter growth.

The main determinant of the ratio of height to diameter growth rates [eqn (5)] is assumed to depend on the meristem activity ratio of eqn (9) according to

\[
\lambda_{h/d,G} = \frac{r_{h/d,\text{min}} + r_{h/d,\text{max}}(r_{M,l/s})_{h/d,G}}{1 + (r_{M,l/s})_{h/d,G}} \quad (10)
\]

There are three parameters in eqn (10): the minimum and maximum values of \( \lambda_{h/d,G} \), obtained at \( r_{M,l/s} = 0 \) and \( \infty \), and a steepness parameter \( q_{h/d,G} \), which alters the steepness of the response in the middle range, and could be used to amplify the response. This equation is drawn in Fig. 2 for three values of the parameter \( q_{h/d,G} \). The meristem activity ratio [eqn (9)] predicted by the EFM is found to vary over the range 0–5 to 1–5, under the conditions applied below.

Following Lockhart’s suggestion (1965) that a minimum turgor pressure is required for cell wall extension to occur, with a strong dependence of extension on the excess turgor pressure, I assume that foliage pressure potential, \( \psi_{P,l} \) [J (kg water)\(^{-1}\)], modifies the height:diameter growth ratio multiplicatively by the factor:

\[
j_{h/d,P,l} = \frac{\psi_{P,l}}{K_{P,l}^{1/2} + \psi_{P,l}^{1/2}} \quad (11)
\]

With adequate water availability and a high turgor pressure, this modifier equals unity, falling to 0.5 when \( \psi_{P,l} = K_{P,l}^{1/2} \).

Most tree physiologists would agree that height growth limitation in trees is the result of water stress at the top of the tree. Here it is assumed that there is a differential effect of water stress on height and diameter growth, affecting the former more than the latter. The plausibility of this assumption may be addressed at the cell level (see Discussion), as well as observing that height growth and diameter growth seem to be at least partially independent processes, spatially and perhaps also temporally. However, in young trees and other plants which are well supplied with water, it seems unlikely that water stress can play a significant role in determining height and diameter growth.

The final expression used for the instantaneous ratio of the height and diameter growth rates [eqn (5)] is obtained by multiplying the nutrient status expression of eqn (10) with the turgor modifier of eqn (11):

\[
\lambda_{h/d} = \lambda_{h/d,G}j_{h/d,P,l} \quad (12)
\]

Height and diameter growth are then calculated with eqn (6). The nutrient status factor is operative under all conditions, reflecting the great plasticity of root:shoot ratios in plants, whereas the turgor modifier is important only under conditions of foliage water stress, which includes trees approaching their limiting height.

**SIMULATIONS**

The model is programmed in the continuous system simulation language, ACSL (Mitchell and Gauthier, 1993). The program for the EFM is available by using a file
The growth rate ratio is calculated from the annual increments in height and diameter. The height: diameter growth rate ratio [Fig. 3D, eqns (5) and (12)], calculated by integrating height and diameter separately over successive years, is immediately stable within 2%—i.e. like stem mass, it is little affected by the initial height: diameter value. During the first 5 years of growth, stem height (Fig. 3B) is affected by the initial h:d value, as is the height: diameter ratio (Fig. 3C). However, after about five years, the height and h:d trajectories (Fig. 3B and C) are not much changed by the initial values.

**Diurnal and seasonal changes in height and diameter growth**

The model is driven by diurnally changing light, air temperature and humidity, and seasonally changing light, daylength, air and soil temperatures, humidity and rainfall. This gives rise to the diurnal and seasonal changes in height growth rate and height: diameter growth rate ratio shown in Fig. 4.

Figure 4A illustrates the diurnal response for 3 d in April. The height growth rate is responding mostly to the changing air temperature, with a small (approx. 3%) modulation of the height: diameter growth rate ratio arising from diurnal changes in substrate concentrations. In the model, it is assumed that foliage and stem [the two components of eqns (8) and (9)] are both at air temperature.
Effect of five treatments on height growth and height:diameter ratios

Relative to the standard ‘control’ environment, five treatments have been simulated: (1) nitrogen deposition is increased from 20 to 200 kg N ha\(^{-1}\) year\(^{-1}\) (+nitrogen); (2) ambient CO\(_2\) concentration is increased from 350 to 700 vpm (+CO\(_2\)); (3) planting density is increased from 0.25 to 1
stems m⁻² (+nstems); (4) air and soil temperatures are increased by 3 °C (+T); and (5) rainfall is decreased by 75% (-water). The 20-year trajectories occurring in these treatments are illustrated in Fig. 5. To help interpret Fig. 5, some pertinent variables are provided in Fig. 6.

It can be seen in Fig. 5A and B that applying +nitrogen, +temperature and +CO₂ all lead to increases in stem mass and stem height whereas +nstems and −water decrease both quantities. However, in the first 13 years, −water increases stem mass and height very slightly; this is due to decreased leaching and improved N nutrition (Fig. 6B and C) opposing the effects of increased water stress. The effects of the treatments on the two ratios of Fig. 5C and D are much more complex, suggesting that there are no simple answers to questions like ‘What is the effect of...’. The answer depends on the particular conditions of the experiment and the time scale.

Increased N increases the height:diameter ratio (Fig. 5C and D), although the higher LAI leads to early (relative to the control) water stress, stomatal closure (Fig. 6A) and decreased foliage turgor (Fig. 6D), which decreases the height:diameter growth rate ratio [eqn (11)].

Increased temperature produces increased growth (Fig. 5A and B) and increased height:diameter ratio (Fig. 5C and D), although these increases are partly due to increased mineralization and higher mineral N concentrations (Fig. 6C). After about five years, the increased water stress (Fig. 5A and D), the increased system N losses (Fig. 6B) and the resulting decreased soil mineral N (Fig. 6C), all combine to depress the height:diameter ratio (Fig. 5C).

Increased CO₂ increases growth (Fig. 5A and B), but decreases the height:diameter ratio (Fig. 5C). However, after some years, the decreased water stress (Fig. 6A and D), the decreased N losses and relative increases in soil mineral N (Fig. 6B and C), lead to steadily increasing height:diameter ratios (Fig. 5C and D).

Increased planting density in this case gives rise to competition for N before competition for light. Stem height (+nstems) keeps pace with the control for the first 5 years (Fig. 5B), but by then soil mineral N is appreciably depleted (Fig. 6C), and the height:diameter growth rate ratio is decreasing accordingly (Fig. 5D). Increased water stress (Fig. 6A and D) is also a factor in decreasing height growth.

Decreasing rainfall produces three effects, as noted earlier. Decreased leaching (Fig. 6B) gives improved soil mineral N (Fig. 6C) which enhances height:diameter ratio. Decreased foliage turgor (Fig. 6D) gives decreased height:diameter ratio. This can be partially offset by decreased stomatal conductance (Fig. 6A) causing decreased photosynthesis which increases height:diameter growth ratio.
DISCUSSION

In the model described above, a minimum hypothesis has been proposed in order to determine the scope of the effects predicted. The relative responses in Fig. 5 seem qualitatively reasonable. Their magnitude could be increased by assuming higher values of the parameter $q_{h/d,G}$ of eqn (10), or changing the parameters of eqn (11). The approach proposed can be divided into two parts for consideration. Equations (10) and (11) are clearly quite subjective and could be modified in many ways: with different equation forms, different components of metabolic activity or water potential, as well as different parameter values. A different forest model would require its own surrogates for these quantities. However, the analysis from eqn (3) to eqn (6) is relatively model-free, that is, applicable to all models. This suggests that these equations can be used in general for attacking the height:diameter problem, even if the particular implementation here [eqns (10) and (11)] with the Edinburgh Forest Model (EFM) does not seem appropriate. Indeed, in so far as I have tried different formulations of eqns (10) and (11), the method appears pleasingly robust.

It is assumed that the stem is cylindrical: see eqn (3) and above. This assumption could be relaxed by taking (say) a negative exponential dependence of stem diameter ($d_{stem}$) on stem height ($h_{stem}$):

$$d_{stem} = d_{stem,0}e^{-qh_{stem}} \quad (13)$$

where $\gamma$ ($m^{-1}$) is a taper factor and $d_{stem,0}$ (m) is the base diameter. Stem volume then becomes [cf. eqn (3)]:

$$V_{stem} = \frac{\frac{1}{4} \pi d_{stem}h_{stem} (1 - e^{-qh_{stem}})}{2\gamma} \quad (14)$$

The analysis from eqns (3) to (6) is no longer possible unless $\gamma$ is assumed to be small. It seems doubtful that the method proposed can be applied to situations where stem shape is a significant factor, at least, in its present formulation.

The height:diameter submodel operates using the values of current internal tree variables. Although these are influenced to an extent by the past environment, including that of the previous year, in the EFM as currently structured, this connection is weak. In some species, height growth depends mainly on the growing conditions of the previous year (e.g. during August to October for some pines) whereas the radial increment is mostly sensitive to the current environment. The model may therefore not always perform well in relation to yearly predictions where there is substantial year-to-year variation in the environment, and where seasonal memory effects are pronounced.

Our assumption that height:diameter growth ratio depends on nutrient status can be argued for in several ways. The effects of say nitrogen fertilization or CO$_2$ enrichment, which affect nutrient status and plant morphology in different ways, are well-documented (e.g. Moorby and Besford, 1983; Newton, 1991): usually (loc. cit.), nitrogen
fertilization promotes height growth, whereas increased CO$_2$ promotes diameter growth. At the level of the single cell, it has been found that in _E. coli_ and _Pseudomonas putida_ both cell size and shape depend on growth rate and nutrient supply (Domach et al., 1984; Givskov et al., 1994).

In plant cells it has been observed that the planes of cell division respond to growth conditions (Lyndon, 1976; Yeoman, 1996). Another possible rationale is that height growth results more from metabolism in the region of the top of the stem (see also Ludlow et al., 1990; Mäkelä, 1990), for which foliage meristem activity is a surrogate, in relation to diameter growth which occurs over the whole length of the stem, including the base of the stem, for which stem meristem activity is a surrogate. However, whatever the strength or otherwise of plausibility arguments, our assumption is only justified if it gives a helpful description of tree growth. There may be other internal tree variables which can fulfil this purpose as well as or even better than those chosen in eqns (8) to (12). Also, it is assumed here that the stem is cylindrical, with a constant height:diameter ratio. This assumption precludes easy comparison of model predictions with field data.

Lockhart (1965) proposed the concept that a minimum turgor pressure is needed for cell wall extension to occur, that is, to be ‘switched-on’. Boyer (1968, Fig. 4) examined the relationship between an externally applied pressure and the specific area growth rate of a sunflower leaf. Boyer’s results suggest that a turgor pressure potential of about 150 J (kg water)$^{-1}$ (0.15 MPa = 1.5 bar) is needed to initiate cell wall extension. Bunce (1977) however found a linear relationship between elongation rate and turgor pressure above a threshold value for soybean leaves. Thus turgor pressure may alter the balance between cell extension (possibly height growth) and cell wall thickening (possibly diameter growth). Equation (11) describes the dependence of height:diameter growth rate ratio on turgor pressure ($P_{\text{tr}}$) assumed here. This is a ‘phenomenological’ equation with parameters whose values have been chosen to give satisfactory operation in the context of the water submodel used in the EFM (Thornley, 1998b). It may be noted that increasing CO$_2$ or increasing N can, under different conditions, either increase or decrease turgor (Fig. 6D).

Phytochrome and light quality have been shown to be related to morphogenesis and stem extension (e.g. Smith, 1981). Another possible modification of eqn (12) for height:diameter growth rate ratio is to introduce a morphogen-dependent factor, whose level depends on light quality. This could be needed if the responses of the currently suggested model to planting density are found to be unsatisfactory. However, an additional submodel describing the synthesis, degradation and possibly the within-plant transport of a morphogen, with its dependence on environmental and plant variables, and its morphogenetic effect, would be a considerable addition to the EFM.

‘Validation’ is still a contentious issue with many biologists, although at last, arguably, its appeal is beginning to diminish, following difficulties with model validation across the whole spectrum of science (e.g. Hopkins and Leipold, 1996). Statistical models, which make contact with reality at few points, and where parameters are unconstrained by scientific principles, can often be shown to work satisfactorily within a given arena. Without doubt this can be a useful matter to demonstrate. Mechanistic simulators, with their multiple and variously weighted objectives, are another proposition entirely. ‘Evaluation’ is then a more helpful term than ‘validation’, allowing a more flexible view of the ingredients of the model to be taken, as well as a more sympathetic tasting of the resulting dish. At the qualitative level, the height:diameter model behaves reasonably. At the quantitative level, an experiment which would allow a meaningful comparison with observational data has not yet been performed. Indeed, such an experiment and comparison would be a massive undertaking, and of doubtful value (Hopkins and Leipold, 1996).

There are, inevitably, some quite important features missing from the height:diameter growth model as currently proposed, as have already been mentioned. No models would be constructed at all if it were not acceptable to build models which only tell part of the story. Any explanation must stop somewhere, leaving an unexplained residue. The scope of a model is always limited. The predictions of a model are always approximate. The failure of a model will usually indicate how that model needs to be changed and perhaps extended. A simple model can be valuable for indicating, or contra-indicating, the utility of a general approach. This has been an important aim in this investigation.

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**LITERATURE CITED**


