

How will climate change affect the way trees allocate carbon to root and shoot?

A R Ludlow & E M Atkinson

Email: info@modelresearch.com

July 16, 2003

Many species of conifer have clear phases of shoot and root growth (Lanner, 1976; Pollard and Logan, 1977; Dougherty, Whitehead and Vose, 1993) and any change in climate which alters the length of each phase is likely to alter the root shoot ratio, with effects on forest respiration and photosynthesis. Hence, we need accurate estimates of root and shoot growing periods to predict growth in a changing environment but most models of carbon and nitrogen allocation in trees do not take account of seasonal phases of growth (eg. Thornley, 1991). In this report we have reanalysed a detailed study of Sitka spruce (*Picea sitchensis*) by McWilliam (1972) which suggests strong links between shoot extension and xylem growth, and between root growth and the formation of next year's buds. The analysis provides a framework for building future models.

McWilliam described the sequence of growth in 22-year-old Sitka spruce trees in Fetteresso Forest, Scotland. His data for 1970 are summarised in Fig. 1 which shows that:

1. budburst was synchronised throughout the tree in the second week in May;
2. the growing season ended throughout the tree in the second week in October;
3. there were two phases of shoot growth. In the first, the previous year's buds expanded to form new shoots. Extension then gave way to a phase in which next year's bud was formed by laying down needle primordia. The switch was latest in the leading shoot, earliest in the lower branches. Such 'determinate growth' is common among conifers, but McWilliam went on to show that
4. xylem cell division was closely synchronised with shoot extension at all levels in the crown (Fig. 1). They started together at bud burst, throughout the tree, and ended together at any one height.
5. elongation of fine roots (and to some extent, phloem growth) was suspended during the phase of shoot extension.

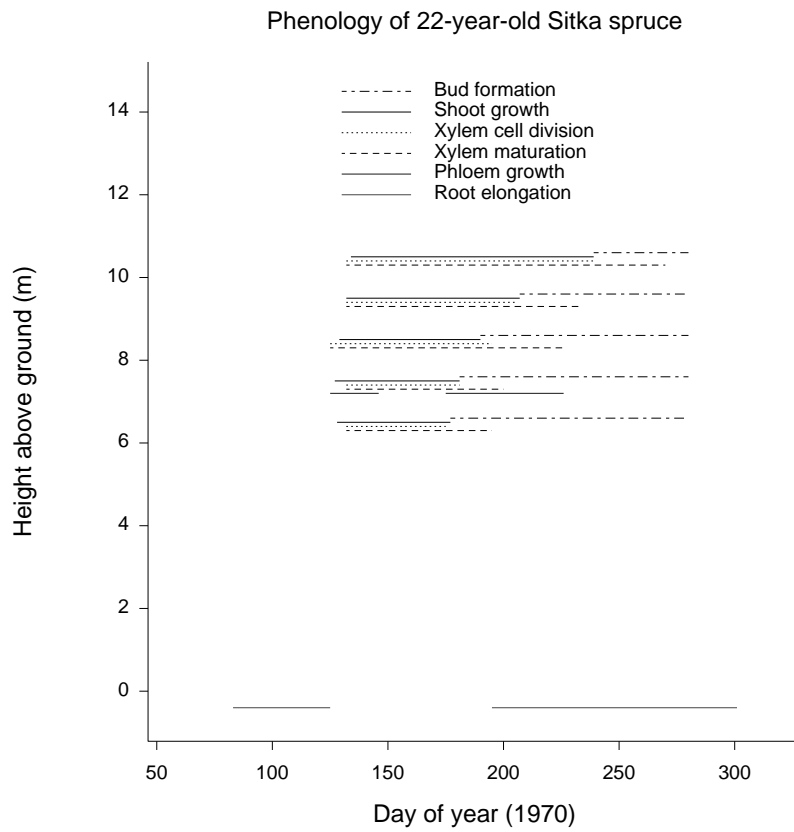


Figure 1: The seasonal pattern of growth in 22-year old Sitka spruce in Feteresso forest, Scotland (abstracted from McWilliam (1972)). Each cluster of lines shows the growth of tissues at a particular height down the tree: 10.5, 9.5, 8.5, 7.5, 6.5 m and fine roots. Within each cluster the lines are in the same vertical order as the key

Figure 1 compares shoot extension and xylem cell division in the same shoots, but McWilliam made some observations along the branch and, summarising his results, he concluded that:

Initiation of expansion of the needles precedes initiation of shoots which precedes formation of xylem in the branches subtending the shoots which precedes formation of xylem in the trunk. Similarly, cessation of needle expansion precedes cessation of shoot elongation which precedes cessation of xylem formation in the branches and in the trunk. This indicates that there may be a stimulus manufactured in the expanding leaves which in turn stimulates shoot elongation and xylem formation as it is transported basipetally.

We argue here that the pattern of changes observed by McWilliam matches what is now known about the transport and effects of auxins (Salisbury and Ross, 1992) although the evidence is all circumstantial.

Auxins are thought to be produced in expanding leaves, from which they spread basipetally. They stimulate elongation of stems (shoot extension) and division of cells in the vascular cambium (xylem cell division) *and* they are known to inhibit root *elongation*, although they promote the development of root initials and of adventitious roots. McWilliam's chronology supports three of these effects. Shoot extension and xylem cell division were synchronised in individual shoots and root elongation ceased at bud-burst.

More recently, Millard and Proe (1989; 1991) have described the pattern of root growth in Sitka spruce seedlings receiving high or low nitrogen treatments. With high nitrogen there was pronounced foliage growth (presumably accompanied by auxin production) and the roots were short, many-branched and thickened. With low nitrogen, the roots were longer, less branched and unthickened. That pattern is consistent with the hypothesis that a secondary effect of nitrogen fertilisation is auxin production in new foliage, and that this inhibits root elongation but it promotes root initials and xylem cell division in the woody roots.

What is known of the transport of auxins is also suggestive. In other plant species, they are known to be transported basipetally through cells next to the vascular cambium (Salisbury and Ross, 1992). They appear not to move in the phloem and their rate of movement has been measured between 5 and 15 mm h⁻¹ (Wareing and Phillips, 1981, p. 107–109). McWilliam did not record the rate of spread of xylem activity, but Denne (1979) observed a similar spread of tracheid formation down the branches and trunk and the rate of spreading was about 8 mm/h which is comparable to the measured flow of auxins.

Modellers have fought shy of plant hormones because it is difficult to quantify their effects, and de Wit and Penning de Vries (1983) have argued that it is better to model the message than the signalling system. In many respects that is true, and we shall be arguing that the correlations that McWilliam observed help in calculating the duration and rates of phases of growth. Nevertheless, it is hard to understand the message unless we understand the pattern of effects of each hormone. Such a clear picture is not yet available but “there is now

conclusive evidence that one thing plant hormones do is control gene activity” (Salisbury and Ross, 1992) and it seems dangerous to leave hormones or seasonal changes in growth out of our calculations.

1 A framework for modelling growth

Whatever the mechanisms, McWilliam’s observations imply that growth occurs in clear phases and that, *for modelling purposes, we need to know what influences the timing of growth.*

Figure 2 links these observations into a framework for modelling growth and allocation. Four processes are considered: shoot extension, xylem growth, formation of next year’s bud, and fine-root growth, and the framework is based on the following hypotheses.

1. The outcome of each process is the product of its duration and its rate.
2. McWilliam’s observations make it simpler to calculate the duration of each process because:
 - (a) The durations of shoot extension and xylem cell division are the same.
 - (b) The number of primordia in each bud, at the start of the year, has a strong influence on duration of shoot extension and hence on length of shoots and number of new tracheids in the xylem.
 - (c) The time left to form next year’s bud, after shoot extension, depends on the length of the growing season.
 - (d) The start of the growing season depends mainly on winter and spring temperatures and is likely to be affected by climate change
 - (e) The end of the growing season depends more on photoperiod and should be less affected by climate change.
 - (f) Root elongation, too, seems to be suspended during shoot extension, so its duration is inversely related to that of shoot extension.
3. The outcomes of synchronised processes, such as shoot extension and xylem cell division, are likely to be correlated because their durations will vary together from year to year and outcome is the product of duration and rate (1. above).
4. Accurate predictions of growth depend on identifying the factors which affect the rates of each of these processes.

In the remaining sections we review experimental evidence in the light of these hypotheses.

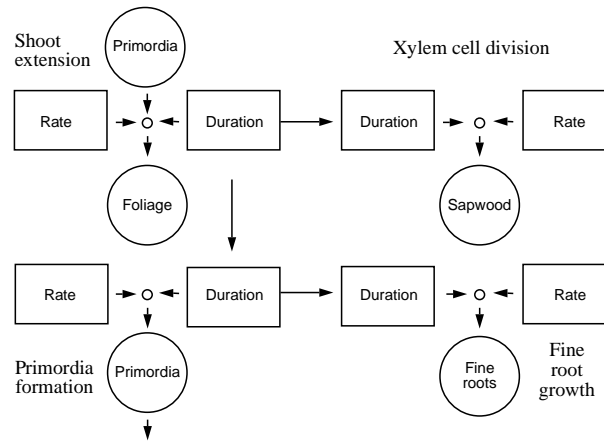


Figure 2: A framework for modelling seasonal growth in Sitka spruce

2 Onset of growth in the spring

McWilliam (1972) found that, during the winter, all tissues were dormant, but the fine roots started growing in March. They continued until budburst which occurred in the second week of May, throughout the tree. Numerous authors have studied the breaking of winter dormancy (Cannell, 1990) and Kramer (1992) has reviewed eight models for predicting bud burst. For example, it can be predicted as the date at which

$$T = a + be^{rC} \quad (1)$$

(Murray, Cannell and Smith, 1989) where T is thermal time measured in degree days above 5°C since 1st January, C is the number of chill days below 5°C since 1st November while a , b and r are parameters: $a = -56$, $b = 602$, and $e^r = 0.991$ for Sitka spruce in Scotland (Murray *et al.*, 1989).

A similar equation could be used for the start of root growth although there are few data with which to estimate parameters (Keinholtz, 1934).

3 The end of the growing season

The end of the growing season has been studied most in seedlings showing free growth (e.g. Burley, 1966) and is believed to be under photoperiodic control, modified by temperature, water stress and mineral nutrients (Cannell, 1990). The end of bud formation and the onset of frost hardiness are related and the latter has been studied in mature shoots by Cannell *et al.* (1985). who developed an empirical model based on photoperiod and autumn temperatures. Since photoperiod plays a dominant role, climate change may have little effect

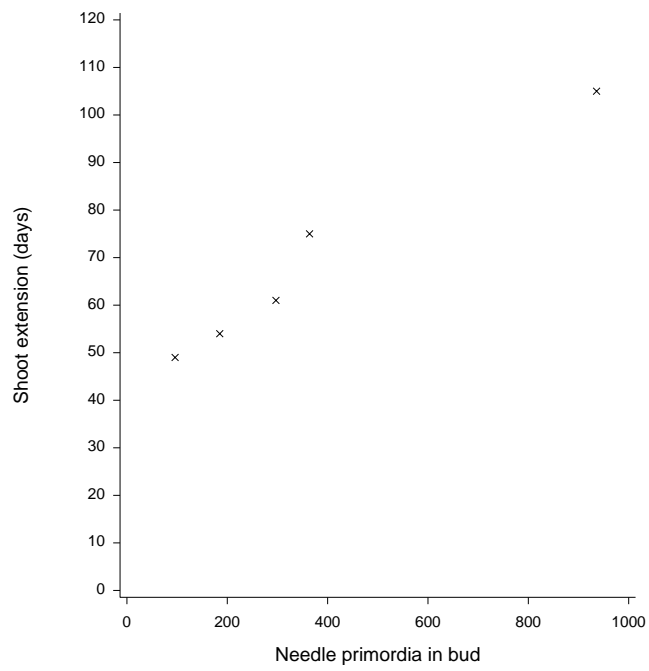


Figure 3: Duration of shoot extension in the leading shoot and branches of Sitka spruce (abstracted from McWilliam, 1972).

on the end of the growing season although, Oleksyn, Tjoelker and Reich (1992) throw doubt on the conventional hypotheses.

4 Shoot extension and xylem growth

4.1 Duration of shoot extension

McWilliam (1972) described the extension of a single bud as follows:

... the stem and leaves elongated rapidly, the basal region elongating first and the apical region elongating last. This was because a wave of maximum cell division proceeded from the base to the apex which was followed, as cell division declined and stopped, by a wave of cell expansion and maturation. With this acropetal advance of cell expansion and maturation, several tissues altered their characteristics.

In other words, the bud formed the previous year contained a number of stem units, each with a single needle primordium. Extension of these stem units involved cell division, followed by cell expansion and maturation, beginning with the most basal.

An obvious hypothesis is that shoot extension continues to completion, so that its duration depends on the number of stem units or primordia laid down the previous year (Cannell, 1990). This leads to a simple model:

$$D_e = \frac{P_{t-1}}{E'_p} \quad (2)$$

where D_e is the duration of shoot extension, P_{t-1} the number of primordia from the previous year, and E'_p is the mean rate of shoot extension in primordia per day. (We use the subscript p to indicate that the units are in primordia, rather than mm, and the 'prime' to indicate that this is a *rate* of extension per day, rather than the total extension over the season.)

Figure 3 shows the relationship between duration and number of primordia, but the fitted line does not go through zero, as one might expect. One explanation is that the mean rate of extension (E'_p primordia per day), varied with height down the tree (Fig. 4). *Hence, we need data giving the number of needles and the duration of shoot extension for several shoots at the same height.*

Such data may be available for other species. For example, Flower-Ellis recorded extension of the leading shoot, twice weekly, in Scots Pine in Jädraås, Sweden, from 1974–1978 (Flower-Ellis, 1982). From 1975 there were four treatments: control, fertilised, irrigated, and a combined treatment of fertilizer with irrigation (Fig. 5).

Figure 5 shows that the duration of extension growth was similar in all four treatments, but that growth was faster (in mm d^{-1}) when irrigation and fertilizer were combined. The primordia at the start of 1975 were laid down before the treatment started, so P_{t-1} , should have been similar in all blocks, and it is surprising that 30% extra growth in the combined treatment should have

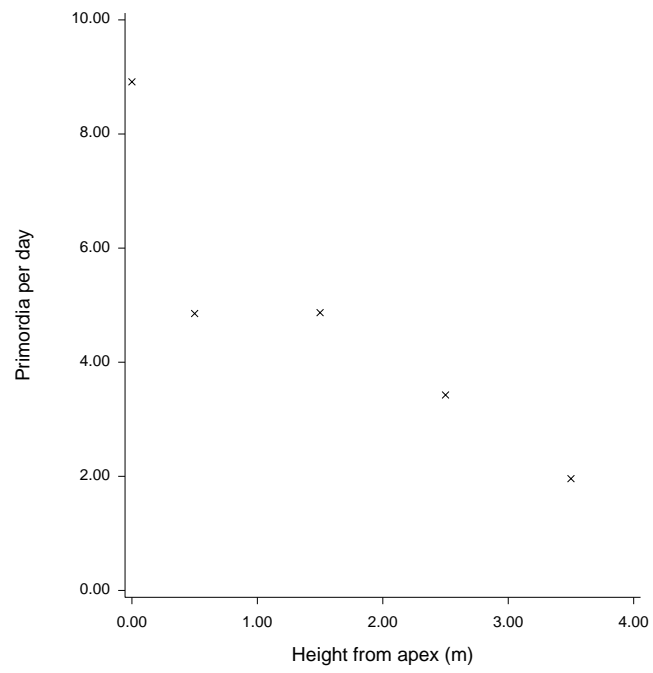


Figure 4: The mean number of primordia per day of shoot extension (E'_p) in Sitka spruce in Feteresso forest (abstracted from McWilliam, 1972).

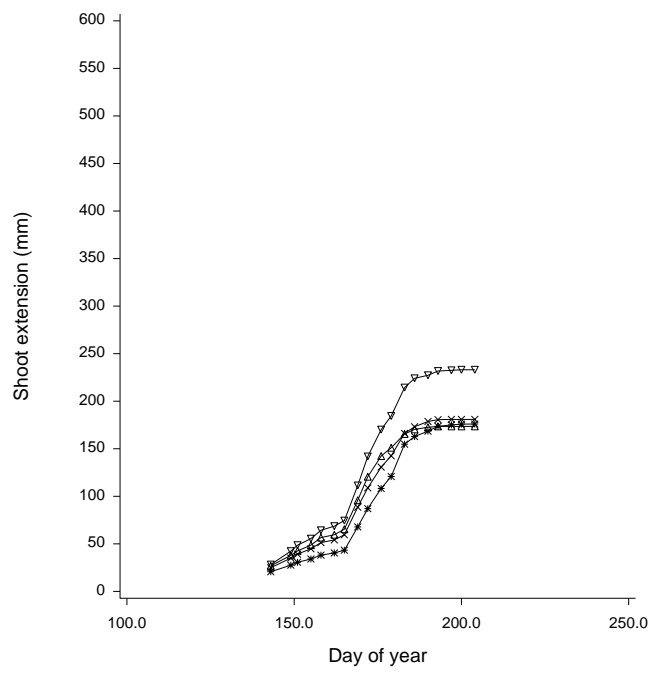


Figure 5: Shoot extension in Scots pine at Jädraås, Sweden, in 1975. Data from Flower-Ellis (1982). Treatments: × = control; ★ = irrigated; △ = fertilized; ▽ = irrigated and fertilized.

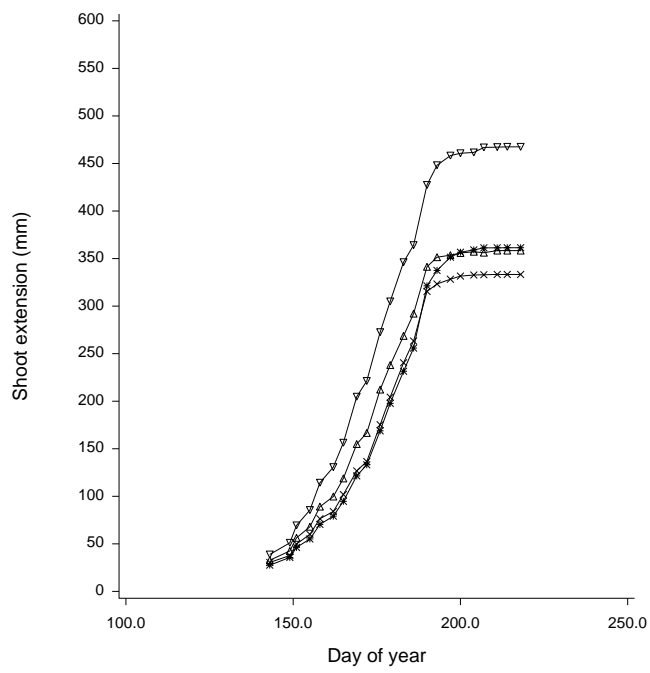


Figure 6: Shoot extension in Scots pine at Jädraås, Sweden, in 1976. Data from Flower-Ellis (1982). Treatments: × = control; ★ = irrigated; △ = fertilized; ▽ = irrigated and fertilized.

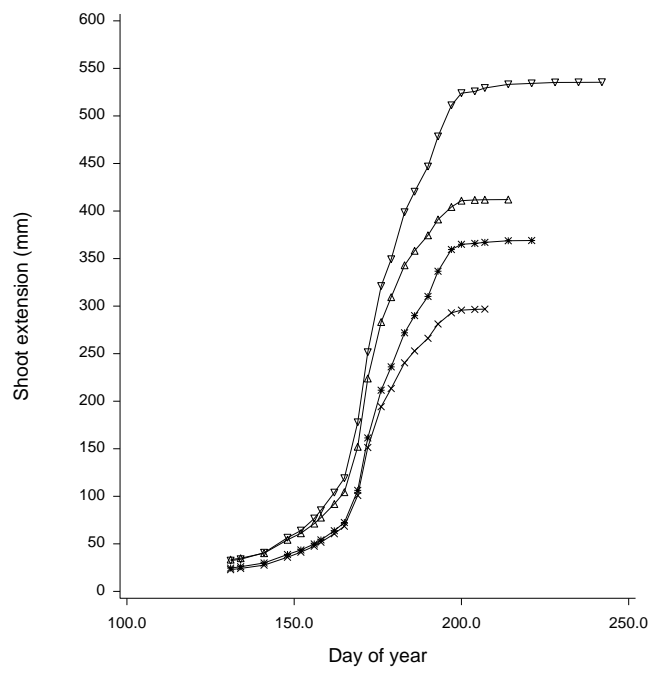


Figure 7: Shoot extension in Scots pine at Jädraås, Sweden, in 1977. Data from Flower-Ellis (1982). Treatments: × = control; * = irrigated; Δ = fertilized; ∇ = irrigated and fertilized.

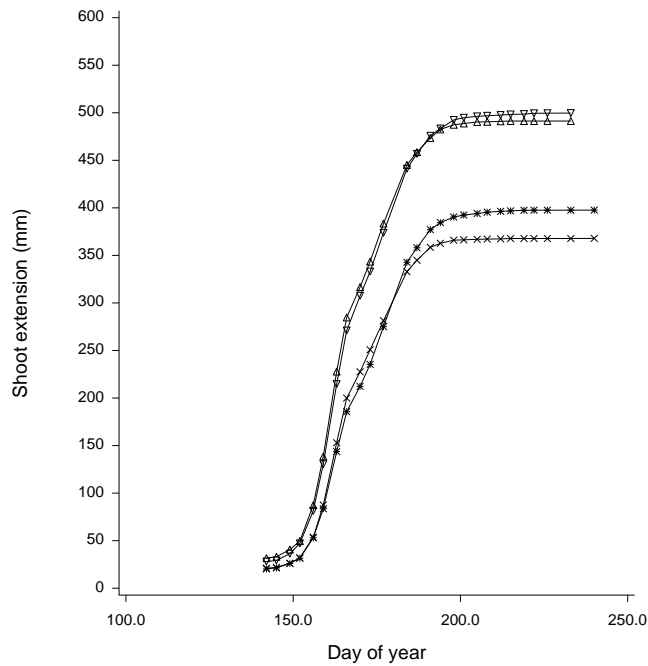


Figure 8: Shoot extension in Scots pine at Jädraås, Sweden, in 1978. Data from Flower-Ellis (1982). Treatments: \times = control; \star = irrigated; \triangle = fertilized; ∇ = irrigated and fertilized.

taken the same time as in the other treatments. In other words, the combined treatment increased the material added to the shoot without affecting the speed at which individual stem-units were developed.

Data from later years are even more surprising because the durations remain similar in all treatments (Figs. 6–8) when we might expect the number of primordia per bud to be greater in the fertilised treatments. This appears to be a species difference. Fertilizer increased both number and size of buds in Sitka spruce (Burley, 1966) while, in Scots pine, the main effect is on bud number (Linder, pers. comm.). Data on the number of needles recorded by Flower-Ellis could be used to test this interpretation.

Further data may be available from the numerous studies of height growth, since height growth and extension of the leading shoot are the same.

4.2 Rate of shoot extension

Figure 9 shows McWilliam's data on extension rates (mm d^{-1}) and rates can also be estimated from Flower-Ellis's data (Figs. 5–8). (Fig. 9). A thorough analysis of the Swecon data, including meteorological records and measurements

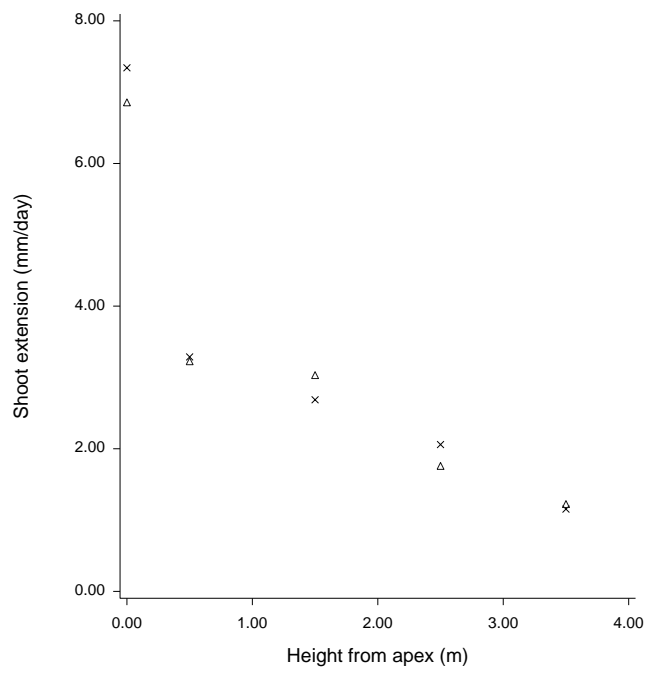


Figure 9: Mean rate of shoot extension ($k(h)E'(h)$ mm/day) of Sitka spruce (*Picea sitchensis*) in Feteresso forest (data from McWilliam, 1972). \times = 1969; Δ = 1970

of internal nutrient concentrations should provide insight into the factors affecting shoot extension.

For the moment we note that it is affected by distance from the apex, nutrients and temperature (Cannell, 1990)

4.3 Duration of xylem growth

One of McWilliam's particular contributions was to record xylem cell division and show that it was synchronised with extension in the same shoot (Fig. 1). This synchrony had not been noticed by other authors because diameter growth continues when the newly formed tracheids expand and mature after shoot extension has ceased. The synchrony of shoot extension and xylem cell division makes it easy to model the duration of xylem growth.

Both cell division and maturation of xylem continued longer in the stem than the branches, so that diameter growth at 1 m continued into October (Fig. 1).

4.4 Rate of xylem growth

There seems to be surprisingly little evidence on internal factors affecting the rate of xylem growth, although numerous tree ring analyses have correlated xylem growth with variations in weather, and studies on the pipe model theory have investigated the relationship between sapwood area and foliage or soil moisture (Grier and Waring, 1974; Waring, 1983; Whitehead, 1978; Whitehead, Edwards and Jarvis, 1984; Berninger and Nikinmaa, 1994). The synchrony between shoot extension and xylem cell division would explain the correlations observed by these authors, although the correlation will be reduced if rates of foliage growth and xylem expansion are affected by different factors.

The number of xylem cells formed was related to the number of primordia in the bud (Fig. 10) but *data from several years are needed to see how the rate of cell division varies with other factors. We also need to measure the effect of internal conditions on the rate of cell expansion and wall-thickening.* Kozlowski (1962) states that diameter growth depends on conditions during the current growing season, so it seems likely that expansion of tracheids is limited by carbon available.

Deans and Ford (1986) measured xylem growth in roots of Sitka spruce of differing ages and found that it was reduced during the period of fastest shoot extension in 15 year-old, but not in 9 year-old trees. Deans and Ford also compared root growth in June with starch depletion at various distances along the root. Close to the stem (< 0.25 m) trees of all ages relied on some imported carbon. Beyond 0.25 m in 20 year-old trees, starch depletion was more than enough for local root thickening, so roots beyond 0.25 m were a net source of carbohydrate in June. Roots in 9 year-old trees were net sinks up to 0.75 m from the stem.

There is rather little nitrogen in wood (0.2% in oak sapwood. 0.1% in oak heartwood (Allen *et al.*, 1974) which implies that wood production *consumes* rather little nitrogen. On the otherhand the process of wood production may

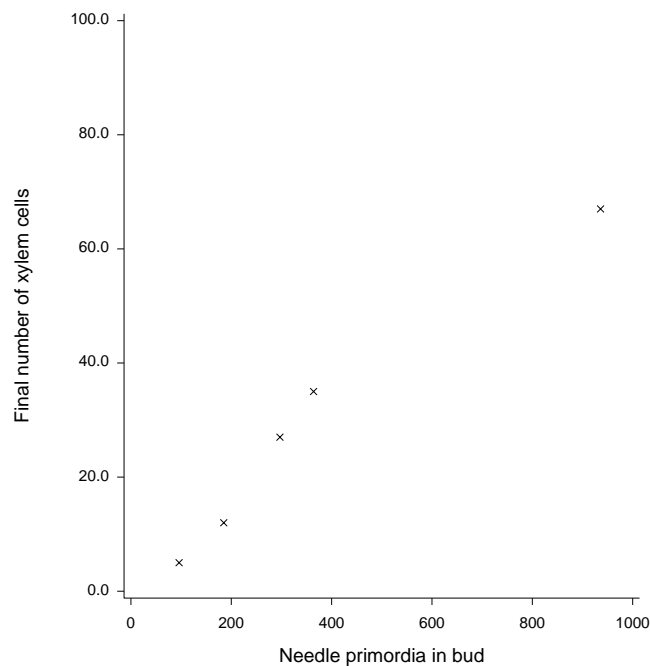


Figure 10: Relation between xylem cells formed and number of needle primordia in the original bud in shoots of Sitka spruce (Data abstracted from McWilliam, 1972)

require *high levels* of nitrogen substratemay even if nutrients are withdrawn after differentiation and available for further wood production. It is difficult to know whether wood production is highly sensitive to nitrogen availability or not.

5 Formation of next year's bud

5.1 Rate of primordia formation

In trees with predetermined growth, the number of primordia formed in a season can be estimated from the number of needles in the shoot which extends the following year. McWilliam (1972) recorded the number of needles formed in 1969, but he did not record the date at which bud formation ceased in that year. If we assume, however, that the date was set by photoperiod, then it should have been similar to the corresponding date the following year, especially since autumn temperatures were similar. From this estimated date for 1969, and the known date at which bud formation started in 1969, we can estimate the time spent in forming primordia. Fig. 11 shows the rate of primordia production

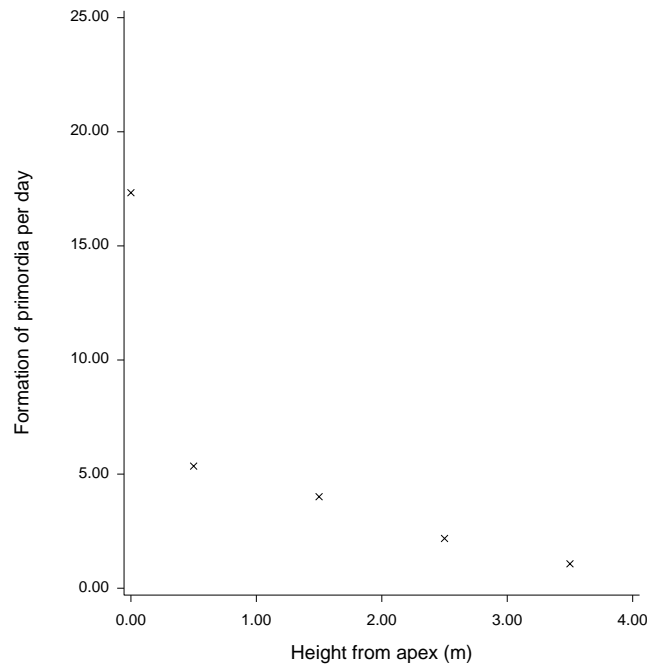


Figure 11: Estimated rate of primordia production in Feteresso forest in 1969 (data abstracted from McWilliam, 1972). The number of primordia formed and the date at which primordia formation started were measured, the date at which primordia formation ended has been estimated as equal to the observed date in 1970.

(P') calculated on that basis from McWilliam's data. *Further data are needed to estimate the effects of temperature and nutrients on P' .*

Burley (1966) compared Sitka spruce seedlings from 48 provenances and found that buds matured faster in the greenhouse than the nursery. However, he did not record the number of primordia produced.

Pollard and Logan (1977) examined a number of factors affecting primordial formation in black spruce (*Picea mariana*) and white spruce (*P. glauca*). A 10°C rise in temperature almost doubled the number of primordia produced, but had no effect on the duration of this phase. In contrast, halving the light intensity from 22,000 lux had little effect (they give the compensation point for spruce as about 1700 lux). In other words, temperature has a large effect on primordia formation while the difference in carbohydrate availability had almost none. Neither species was affected by photoperiods between 8 and 15 hours, although production dropped sharply when photoperiod was reduced from eight to two hours. Soil moisture potential had a significant effect on black spruce, but less on white, although the authors suggest that the experiment may

have underestimated the effect.

Data collected by Flower-Ellis may throw valuable light on the rate of primordia production. As observed in the previous section, the duration of shoot extension was similar in fertilised and control treatments (Figs. 5–8) although the rate in mm d^{-1} was almost doubled in the *IF* treatment in 1975. If duration depends on the number of primordia formed the previous year, this observation implies that the number of primordia per bud was similar in fertilised and control treatments. *The number of buds may have been larger (Linder, pers. comm.) or the primordia formed may have had more cells. These questions need to be resolved by analysing the data further.* The experiment provides a unique combination of detailed measurement over a long period with sustained differences in treatment.

It is of particular interest in Figs. 5–8 that irrigation plus fertilizer delivered a more rapid effect than fertilizer on its own. The *F* treatment only caught up the *IF* treatment in 1978. Irrigation alone was better than the control only in 1977, which followed the long dry summer of 1976 (was 1977 itself dry?).

6 Root growth

There is a large literature showing that the root shoot ratio in plants is sensitive to the balance of carbon assimilation and nutrient uptake, so that high nutrient uptake promotes foliage growth and low uptake causes a higher share of the growth to be in roots (White, 1935; Ingestad and Lund, 1979; Linder and Axelsson, 1982; Axelsson and Axellson, 1986). Many process-based models of forest growth now simulate this response (Thornley, 1972; Reynolds and Thornley, 1982; Mäkelä and Sievanen, 1987; Thornley, 1991).

In absolute terms the root growth may not be greater when nutrients are scarce, but the proportion alters. For example, Millard and Proe (1989; 1991) found roots in Sitka spruce seedlings to be shorter and thicker in high than in the low nitrogen treatment, although root weight was similar. The foliage weight in the high nitrogen treatment was very much larger, so foliage growth was relatively greater in high nitrogen treatments.

Coutts and Philipson (1977) describe an experiment in which Lodgepole pine (*Pinus contorta*) seedlings were grown with divided roots, so that half grew in high nutrient and half in low nutrient concentrations. After 56 days, some of the plants were switched to a regime of high nutrient concentration for both halves. The results are summarised in Table 1.

After 56 days, the roots in high nutrient concentration (rows 1 and 2) weighed about three times as much as those in low concentration (rows 3 and 4). Hence, high nutrient supply increased the sink strength of the growing roots, and so diverted more carbon into the nutrient rich half.

At 56 days some plants were switched to uniform high nutrient concentration (middle two rows). There was no change in external environment for the root already in high nutrients, but its partner, not in high nutrients, suddenly became a stronger carbon sink. In other words, roots already in high nutrients faced

Table 1: Root dry-weight (g) in a split root experiment (Coutts and Philipson, 1977). Half the roots of each plant received high nutrient concentrations and half low for 56 days. The some plants were switched to uniform high concentrations

Nutrient regime	Time (days)		
	56	84	133
High throughout; other half low throughout	0.6	1.5	-
High throughout; other half low then high	0.6	1.2	3.1
Low then high; other half high throughout	0.2	0.5	1.5
Low throughout; other half high throughout	0.2	0.4	-

Table 2: Actual and relative growth (from 56–84 days) under each regime (Coutts from and Philipson, 1977)

Regime	56–84 days		84–133	
	Actual growth (g)	Relative growth (d^{-1})	Actual growth (g)	Relative growth (d^{-1})
High N, continuous weak competition	0.9	0.037		
High N, increased competition	0.6	0.026	1.9	0.020
Increased N, continuous strong competition	0.3	0.028	1.0	0.021
Low N, continuous strong competition	0.2	0.018		

increased competition for carbon from day 56 (Table 1, row 2). In contrast, the previously low nutrient roots of switched plants faced no change in competition, but their external environment was changed (row 3). Table 2 gives growth rates and summarises the changes in competition and nutrient supply for each root and treatment.

The highest absolute and relative growth rates were with *high nutrient and low competition* (Table 2, row 1).

The effect of *increased competition* on high nutrient roots was to reduce absolute and relative growth rates (compare rows 1 and 2).

The effect of *increased nutrients* was to increase absolute and relative growth rates (compare rows 3 and 4) and, most interestingly, the relative growth rate was then as great as for roots which had been in high N all the time (compare rows 2 and 3). This is consistent with the hypothesis that growth was proportional to sink size when both halves were in high N.

This experiment is rich in comparisons, and can be used to estimate the effects of nutrients on local growth rate, competition from other parts of the rooting system, and even on changes in relative growth rate with time. To estimate these effects, I fitted a factorial model, using GLIM. The response variable was relative growth rate and the predictors were all factors with two levels: Nutrient (high, low), Competition (high, low), Period (56-84 days, 84-133). The relative growth rate was then predicted by

$$\begin{aligned} \frac{dW_r}{dt} \frac{1}{W_r} = 0.028 & \times 1.16 & ; \text{ if nutrient is high} \\ & \times 0.88 & ; \text{ if competition is high} \\ & \times 0.68 & ; \text{ for second period} \end{aligned} \quad (3)$$

In other words, the level of nutrients used in the experiment gave an increase in root growth rate of 16%, while competition from fertilized roots reduced growth rate by about 12%.

The growth rate also fell with time, which could have been due to several processes.

1. As the plant grew, the leaf area became a diminishing proportion of the total, so a higher proportion of assimilated carbon would be lost in respiration;
2. New leaves start to shade the old so that foliage intercepts light less efficiently;
3. Sinks in other parts of the plant were increasing, in competition with the growing roots;
4. Within the roots, the meristems at the tip and in the vascular cambium become a decreasing proportion of total root weight, so the size of the growth sink decreases in proportion to root weight.

A detailed analysis of these processes would be helpful.

Water stress also affects root growth and Khalil and Grace (1992) showed that total fine root length was less in water stressed plants. However, their plants grew more fine roots in the moist part of the soil, and the roots passing through dryer regions of soil thickened more than in unstressed plants.

Thus, the rate of root growth is influenced by a complex of factors including temperature, water and nutrients and a good review of these factors is needed.

7 Implications for modelling

Allocation of carbon is treated in a variety of ways in current forest growth models. At the simplest level, the carbon assimilated has been allocated according to constant allocation coefficients (c.f. McMurtrie and Wolf, 1983).

Other models have addressed two common observations:

- Changes in nitrogen supply are known to affect the ratio of root to shoot growth;
- Sapwood area is observed to be well correlated with the weight or area of foliage it supports.

Mäkelä (1986; 1988a;1988b; 1990) combined a functional balance model for root : shoot growth with a pipe model linking sapwood area to foliage growth. Allocation between root and shoot depends on the ratio of carbon assimilation to nitrogen uptake, so that a fall in nitrogen or a rise in carbon causes more carbon to be allocated to root growth.

Within the shoot, the allocation between foliage and sapwood is calculated using the pipe model (Shinozaki et al., 1964a,b) so that the total area of sapwood is linearly related to the total weight of foliage. Valentine (1985; 1987; 1988a,b; 1990) had used the pipe model to allocate carbon and other authors have since used these ideas (Ludlow, Randle and Grace, 1990)

All of these models use allocation coefficients or functions to hand out carbon to different tissues. However, the growth of each tissue depends only on the conditions within that tissue, whether these are temperature, nutrients or carbon availability. Models by Thornley (1991) and Dewar (1993) are based on that approach, but the analysis here suggests that even their models fail to capture all of the internal influences on growth of tissues. In particular, growth does not depend in a simple way on internal C and N, at least at some times of year. For example, Ford and Deans (1977) found a trough in elongation of fine roots in Sitka spruce on 24th June, while soluble carbohydrates had peaked on the 6th and soluble starch rose after that. Thus, root elongation was declining at a time when carbon was being stored. This is consistent with the hypothesis that auxin from expanding leaves inhibits root elongation.

Similarly, Sofronova (1992) showed large differences in height growth between suppressed and dominant trees, even though internal carbohydrate concentrations were very similar, and this is consistent with the hypothesis that expansion of foliage in the suppressed trees was reduced by low light intensity, or the spectrum reaching shaded leaves.

A further problem is that we do not understand the dynamics or the mechanisms of storage in plant tissues. Presumably carbon is stored when other factors limit growth, whether these are nitrogen, auxin or other hormones or nutrients. Until we quantify the way growth rates depend on these factors we will not have a clear understanding of the mechanisms.

7.1 Necessary complications

Taken together the evidence suggests that:

1. Growth processes such as cell division and cell expansion occur in different tissues at different times of year, and different environmental variables may be more important for one process than another (temperature, say, for cell division; water availability for cell expansion). Hence, the timing of high

rainfall, warm periods, nutrient availability, or other environmental factors may affect the pattern of allocation.

2. Changes in climate or CO₂ levels can be expected to affect the timing of growth periods, as well as the timing of environmental factors, so growth needs to be modelled at a seasonal scale if allocation patterns are to be predicted.
3. Substrate concentrations are not good predictors of seasonal patterns of growth.
4. Sinks which compete for substrates may promote each other's growth by chemical signals. For example, it is suggested here that extending leaves produce auxin which increases a competing cambial sink. This creates a resource-limited positive feedback which needs to be simulated and understood.
5. We need to understand the control of carbohydrate storage and nutrient cycling within the tree.

8 Data needed to develop a model of allocation based on phenology

To model allocation in a mechanistic way we need to find the factors that determine the duration of shoot extension, bud formation, and root growth, and then to quantify the internal factors which affect the rate of these processes. Rates of cell division, cell expansion and differentiation are no doubt influenced by different factors.

A practical approach is to assume that the durations can be calculated from the length of the growing season and the number of primordia from the previous year, but that the rates of growth are limited by carbon and nitrogen availability. In other words, sinks are switched on or off by hormones, but their growth rates are limited by substrate, and so by competition between active sinks.

Data on rates may not yet be available, but we should be able to quantify the factors affecting durations from existing data, especially data from the SWE-CON project on Scots pine and, more recently, from experiments on Norway spruce at Flakaliden, Sweden.

The first step in analysis is to assemble data on needle numbers and periods of shoot growth and bud formation for a variety of treatments, together with local climate data. From these we may calculate actual growth rates for the leading shoot, relating the actual growth rates to environmental factors.

From the chemical composition of each tissue it should be possible to work out how much carbon and nitrogen were needed to form the observed new growth and then to deduce the actual sink activity. The aim would be to reconstruct the actual flows into new growth. A problem is to distinguish between structural nutrients or carbohydrate and those which are mobile.

Data on the concentration of nutrients in buds would be useful because they would show whether bud formation is especially sensitive to nutrient availability. *Total foliage growth is increased by N, S, P and Fe (Ericsson, 1990) but are these most needed during the phase of shoot extension or do they act by influencing bud size, and hence the sink-size of growing foliage in the following year?*

Finally, the data from the SWECON project (and from Flakaliden) should give further information on whether nutrients and irrigation act by multiplying the number of sinks when buds are formed, or by influencing the rate of the extension phase. Changes in growth rate appear to affect all the curves in Fig 6–8 at the same time, suggesting a strong effect of weather variables that would have to be estimated in any analysis.

Once that is done, an analysis similar to equation (3) should give estimates that are easily used in a model based on sink size and sink strengths.

References

- Allen, S., Grimshaw, H., Parkinson, J., and Quarmby, C. (1974). *Chemical analysis of ecological materials*. Blackwell, Oxford.
- Axelsson, E. and Axelsson, B. (1986). Changes in carbon allocation patterns in spruce and pine trees following irrigation and fertilisation. *Tree Physiology*, **2**, 189–204.
- Berninger, F. and Nikinmaa, E. (1994). Foliage area-sapwood area relationships of Scots pine (*pinus sylvestris*) trees in different climates. **24**, 2263–2268.
- Burley, J. (1966). Genetic variation in seedling development of Sitka spruce, *picea sitchensis* (Bong). *Carr. Forestry*, **39**, 68–94.
- Cannell, M. (1990). Modelling the phenology of trees. *Silva Carelica*, **15**, 11–27.
- Cannell, M., Sheppard, L., Smith, R., and Murray, M. (1985). Autumn frost damage on young *picea sitchensis* 2. Shoot frost hardening, and the probability of frost damage in Scotland. *Forestry*, **58**, 147–166.
- Coutts, M. and Philipson, J. (1977). The influence of mineral nutrition on the root development of trees. III. plasticity of root growth in response to changes in the nutrient environment. *Journal of Experimental Botany*, **28**, 1071–1075.
- Denne, M. (1979). Wood structure and production within the trunk and branches of *picea sitchensis* in relation to canopy formation. *Canadian Journal of Forest Research*, **9**, 406–427.
- Dewar, R. (1993). A root-shoot partitioning model based on carbon-nitrogen-water interactions and Münch phloem flow. *Functional Ecology*, **in press**, .

- Dougherty, P., Whitehead, D., and Vose, J. (1993). Environmental influences on the phenology of pine. In H. Gholz, R. McMurtrie, and S. Linder, editors, *A comparative analysis of pine forest productivity*, page Chapter 7. to be announced.
- Ericsson, T. (1990). Dry matter partitioning at steady state nutrition. In *Above- and below-ground interactions in forest trees and acidified soils*, Air Pollution Report 32, pages 236–243.
- Flower-Ellis, J. (1982). Structure and growth of some young scots pine stands: (2) effects of irrigation and fertilisation on the amount, rate and duration of leading shoot growth. Technical Report 30, Swedish Coniferous Forest Project, Institute of Ecology and Environmental Research, Swedish University of Agricultural Sciences, Fack, S-750 07 UPPSALA, Sweden.
- Ford, E. and Deans, J. (1977). Growth of a sitka spruce plantation: spatial distribution and seasonal fluctuations of lengths, weights and carbohydrate concentrations of fine-roots. *Plant and Soil*, **47**, 463–485.
- Grier, C. and Waring, R. (1974). Conifer foliage mass related to sapwood area. *Forest Science*, **20**, 205–206.
- Ingestad, T. and Lund, A.-B. (1979). Nitrogen stress in birch seedlings. *Physiol. Plant.*, **45**, 137–148.
- Keinholtz, R. (1934). *Botanical Gazette*, **96**, 73–92.
- Khalil, A. and Grace, J. (1992). Acclimation to drought in *acer pseudoplanatus* L. (Sycamore) seedlings. *Journal of Experimental Botany*, **43**, 1591–1602.
- Kozlowski, T., editor (1962). *Tree growth*. Ronald Press.
- Kramer, K. (1992). Phenological reactions of the main Dutch tree species to climate change described by a simulation model of the annual cycle. Interim Report of the N.O.P.-project. Technical report, Institute of Forestry and Nature Research, Wageningen. Dorschkamp report 696.
- Lanner, R. (1976). Patterns of shoot development in *pinus* and their relationship to growth potential. In M. Cannell and F. Last, editors, *Tree physiology and yield improvement*, pages 223–243. Academic Press, London.
- Linder, S. and Axelsson, B. (1982). Changes in carbon uptake and allocation patterns as a result of irrigation and fertilisation of a young *pinus sylvestris* stand. In R. Waring, editor, *Carbon uptake and allocation in sub-alpine ecosystems as a key to management*, pages 38–44. Oregon State University, Corvallis, U.S.A.
- Ludlow, A., Randle, T., and Grace, J. (1990). Developing a process-based growth model for Sitka spruce. In R. Dixon, R. Meldahl, G. Ruark, and W. Warren, editors, *Process modeling of forest growth responses to environmental stress*, pages 249–262, Portland, OR, U.S.A. Timber Press.

- Mäkelä, A. (1986). Implications of the pipe-model theory on dry matter partitioning and height growth in trees. *J. Theor. Biol.*, **123**, 103–120.
- Mäkelä, A. (1988a). Parameter estimation and testing of a process-based stand growth model using Monte Carlo techniques. In A. Ek, S. Shifley, and T. Burk, editors, *Forest Growth Modelling and Prediction*, pages 315–322, St. Paul, MN, U.S.A. USDA Forest Service North Central Forest Experiment Station.
- Mäkelä, A. (1988b). Performance analysis of a process-based stand growth model using Monte Carlo techniques. *Scandinavian Journal of Forest Research*, **3**, 315–331.
- Mäkelä, A. (1990). Adaptation of light interception computations to stand growth models. In H. Jozefek, editor, *Silva Carelica*, volume 15, pages 221–239, Finland. University of Joensuu.
- Mäkelä, A. and Sievänen, R. (1987). Comparison of two shoot-root partitioning models with respect to substrate utilization and functional balance. *Annals of Botany*, **59**, 129–140.
- McMurtrie, R. and Wolf, L. (1983). Above and below ground growth of forest stands: A carbon budget model. *Anal. Bot.*, **52**, 437–448.
- McWilliam, A. (1972). *Some effects of the environment on the growth and development of Picea sitchensis*. Ph.d. thesis, University of Aberdeen.
- Millard, P. and Proe, M. (1989). The internal cycling of nitrogen in Sitka spruce. In *Importance of root to shoot communication in the responses to environmental stress*. British Plant Growth Regulator Group, Monograph 21.
- Millard, P. and Proe, M. (1991). Nitrogen storage and internal cycling for the seasonal growth of Sitka spruce. *Plant, Cell and Environment*, **submitted**.
- Murray, M., Cannell, M., and Smith, R. (1989). Date of budburst of 15 tree species in Britain following climatic warming. *Journal of Applied Ecology*, **26**, 693–700.
- Oleksyn, J., Tjoelker, M., and Reich, P. (1992). Growth and biomass partitioning of populations of European *pinus sylvestris* L. under simulated 50° and 60° n daylengths; evidence for photoperiodic ecotypes. *New Phytologist*, **120**, 561–574.
- Pollard, D. and Logan, K. (1977). The effects of light intensity, photoperiod, soil moisture potential, and temperature on bud morphogenesis in *picea species*. *Canadian Journal of Forest Research*, **7**, 415–421.
- Reynolds, J. and Thornley, J. (1982). A shoot-root partitioning model. *Annals of Botany*, **49**, 585–597.

- Salisbury, F. and Ross, C. (1992). *Plant physiology*. Wadsworth, Belmont, California, 4th edition.
- Shinozaki, K., Yoda, K., Hozumi, K., and Kira, T. (1964a). A quantitative analysis of plant form – the pipe model theory. i. basic analyses. *Japanese Journal of Ecology*, **14**, 97–105.
- Shinozaki, K., Yoda, K., Hozumi, K., and Kira, T. (1964b). A quantitative analysis of plant form – the pipe model theory. ii. further evidence of the theory and its application in forest ecology. *Japanese Journal of Ecology*, **14**, 133–139.
- Sofronova, G. (1992). Dynamics of carbohydrate distribution in Scots pine. In M. Mecke and P. Hari, editors, *Production process of Scots pine; geographical variation and models*. .
- Thornley, J. (1972). A balanced quantitative model for root-shoot ratios in vegetative plants. *Annals of Botany*, **36**, 401–404.
- Thornley, J. (1991). A transport-resistance model of forest growth and partitioning. *Annals of Botany*, **68**, 211–226.
- Valentine, H. (1985). Tree growth models: Derivations employing the pipe-model theory. *J. Theor. Biol.*, **117**, 579–585.
- Valentine, H. (1987). A carbon-balance model of a self thinning stand with the pipe-model theory. Wp-87-56, IIASA, Vienna, Austria.
- Valentine, H. (1988a). A carbon-balance model of stand growth: a derivation employing pipe-model theory and the self-thinning rule. *Annals of Botany*, **62**, 389–396.
- Valentine, H. (1988b). Derivation of a carbon-balance model of a self thinning stand with the pipe-model theory. In A. Ek, S. Shifley, and T. Burk, editors, *Forest Growth Modelling and Prediction*, pages 353–360, St. Paul, MN, U.S.A. USDA Forest Service North Central Forest Experiment Station.
- Valentine, H. (1990). A carbon-balance model of forest growth with a pipe model framework. In R. Dixon, R. Meldahl, G. Ruark, and W. Warren, editors, *Process modeling of forest growth responses to environmental stress*, pages 33–40, Portland, OR, U.S.A. Timber Press.
- Wareing, P. and Phillips, I. (1981). *Growth and differentiation in plants (3rd Edition)*. Pergamon International Library, Oxford.
- Waring, R. (1983). Estimating forest growth and efficiency in relation to canopy leaf area. *Advances in Ecological Research*, **13**, 327–354.
- White, H. (1935). The interaction of factors in the growth of Lemna. XII. The interaction of nitrogen and light intensity in relation to root length. *Annals of Botany*, **1**, 649.

Whitehead, D. (1978). The estimation of foliage area from sapwood basal area in scots pine. *Forestry*, **51**, 35–47.

Whitehead, D., Edwards, W., and Jarvis, P. (1984). Conducting sapwood area, foliage area, and permeability in mature trees of *picea sitchensis* and *pinus contorta*. *Canadian Journal of Forest Research*, **14**, 940–947.