

## Chapter (non-refereed)

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## DRY MATTER PARTITIONING IN TREE CROPS

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### I. INTRODUCTION

It is now a truism of crop physiology that, during crop evolution and domestication, yield has been increased mainly by increasing the proportion of assimilates partitioned to the harvested parts of the plants, and much less (or not at all) by increasing total biomass production (Evans 1976). Indeed, it has proved very difficult to find evidence for an increase, during domestication in the maximum light-saturated  $\text{CO}_2$  exchange rate per unit leaf area of wheat, maize, sorghum, sugar cane, cotton, cowpea and pearl millet (Gifford & Evans 1981). In all these crops, genetic improvement in yield has generally been achieved by altering the size of plant parts, developmental processes, and adaption to the 'agronomic' environment, all resulting in

increased partitioning of dry matter to the organs that are harvested (Evans 1975).

The purpose of this review is to consider the opportunities that exist in tree crops to increase yield by changing the partitioning of dry matter. These opportunities are sought in part empirically, by reviewing widely scattered information on dry matter partitioning in trees, and in part by considering the factors that influence or control assimilate partitioning. McMurtrie (this volume) extends our understanding further, by using conceptual models to explore the effects on tree growth of changes in assimilate partitioning. It is important to consider some aspects of mineral nutrient, as well as carbon, partitioning. However, no attempt is made to cover the extensive literature on source-path-sink relationships (see Warren-Wilson 1972; Wareing & Patrick 1975; Moorby 1977; Thornley 1977; Gifford & Evans 1981).

The framework of this review is to consider (a) the relevance to tree crops of the notion of 'harvest index', (b) the limited factual information on carbon budgets of whole trees and forests, (c) root/shoot interactions, (d) the effects of fruiting on dry matter partitioning, and (e) partitioning between leaves, branches and stems.

## II. HARVEST INDEX

The notion of harvest index (*H.I.*) was devised primarily to assess dry matter partitioning in annual grain crops, defined as: dry weight of harvested part/total above-ground dry weight at harvest. Let us consider this concept with respect to tree crops.

### A. Defining yield

A premise of the *H.I.* concept, and indeed of this review, is that yield can be adequately defined in terms of dry weight. However, different harvested parts can have greatly different values. The most lucrative aspects of harvest index to explore are often the opportunities to increase the proportion of dry matter partitioned to the highest value products. However, it is beyond the scope of this review to consider, for instance, factors affecting the relative value of fruits and fuelwood, or the quality and size distributions of forest tree boles.

A second aspect of harvest index to explore is the possibility of increasing the size or number of tree parts that can be removed as yield. The extreme example of this is the multipurpose tree, where even the litterfall might be of value for soil improvement. A less extreme example is whole-tree harvesting in forestry (eg Keays 1971). A further example occurs in tea (*Camellia sinensis*), where yield consists of young shoots with 'two-leaves-and-a-bud'. These are the only parts which make good quality beverage. Each shoot is plucked at the end of a period of slow exponential growth lasting about 35 days. If the shoots were allowed to grow to 'three-leaves-and-a-bud', they would double their dry weights, and take only a further 7 days to do so (Tanton 1979). Thus, if tea bushes were selected in which this third leaf could be used to

make good quality tea, yield might be substantially increased. There are, perhaps, other instances in which *H.I.* could be increased, not by changing dry matter partitioning, but by redefining yield.

## B. Harvest index and yield

There is a considerable literature in the agricultural sciences showing that there is a strong association between *H.I.* and yield, and it has been suggested that measurement of *H.I.* might advance our understanding of crop performance (eg Singh & Stoskopf 1971; Donald & Hamblin 1976). However, Charles-Edwards (1982) warns against this suggestion, on two grounds: (a) correlations between a ratio (*H.I.*) and a measurement from which that ratio is derived (yield) are 'false' and can be obtained using random numbers, and (b) *H.I.* is actually a complex measure of performance which integrates phenological, physiological and environmental factors affecting yield. Thus, genetic improvements in the yield of cereals in Britain during the period 1900 to 1980 were accompanied by a large increase in *H.I.* (Austin *et al.* 1980), but the true determinants of increased yields were probably a decline in the duration of the vegetative growth phase, and an increase in the amount of light intercepted during the grain-filling phase (Charles-Edwards 1982). Thus, when looking for ways of increasing the yield of tree crops, we should examine the whole-plant processes that determine *H.I.*; it is not sufficient to say that yield increase is associated with an increase in *H.I.*

Finally, we should recognize that the relationship between yield and *H.I.* is always likely to be parabolic; that is, there will be an optimum value beyond which continued increase in the proportion of assimilates devoted to the yielded part occurs at the expense of new light-intercepting foliage, new roots, or essential structural parts.

## C. Harvest increment of tree crops

The harvest indices of annual crops are calculated over their lifetimes, so for the purposes of comparison the same should be done for perennials (eg Pritts & Hancock 1983). However, in tree crops, we are also interested in the increment apportioned to a harvested part over a period of years within the lifespan, which we may call the harvest increment (*H.Incr.*)<sup>1</sup>. Clearly, the value of *H.Incr.* will depend on the age of the trees and span of years chosen.

The *H.Incr.* values of forest trees and most fruit trees are, in fact, quite high. Thus, Cannell's (1982) 'forest production data set' shows that the stems took 40–60% of the current annual above-ground dry matter increment in a large number of both broadleaved and coniferous stands around the world

<sup>1</sup> *H.Incr.* = Increment in harvested part/total above-ground increment; where the interval may be one or several years during the life of the trees.

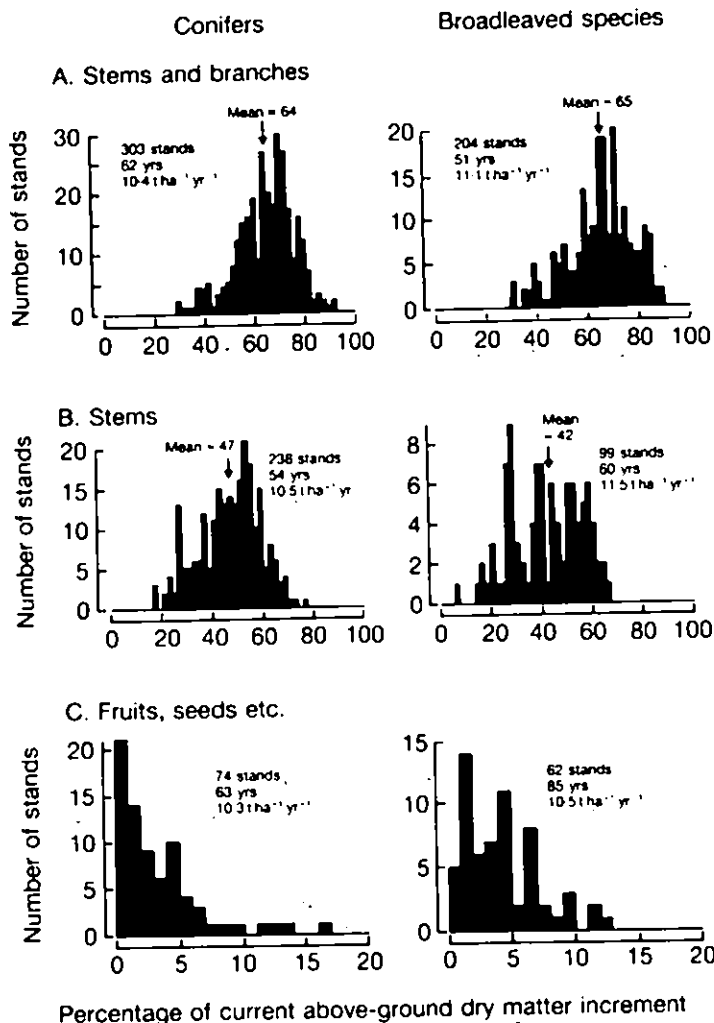


FIGURE 1. Percentage of the current annual increment in above-ground dry matter of forest stands taken by: A. stems and branches; including bark, B. stems only, including bark, and C. reproductive structures (fruits, seeds, etc).

Values were taken from Cannell (1982), using all data sets in which estimates had been made of foliage, branch and stem production. C does not include those stands that had zero values for reproductive structures. Many studies did not include good estimates of tree mortality or woody litterfall. Each histogram gives the number of stands, the average age of the stands, and their average current above-ground dry matter production.

(Fig. 1B). If branches are included with stems, then the *H.Incr.* of many stands are in the range 60–80% (Fig. 1A). Furthermore, these values are

probably under-estimates, because many studies failed to give values for woody litterfall or tree mortality.

The proportion of above-ground dry matter increment taken by the reproductive structures of forest trees is usually less than 10% (Fig. 1C), although higher values may be recorded in 'mast' years, heavy coning years, and perhaps if accurate estimates of pollen production were made. The *H.Incr.* measured on young fruit trees ranges from 23% to 75% (Table I). Despite biennial bearing (which may be related to seed-produced hormones rather than to shortage of assimilates), mature fruit trees may have average *H.Incr.* values exceeding 60%, which is considered to be near the maximum *H.I.* (= *H.Incr.*) of cereals, which have to produce new structural tissues each year (Austin *et al.* 1980). Carbon allocation models for wild annual species suggest that the maximum reproductive yield is obtained when the switch from vegetative to reproductive growth occurs at the time when the vegetative mass is equal to final reproductive yield, that is when *H.I.* is no more than 50% (King & Roughgarden 1983). Selected progenies of oil palm are able to sustain a *H.Incr.* (bunch index) of about 50% (Corley *et al.* 1971b; Breure & Corley 1983).

Tea and *Hevea* rubber have *H.Incr.* values of less than 15% (Table I), which is one of the main reasons why the mean annual yield of these crops is usually only 1 to 3 t ha<sup>-1</sup> yr<sup>-1</sup> of dry matter, compared with 5 to 15 t ha<sup>-1</sup> yr<sup>-1</sup> in many tropical timber, fuelwood and fruit trees.

### III. ANNUAL CARBON BUDGETS

The first step to understanding whole-plant processes that might influence the *H.Incr.* of trees is to examine yield in the context of the total annual carbon budget. Unfortunately, few complete carbon budgets have been constructed for trees, and most of them suffer serious limitations (see Jarvis & Leverenz 1983). However, sufficient information exists to establish the relative magnitude of the different biomass components and carbon fluxes, which form a basis for the conceptual models of McMurtrie and Wolf (1983) and McMurtrie (this volume).

Figure 2 presents two carbon budgets for forest trees, in which attempts were made to determine all the components by measurement. However, there was considerable uncertainty about the magnitude of root respiration and woody litterfall (Agren *et al.* 1980; Edwards *et al.* 1981). Also note that the two stands differed markedly in age, size and site conditions. Two further budgets are presented later (Fig. 7, for the same stands as Fig. 2A), but other published budgets for trees are incomplete, or were balanced by assigning a remainder to one of the processes (Schulze 1970; Schulze *et al.* 1977; Kinerson *et al.* 1977; Kira & Yabuki 1978).

In the absence of other data, Figure 3 presents four of the best current net-dry-matter-production budgets published for forests (that is, omitting respiration), in which good estimates were made of each component, including fine root turnover.

The most striking feature of all these budgets is the high proportion of dry matter allocated to root respiration and fine root turnover. Thus, in Figures

TABLE I. Harvest increment<sup>1</sup> of some tree crops

Tree crop	Yield	Age (years)	Increment period (years)	Harvest increment (%)	Source
Forest trees	Stems and branches	Average 57	1 to 10	40-85	Cannell 1982; Fig. 1A
	Stems	Average 57	1 to 10	20-70	Cannell 1982; Fig. 1B
Apple	Fruits	2	0.5	40	Maggs 1963
	Fruits	2	0.6	44	Avery 1969
	Fruits	2-5	3	23-74	Avery 1970
	Fruits	3-4	1	53	Hansen 1971a
	Fruits	3-4	1	27-72	Heim <i>et al.</i> 1979
Peach	Fruits	4-15	1	35-70	Chalmers & Ende 1975
Citrus	Fruits	2-3	1	up to 52	Lenz 1979
Coffee	Fruits (seeds)	3-4	1.3	44(30)	Cannell 1971
	Fruits (seeds)	4	0.3	75(50)	Cannell 1971
Oil palm	Bunch (oil)	17-22	5	27(11)	Rees & Tinker 1963
	Bunch (oil)	7-18	11	43(17)	Corley <i>et al.</i> 1971a
	Bunch (oil)	10	1	25-54(10-22)	Corley <i>et al.</i> 1971b
Tea	Young shoots	6	1	11	Magambo & Cannell 1981
Hevea rubber	Latex	6	1	3-11	Templeton 1969

<sup>1</sup> Dry weight increment in the harvested part/dry weight increment in all above-ground parts.

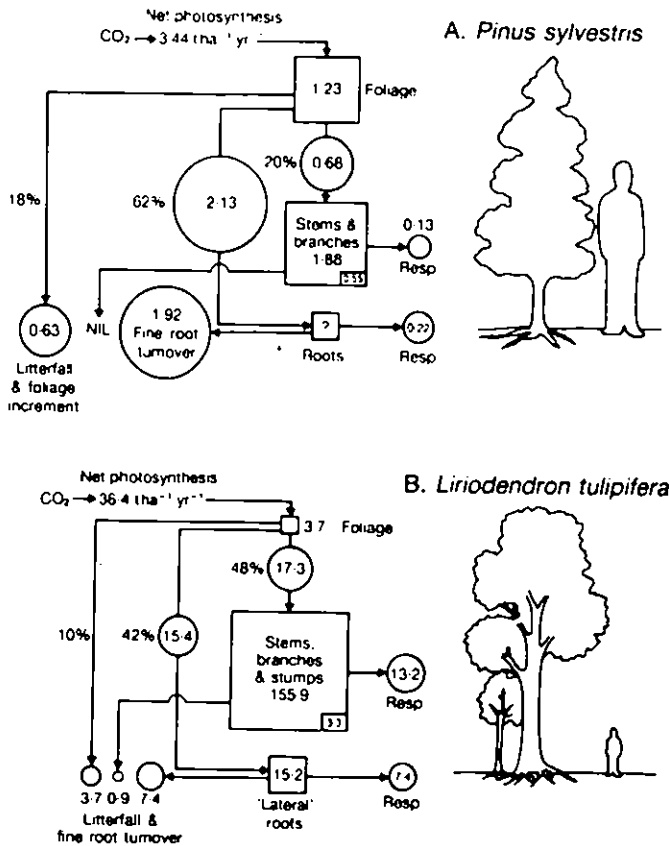


FIGURE 2. Current annual dry matter budgets of two contrasting forests. Both budgets were balanced using measurements of net photosynthesis, biomass increments, respiration, litterfall and fine root turnover.

A. *Pinus sylvestris*, 14 years old,  $60^{\circ}49'N$  in Sweden, poor sandy iron-podzol (Ågren *et al.* 1980).

B. *Liriodendron tulipifera*, broadleaved woodland, up to 50 years old,  $35^{\circ}58'N$  in Tennessee, deep alluvial silt-loam (Edwards *et al.* 1981).

Squares: biomass ( $\text{t ha}^{-1}$ ); circles: fluxes ( $\text{t ha}^{-1} \text{ yr}^{-1}$ ). Values can be converted to  $\text{g C m}^{-2} \text{ yr}^{-1}$  by multiplying by 50. The areas of the squares and circles are proportional to the values, but the scales differ in A and B. The small boxes within the woody biomass squares give the annual net wood increments ( $\text{t ha}^{-1} \text{ yr}^{-1}$ ). The budget for B includes the understorey canopy, but omits the ground flora, and small losses from predators and herbivores. Note that the percentage dry matter going to foliage is equal to the litterfall plus the increment in living foliage.

2A and 2B the roots took 62% and 42%, respectively, of the total carbon, while in Figure 3 they took between 24% and 66% of the current net dry matter production. These percentages represented 2.1 to  $16.8 \text{ t ha}^{-1} \text{ yr}^{-1}$  of dry matter, often exceeding the dry matter used each year to produce new foliage. The second feature to note is that, whereas the *H.Incr.* values for



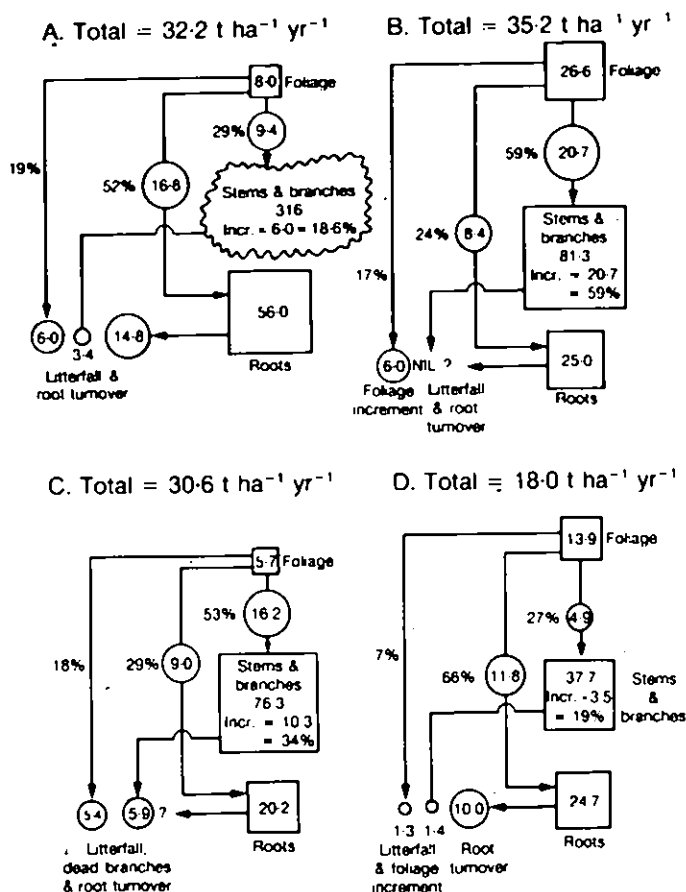


FIGURE 3. Current annual net dry matter production budgets of four forest stands (excluding respiration).

A. Tropical rainforest, Venezuela, on infertile leached lateritic soil (see Cannell 1982, p. 372). (A fairly complete budget also exists for the Pasoh tropical rainforest, Malaysia; see Cannell 1982, p. 196.)

B. *Picea sitchensis*, Scotland, aged 17, peaty gley soil (see Cannell 1982, p. 242).

C. *Pinus taeda*, North Carolina, aged 14, sandy loam (see Cannell 1982, p. 326, assuming 5.5 t ha<sup>-1</sup> yr<sup>-1</sup> increment in dead branches).

D. *Abies amabilis*, Washington State, aged 23, sandy, gravelly clay loam (see Cannell 1982, p. 289).

Squares: biomass (t ha<sup>-1</sup>); circles: fluxes (t ha<sup>-1</sup> yr<sup>-1</sup>). The large biomass of stems and branches in A (316 t ha<sup>-1</sup>) is not drawn to scale, but all other biomass and flux values are represented by squares or circles on the same scale. See legend to Fig. 2.

woody parts in these stands were quite high, the net increment of woody parts often represented a small part of the total carbon budget. For instance, the *H.Incr.* of woody parts in Figure 2A was 47% [0.55/(0.55+0.63)], whereas the annual net increment of woody parts represented only 16% of the total

fixed carbon (0.55/3.44). Third, note how very different the allocation patterns were in the different stands. We do not know to what extent the differences were due to species, stand age, management, climate, site conditions or errors in measurement. Nevertheless, the magnitude of the differences suggests that important variation exists, some of which may be exploitable. Finally, note that the respiratory losses from foliage and fine roots were proportional to their biomasses, whereas the respiratory losses from woody parts were a function of their surface areas, and so were small relative to their biomasses (Butler & Landsberg 1981). However, whereas the surface area of woody parts increases with tree size, the biomass and respiratory burden of foliage and fine roots remain relatively constant after canopy closure (Rauner 1976; McMurtrie, this volume). This fact means that the *net* dry matter increment of woody parts represents a decreasing proportion of the total net increment with increase in the tree size.

#### IV. ROOT/SHOOT INTERACTIONS

It is widely believed that a functional equilibrium exists between the size and activity of the shoots (which fix carbon) and the size and activity of the fine roots (which take up nutrients and water). In a constant environment favouring continuous growth, the ratio of root/shoot relative growth rates tends to be constant. The root/shoot equilibrium tends to be adaptive; in particular, assimilates are used preferentially by the shoots if conditions limit photosynthesis, and preferentially by the roots if conditions limit nutrient or water uptake.

The root/shoot equilibrium is virtually the only aspect of partitioning in plants that has been modelled non-empirically. In almost all the major plant and crop growth models (ELCROS, SIMCOT, GOSSYM, SIMAIZ, etc) carbon partitioning has been simulated by assuming a specified allometry, by predefining patterns of partitioning, or by pre-assigning priorities to different sinks (Hesketh & Jones 1976; Loomis *et al.* 1979; Penning de Vries & Laar 1982).

Here, I shall briefly consider the predictions of different approaches to modelling root/shoot interactions, and then describe the observed effects on root/shoot partitioning of some environmental, management and plant factors.

##### A. Root/shoot models

There have been basically three approaches to modelling root/shoot assimilate partitioning: (a) the 'whole-plant view' proposed by Davidson (1969) and extended by Thornley (1977) and Charles-Edwards (1976, 1981, 1982), (b) the 'resistance-utilization' approach of Thornley (1977), and (c) a 'storage-pool' model proposed by Reynolds and Thornley (1982). All of them are relevant to trees if we redefine roots as only the fine roots, and shoots as the foliage.

The whole-plant view is based on the relationship:

$$W_R \sigma_R / f_m = W_S \sigma_S / f_c \quad (1)$$

where  $W_R$  is the root mass,  $W_S$  is the shoot mass,  $\sigma_R$  is the specific activity of the roots (eg the rate of nitrogen uptake per unit root mass),  $\sigma_S$  is the specific activity of the shoots (normally the rate of carbon assimilation per unit shoot mass),  $f_m$  is the nutrient composition of an increment of new plant dry matter (eg percentage nitrogen), and  $f_c$  is its carbon composition. The root/shoot ratio  $W_R/W_S = f_m \sigma_S / f_c \sigma_R$  and the proportion partitioned to roots becomes:

$$\text{root fraction} = f_m \sigma_S / (f_c \sigma_R + f_m \sigma_S) \quad (2)$$

Equation (2) states that the proportion of new plant dry matter partitioned to roots will decrease if (a) the root specific activity,  $\sigma_R$ , increases (eg with improved nutrition, see below), (b) the nutrient composition of new plant dry matter,  $f_m$ , decreases (eg with increased partitioning to wood, see below), and (c) the rate of carbon assimilation by the shoots,  $\sigma_S$ , decreases (eg as a result of shading) (see Fig. 4A).

The balanced 'resistance-utilization' model of Thornley (1977) makes the assumptions that (a) carbon, C, and nitrogen, N, are transported passively, at rates dependent upon concentration gradients divided by resistances in the pathway, and (b) the rates at which C and N are utilized by the shoots and roots depend upon their masses and the concentrations of C and N in the substrate (Fig. 4B). This model predicts similar changes in partitioning to those expressed in Figure 4A, resulting from changes in substrate C/N ratio. Under steady-state conditions, the relative growth rates of shoots and roots are in constant ratio to each other, and if the root/shoot ratio is perturbed, this brings about changes in C and N substrate concentrations that lead to a return to steady-state conditions (Fig. 4B).

The 'storage-pool' model proposed by Reynolds and Thornley (1982) does not invoke assimilate transport resistances, which cannot easily be measured, but instead supposes that there are two storage pools, one for C and one for N (Fig. 4C). The model is a further advance, in that it allows suboptimal and optimal partitioning strategies to be compared, assuming that an optimal strategy is one giving the greatest plant relative growth rate. The model suggests that, when  $\sigma_R$  is low (in nutrient-poor conditions), the root/shoot ratio will be lower with an optimal strategy than with a fixed or suboptimal strategy, but the situation will be reversed when  $\sigma_R$  is high. Trees, which must endure a range of environments, may not adopt optimal partitioning strategies in their native environments. They may, for instance, partition less to foliage and more to roots than would be needed to maximize their relative growth rates, and hence to perform well as crop plants (see Bowen, this volume).

## B. Effects of nutrition

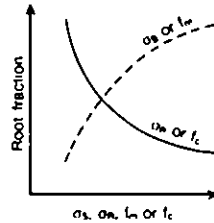
There are numerous papers, on woody and herbaceous species, showing that high levels of nutrient supply increase shoot growth relative to root growth (Ledig 1983 lists 24 papers): A few papers give sufficient information to allow estimates to be made of specific root activity in relation to nutrient supply, elemental composition and root/shoot partitioning. Two examples are given

## A. Whole plant view

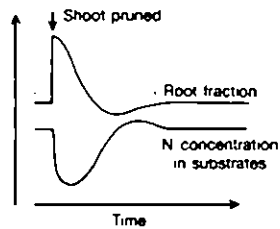
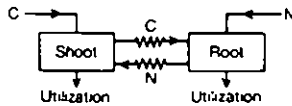
$$\text{Root fraction} = f_r \sigma_r / (f_r \sigma_r + f_s \sigma_s)$$

$\sigma_r, \sigma_s$  = root and shoot specific activities

$f_r, f_s$  = carbon and nutrient elemental composition



## B. Resistance-utilization model



## C. Storage-pool model

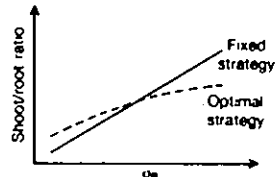
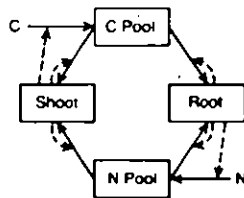


FIGURE 4. Models of root/shoot interactions in plants, and their predictions.  
 A. Whole-plant view of Davidson (1969), modified by Thornley (1977) and Charles-Edwards (1982).  
 B. Resistance-utilization model (balanced version) of Thornley (1977).  
 C. Storage-pool model of Reynolds and Thornley (1982).

in Figure 5. In both instances, specific root activity ( $\sigma_R$ ), percentage N content of the tissues, and partitioning to shoots increased with increase in N supply. Also, the form of the relationships between  $\sigma_R$  and the proportion of dry matter partitioned to roots and shoots was similar to that expressed in equation (2) (Fig. 4A). Furthermore, Ingestad's experiments showed that birch seedlings adapted rapidly to changes in rate of N supply so that tissue concentrations of N and growth rates were balanced in the manner predicted by Thornley's models. Also, it should be noted that increased N supply increased the proportion of dry matter partitioned to stems (Fig. 5B).

In the past, explanations for increased above-ground dry matter production in trees in response to improved nutrition have been sought mainly in terms of increased foliage biomass and/or photosynthetic rates. But, bearing in mind the high carbon cost of fine roots, more researchers are realizing that greater

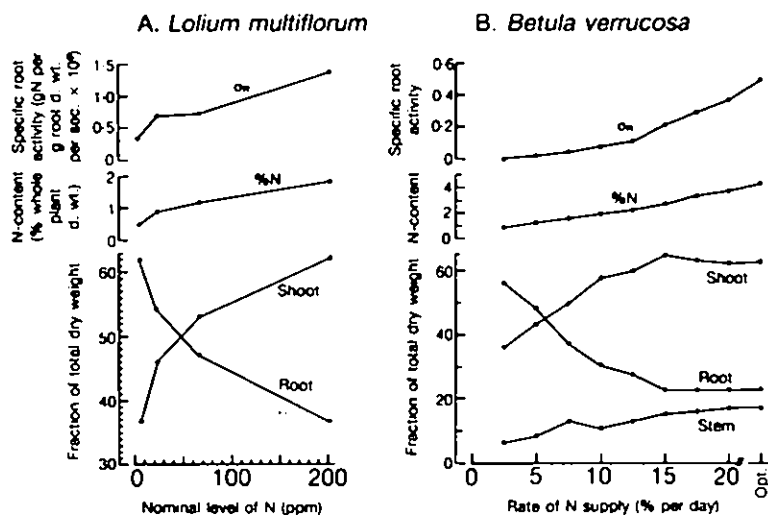


FIGURE 5. Effects of differences in N level or supply rate on the specific root activity, the percentage N in plant dry matter, and the proportion of dry matter in plant parts. A. *Lolium multiflorum* grown in sand culture with different nominal levels of N provided in watering solutions (Charles-Edwards 1982).

B. *Betula verrucosa* seedlings grown with their roots in a nutrient mist, supplying N at different rates according to demand for 80 days, maintaining constant N concentrations in the tissues (Ingestad & Lund 1979; Ingestad 1979).

weight must be given to the effect of improved nutrition on root/shoot partitioning (Linder & Rook 1984).

Maggs (1961) showed that N nutrition of young pot-grown apple trees increased the total annual dry matter production per tree by only 1.3%, but it altered root/shoot partitioning so as to increase above-ground dry matter production by 5.9% (Fig. 6A). More dramatically, Keyes and Grier (1981), working on 40-year-old stands of *Pseudotsuga menziesii* in Washington State, showed that trees growing in a fertile soil produced only about 17% more total dry matter per hectare per year than similar trees growing in an infertile soil, but the former were producing about 88% more dry matter above-ground, largely owing to decreased fine root turnover (Fig. 6B).

However, the best data on the effects of improved nutrition on assimilate partitioning in trees were reported by Linder and Axelsson (1982), who supplied a complete nutrient solution, daily from mid-May to mid-September for six years, to plots of the *Pinus sylvestris* trees illustrated in Figure 2A. Figure 7 shows the measured annual carbon budget of the trees at age 20 compared with untreated controls. The treated trees were over twice as large in dry biomass as the untreated trees, and were fixing over twice as much dry matter per year (22.24 compared with 11.60 t ha<sup>-1</sup> yr<sup>-1</sup>, with leaf area index 3.0 compared with 1.4). Most importantly, the treated trees partitioned only about 31% of their assimilates to roots, compared with 59% in the untreated trees – representing a similar dry weight of 6.9 t ha<sup>-1</sup> yr<sup>-1</sup> in both cases. Fine

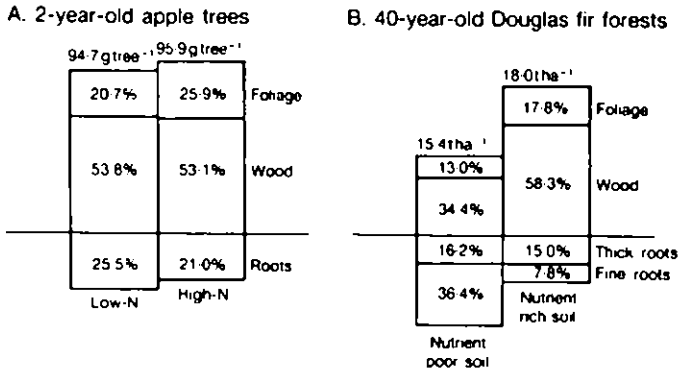


FIGURE 6. Effects of nutrition on the annual production and distribution of dry matter in trees.

- A. Two-year-old apple trees grown in pots outside at East Malling, Kent, England, in a low-N compost; the high-N treatment received  $2 \text{ g tree}^{-1}$  of ammonium nitrate every two weeks during the growing season (Maggs 1961).
- B. Forty-year-old stands of *Pseudotsuga menziesii* in Washington State, USA, growing either in infertile loam-sand, low in N, and with a low base saturation, or in fertile colluvial soil, with 33% base saturation (Keyes & Grier 1981). Fine root increments were estimated by soil core sampling and root observations through underground windows.

root turnover, derived as the residual term needed to balance the budgets, was only  $2.48 \text{ t ha}^{-1} \text{ yr}^{-1}$  on the treated trees compared with  $4.00 \text{ t ha}^{-1} \text{ yr}^{-1}$  on the untreated trees. In consequence, improved nutrition greatly increased partitioning to foliage (from 12% to 20%) and to wood (28% to 49%) and increased the proportion of assimilates used in stem growth from 8% to 14%.

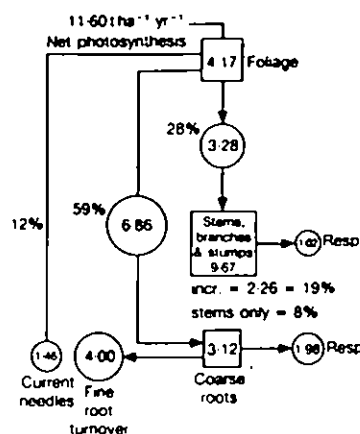
If we look again at the dry matter increment budgets for the three conifer plantations given in Figure 3B, C and D, we find that the stands that produced most above-ground and total dry matter (B =  $35.2 \text{ t ha}^{-1} \text{ yr}^{-1}$ , C =  $30.6 \text{ t ha}^{-1} \text{ yr}^{-1}$ , D =  $18.0 \text{ t ha}^{-1} \text{ yr}^{-1}$ ) also partitioned least to roots (B = 24%, C = 42%, D = 66%). It is tempting to suggest that one of the factors involved was a difference in soil fertility, although differences also existed in age, species and water relations.

In conclusion, there is growing evidence that decreased partitioning to fine roots is one of the most important mechanisms by which improved nutrition increases above-ground dry matter production. This fact could not have been appreciated in tree nutrition studies that did not include estimates of fine root turnover (eg Brix & Ebell 1969; Miller & Miller 1976).

### C. Effects of water stress and shade

Root/shoot models predict that a drought-induced decrease in root-specific activity with respect to water uptake would increase root relative to shoot growth. Gales (1979) found 19 papers which reported this predicted effect,

## A. Untreated



## B. Nutrient solution

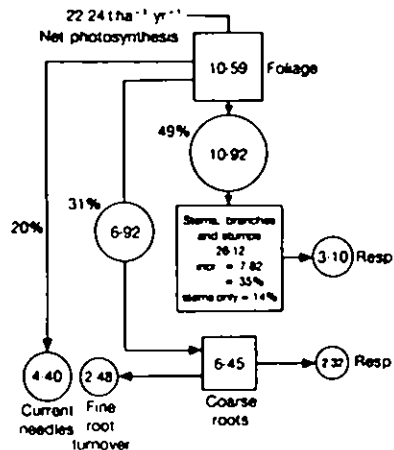


FIGURE 7. Current annual dry matter budgets of 20-year-old *Pinus sylvestris* trees, A untreated, and B supplied for 6 years with a complete nutrient solution from mid-May to mid-September representing 3 mm of water per day. The trees were in the same location as those illustrated in Fig. 2A, at age 14. Squares: biomass (t ha<sup>-1</sup>); circles: fluxes (t ha<sup>-1</sup> yr<sup>-1</sup>). The areas of the squares and circles are proportional to the values. These values can be converted to kg Cha<sup>-1</sup> yr<sup>-1</sup>, as given by Linder and Axelsson (1982), by multiplying by 500.

and nine which did not. It appeared that, where levels of soil nutrients were low (especially P), drought could exacerbate nutrient deficiency as well as induce water stress, and the net effect was increased or unchanged root/shoot relative growth rates. However, when P levels were high, water stress generally increased the root/shoot ratio, and indeed it is often recommended practice to withhold irrigation to promote deep rooting when establishing tropical trees in drought-prone areas. Conversely, if irrigation can be maintained throughout the year, this may decrease the carbon demand of the roots, and, like nutrition, increase above-ground dry matter production (Evans 1980).

Numerous shading experiments have shown that the resulting decrease in shoot-specific activity (net photosynthetic rate) is accompanied by greater partitioning to the shoots (see Ledig 1983). Where this effect has not been found, the results can often be explained by confounding with nutrient levels, water stress or ontogenetic drifts in root/shoot relative growth rates. Increased shoot growth in shade argues in favour of growing shoot- or leaf-yielding plants such as forage crops, spinach or tea in the understorey of agroforests (Cannell 1983). One may also speculate that high levels of solar radiation and seasonal droughts in the tropics would favour higher root/shoot relative growth rates than in temperate regions. Cripps (1971) noted that the root/shoot ratios of young apple trees in Western Australia were about 1:1, whereas similar trees in England had root/shoot ratios of about 1:2. He suggested that this was why reduced shoot growth and early cropping occurred naturally in

Western Australia, but has to be induced by using dwarfing rootstocks or chemicals in England.

#### D. Effects of pruning

Shoot pruning temporarily checks root growth, while root pruning temporarily checks shoot growth. As would be predicted using Thornley's models, the more is pruned off, the greater is the check in growth, and the longer it takes for the plants to recover the root/shoot relationship that existed before pruning (beans, Brouwer 1962; apple, Maggs 1965; orange, Alexander & Maggs 1971; peach, Richards & Rowe 1977). Thus, shoot pruning is a means of promoting new shoot growth (eg when stimulating a 'pruning response'), and root pruning is a means of promoting new root growth (eg when undercutting nursery seedlings).

#### E. Seasonal and plant factors

In trees, the functional balance between roots and shoots is normally perturbed by changes in the environment, and by periodicity in the activity of the shoot meristems. In temperate regions, assimilates are usually used preferentially by the shoots during elongation or 'flushing' in spring or early summer, and preferentially by the roots in autumn (Fig. 8A; Cannell & Willett 1976; McLaughlin *et al.* 1979; Isebrands & Nelson 1983). Work on conifer seedlings showed that, over a succession of seasons, the root/shoot relationship remained in balance, but within any season the trees developed a relatively high root/shoot ratio in the autumn, which was restored to equilibrium when shoot elongation occurred the following spring (Cannell & Willett 1976). Furthermore, the shorter the period of shoot elongation, the greater the root/shoot ratio each autumn (Fig. 8A comparing Oregon and Alaskan provenances). In tropical regions, we would expect assimilates to be used preferentially by the shoots during periods of rapid shoot growth at the start of (or during) each rainy season, and preferentially by the roots during dry and/or cool seasons, as is roughly the case for coffee in Kenya (Fig. 8B). There are, of course, numerous variations on the two partitioning patterns shown in Figure 8, and neither describes the movement of storage carbohydrates.

Tree shoot growth is often intermittent, even in constant environments. In seedlings of temperate-zone pines and oaks, intermittent shoot growth is often paralleled by equal and opposite fluctuations in root growth (eg pines, Drew & Ledig 1980; Drew 1982; oaks, Reich *et al.* 1980). Similar fluctuations may also occur in tropical trees with periodic shoot growth. Alternatively, Borchert (1973, 1976) suggested that root growth may be constant, but that rapid shoot growth periodically outstrips the ability of the roots to supply the shoots with water, thereby inducing water stress, checking leaf expansion, and producing intermittent shoot elongation.

Whatever the mechanism, endogenously or environmentally induced perturbations in root/shoot relationships seem eventually to be restored by



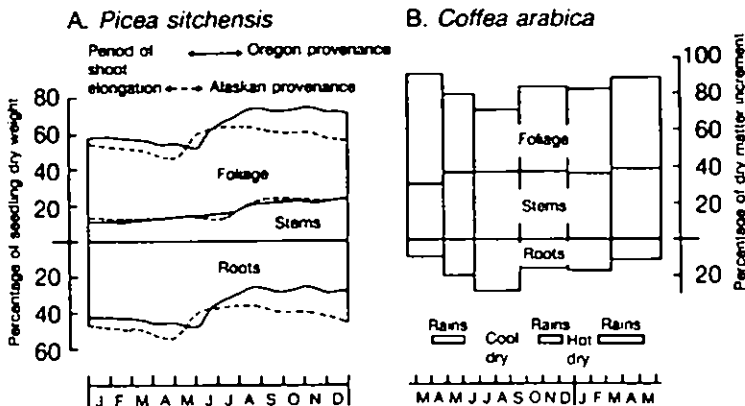


FIGURE 8. Seasonal changes in the distribution of dry matter in trees.

- A. *Picea sitchensis* seedlings of Denmark, Oregon ( $42^{\circ}51'N$ ) and Cordova, Alaska ( $60^{\circ}30'N$ ) provenance, during their second year, growing in pots in a nursery at Bush, Midlothian, Scotland (Cannell & Willett 1976; from their Fig. 3).
- B. *Coffea arabica* trees, during their fourth year, growing in deep loam at Ruiru, Kenya. The leaf fraction includes flower buds, but there were no fruits because the trees were deblossomed (Cannell 1971). Note that this figure shows the distribution of *increment*, whereas A shows the distribution of *biomass*.

feedback mechanisms as predicted in root/shoot models. When examining root/shoot ratios in trees, it is important to distinguish the long-term equilibrium from the short-term fluctuations (Cannell & Willett 1976).

To complete this account, attention should be drawn to the genetic differences in root/shoot balance that exist between and within tree species. Ledig (1983) suggested that species of early seral stages have smaller root/shoot relative growth rates than those from later seral stages. There has also been debate about the optimal root/shoot investment strategy of trees and other plants in xeric and mesic habits with regard to survival, growth and the carbon cost of constructing and maintaining mesophytic and xerophytic leaves (see Orians & Solbrig 1977; Mooney *et al.* 1978). Clearly, within-species variation in root/shoot relationships may offer important opportunities for genetic advance in yield.

## V. FRUITING

### A. Fruits and seeds as priority sinks

Whereas the growth rates of roots and shoots may fluctuate with time, and may often be below their potential rates, the growth rates of seeds tend to be constant during the period of endosperm filling (eg cereals, Biscoe & Gallagher 1977; Martinez-Carrasco & Thorne 1979; coffee, Cannell 1974). Within limits, the final weights of seeds (beans, grains and nuts) are often inherently fixed, and are less variable than other components of seed or fruit yield (Harper

1977). Seeds may therefore be described as 'priority sinks', or as having a large 'sink strength' or 'mobilizing ability' (Wareing & Patrick 1975). More exactly, they seem to be able to generate and maintain steep gradients in sieve-tube assimilate concentrations or pressure potentials so as to promote assimilate flow from distant leaf sources (Gifford & Evans 1981; Thorpe *et al.* 1983). In this sense, the fleshy parts of fruits are less competitive sinks, because their growth rates and final sizes are more affected when, for instance, there is a decrease in leaf/fruit ratio (eg coffee, Cannell 1974; apple, Heim *et al.* 1979). Seeded fruits can draw assimilates from leaves at least one metre away, so it is possible to manipulate trees so that the fruits are to some extent physically separated from the foliage (Parry 1974; Hansen 1977). We may expect that fruits of different species differ in 'sink strength', depending upon the numbers and sizes of the seeds they contain, and perhaps on the numbers of cells developed during their early stages of growth. Golden Delicious apples seem to be weaker sinks than Graasten apples, in that their growth rates are lower at a given leaf/fruit ratio, and they are less able to attract assimilates from distant leaves (Hansen 1977).

The total assimilate demand per tree of the seeds and fruits depends on their number. Most mature trees are capable of producing more flowers, in some years, than they can sustain to fruit maturity. Their strategy is to adjust fruit numbers to match assimilate and nutrient resources by flower or fruit abortion. June drop of apples in Europe has counterparts in cherelle wilt of cacao, abortion of button coconuts, and citrus and coffee fruit drop two to four months after anthesis. Young fruits often seem, at some stage, to be weak sinks compared with the shoot tips, especially when there is environmental stress (eg Quinlan & Preston 1971). Lloyd (1980) suggested that the optimal strategy to produce full-sized fruits and seeds was to initiate the maximum number of flowers that could be supported; then, if future resources were certain to be limiting, abortion would occur early, whereas if resources were less certain to be limiting, or if there was a high risk that fruits would be lost later on from pests, pathogens or predators, abortion would be delayed. In Arabica coffee, fruit drop rarely occurs after the stage of fruit expansion (before endosperm filling) possibly because, in its native shady habitat, coffee initiates relatively few flowers, so that it is likely that all can be sustained to produce full-sized seeds (Cannell 1974). By contrast, mango can drop its fruits at any time during their development, possibly because such large fruits are likely to be attacked at any stage by pests, pathogens or predators. It might be argued that, when fruit or nut trees are brought into cultivation, we increase the certainty of resources being adequate to sustain fruit and seed growth, and so we need to decrease the trees' susceptibility to flower or fruit abortion. Conversely, if the trees bear irregularly in nature, and we manage them to bear fruits every year, some propensity for flower or fruit abortion might be desirable.

Oil palm is an interesting special case, in which the single, large vegetative apex seems to take precedence over the fruit bunches for carbohydrates and nutrients. Defoliation decreases fruit production by increasing abortion of young inflorescences or by restricting fruit growth, but it rarely decreases the growth rate of the vegetative growing points (Corley 1973).

So far, I have assumed that carbon is the resource limiting fruit and seed growth, but very often it is a mineral element (Harper 1977; Thompson & Stewart 1981; Swank *et al.* 1982). The mineral content of seeds is four to seven times greater than that of wood. In Arabica coffee in Kenya, the flower buds alone took nearly 40% of the total P uptake of the trees during a dry season and, during an 87-day period, the fruits on heavily fruiting trees took 89%, 95%, 98% and 99% of the total tree uptake of Mg, K, N and P, respectively, compared with 72% of the dry matter (Cannell 1971; Cannell & Kimeu 1971).

### B. Effects of fruits on partitioning

In forest trees, it might be argued that fruiting has little effect on vegetative growth because (a) the reproductive parts represent a relatively small proportion of the total above-ground dry matter increment (Fig. 1C); (b) green fruits photosynthesize and refix respiratory  $\text{CO}_2$ , and (c) fruiting often enhances leaf photosynthesis. However, there is ample evidence that cone and seed production can reduce wood and/or foliage production (conifers, Danilow 1953; Eis *et al.* 1965; broadleaves, Harper 1977; Tuomi *et al.* 1982).

The production of 75 cones  $\text{tree}^{-1}\text{yr}^{-1}$  on the 14-year-old *Pinus sylvestris* trees illustrated in Figure 2A would represent 6% of the annual photosynthetic production (Linder & Troeng 1981). In 120-year-old *P. sylvestris* stands in Sweden, cone production of  $0.21 \text{ t ha}^{-1}\text{yr}^{-1}$  dry weight, with an additional estimated respiratory cost equal to 50% of the cone dry weight, was estimated to represent 10–15% of the carbon cost of stemwood production (Linder & Troeng 1981). Earlier, Fielding (1960) reached a similar conclusion for *Pinus radiata* in Australia, but ignoring respiratory costs; over a 40-year rotation, trees produced about  $1.1 \text{ t ha}^{-1}\text{yr}^{-1}$  of cones and pollen, which was equivalent to about  $3.0 \text{ m}^3 \text{ ha}^{-1}\text{yr}^{-1}$  of stemwood, or 16% of the mean annual increment on medium-quality sites. In both the *P. sylvestris* and *P. radiata* studies, the mineral nutrient cost of cone production might well have been 40–50% of the mineral cost of stemwood production (Matthews 1963).

Clearly, the carbon and mineral costs of fruiting will not be solely at the expense of wood production, but, even so, selection for non-fruiting forest trees could enhance stemwood production by several per cent. Conversely, inadvertent selection by tree breeders for enhanced fruiting at maturity might cancel out a significant proportion of the genetic gain observed within juvenile progeny tests.

In dioecious species (eg *Populus* spp. and *Fraxinus excelsior*), it has been suggested that male trees grow faster than females, because they carry a smaller reproductive burden (Matthews 1963; Harper 1977), and this is often the case if the females have a consistently large percentage fruit set (Grant & Mitton 1979). However, in other cases, the males may grow slower than the females, because the expenditure on male reproductive structures is concentrated in the spring and so reduces or delays foliage development (Gross & Soule 1981).

In fruit trees, the heavy demands of the fruits greatly distort the pattern of carbon partitioning among vegetative parts, including the root/shoot balance.

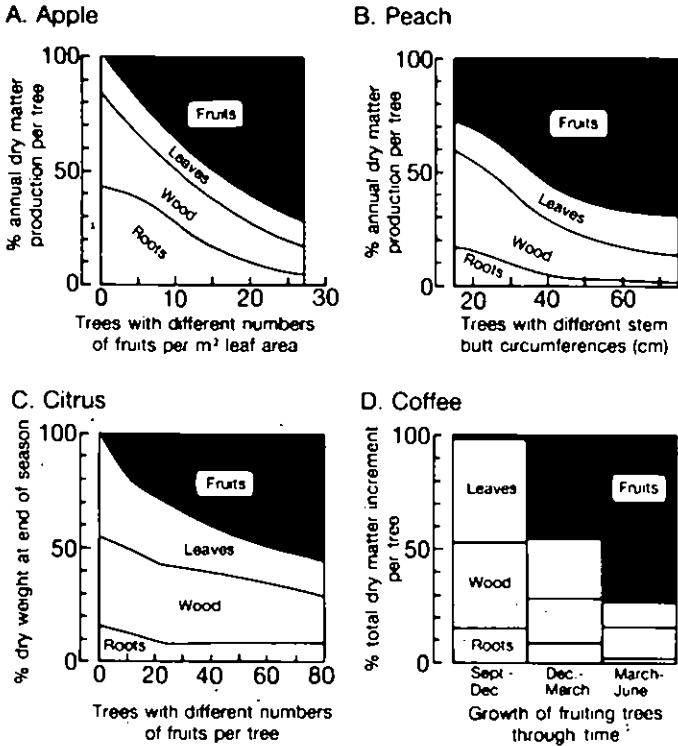


FIGURE 9. Partitioning of dry matter in fruit trees.

- A. Apple (Golden Delicious), 3-4 years old, growing in pots in England and France (Heim *et al.* 1979).  
 B. Peach (Golden Queen), 4-15 years old, growing in Australia (Chalmers & Ende 1975).  
 C. *Citrus madurensis* (Lenz 1979).  
 D. *Coffea arabica*, 4 years old, growing in Kenya (Cannell 1971).

Studies on apple, peach and coffee have all shown that root growth suffers most (Fig. 9, also Maggs 1963; Avery 1970; Hansen 1971a). In England, relatively light crops of fruits greatly reduce new root growth on apple trees during July to October (Head 1969). The explanation usually given is that the roots are furthest from the leaves, and that over such long distances there is a path resistance to assimilate movement (Heim *et al.* 1979), although the resistance to assimilate flow in both angiosperm and gymnosperm phloem is very low (Watson 1980). An alternative explanation is that the root apices are inherently 'weak' sinks compared with the shoot apices, but there is no evidence for this in the vegetative plant (Warren-Wilson 1972). Stem and branch growth is less restricted by fruiting than root growth, and, in apple and peach, the proportion of the total dry matter increment taken by leaves is relatively constant, irrespective of fruiting level (Fig. 9). Fruiting, therefore, reveals an order of priority among the carbon sinks which may be expressed

as differences in their growth rates at different leaf/fruit ratios; the order is usually seeds > fleshy fruit parts = shoot apices and leaves > cambium > roots > storage. If true, this will also be the sequence in which vegetative parts are first affected by fruiting; that is, assimilates will be withdrawn from storage first, then withheld from roots, and so on.

If fruiting greatly decreases the mass of fine roots,  $W_R$ , relative to the foliage mass,  $W_S$ , and equation (2) is to hold, then there must be a corresponding increase in specific root activity,  $\sigma_R$ , or a decrease in plant elemental composition,  $f_m$ . (There is ample evidence that  $\sigma_S$  does not decrease.) Studies on apple (Hansen 1971a, b), coffee (Cannell & Kimeu 1971), and tomato (Richards *et al.* 1979) have shown that, at moderate fruiting levels, the main change in

TABLE II. Rate of uptake of nutrients per unit of root dry weight ( $\text{mg g}^{-1}$  harvest interval<sup>-1</sup>) in 4-year-old Golden Delicious apple and Arabica coffee trees, expressed as a percentage of that in non-fruiting trees

Crop	Fruiting level	N	P	K	Ca	Mg
Apple	Heavy <sup>1</sup>	146	170	299	166	157
Coffee	Moderate <sup>2</sup>	165	500	216	176	150
Coffee	Very heavy <sup>3</sup>	101	86	162	86	110

<sup>1</sup> Derived from Hansen (1971a and b), for the period of one year, assuming the fruiting and non-fruiting trees had an average of 1,000 g and 350 g roots tree<sup>-1</sup> respectively during the year. The fruits took 53% of the total dry matter increment. The trees were grown in containers outdoors in Denmark.

<sup>2</sup> From Cannell (1971) and Cannell and Kimeu (1974) for an 82-day period. Root weight included only those roots < 1 mm diameter. The fruits took 29% of the total dry weight increment. The trees were growing in a plantation in Kenya.

<sup>3</sup> As for 2, for an 87-day period during which the fruits took 72% of the total dry matter increment.

equation (2) is a large increase in  $\sigma_R$  (Table II). In tomato, the overall plant  $f_m$ , including fruits, remains relatively constant, while in apple and coffee, fruiting trees can have higher concentrations of some nutrients (eg Ca) in their leaves than non-fruiting trees (Hansen 1971b; Cannell & Kimeu 1971). However, at very high fruiting levels,  $\sigma_R$  values in coffee can fall below those in non-fruiting trees (Table II), associated with almost zero root growth and 'dieback' of the shoots. Thus, 'overbearing dieback' may be due more to the high demand of the fruits for mineral nutrients, combined with the distance of the roots from assimilate sources, rather than to direct diversion of assimilates from shoots to fruits.

## VI. ABOVE-GROUND VEGETATIVE PARTS

### A. Effect of harvesting vegetative parts

Whereas the removal of fruits from trees *increases* vegetative growth and the potential to produce future fruit yield, the removal of vegetative parts such as

foliage, fuelwood or extractives *decreases* vegetative growth and the potential to produce future vegetative yield. Thus, in tea, the plucking of young shoots, representing only 8.3% of the total annual dry matter production, decreased total dry matter production by 35.7%, compared with unplucked bushes (Fig. 10A). And, in rubber, the removal of latex, representing only 7.2% of the total annual dry matter production above-ground, decreased total dry matter production by 29.6%, compared with untapped trees (Fig. 10B). Thus, the energy cost of vegetative yield is much greater (about 4 times) than the energy content of the parts that are harvested.

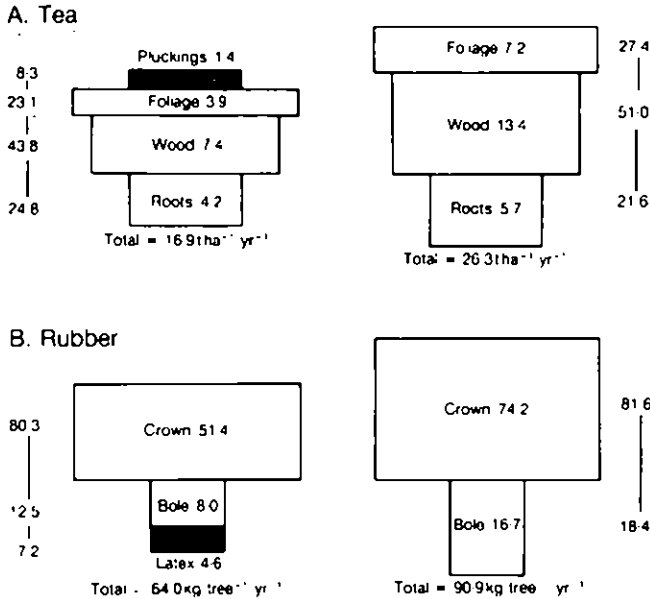


FIGURE 10. Effect of removing vegetative yield on the current annual production and distribution of dry matter in trees ( $\text{t ha}^{-1} \text{yr}^{-1}$ ). Marginal numbers are percentages. A. Tea, plucked and unplucked bushes in Kenya (Magambo & Cannell 1981). B. *Hevea* rubber, tapped and untapped trees in Malaysia, means of six clones (Templeton 1969).

Simmonds (1982) suggested that high-yielding rubber clones might be selected by looking for clonal differences in the inverse relationship between the amount of latex removed and the decrement in total tree dry matter production (see Raven, this volume). Templeton (1969) had earlier shown that the removal of latex from rubber had less effect on total dry matter production in some clones than others. A similar approach could be adopted in the selection of high-yielding fodder and fuelwood trees.

## B. Partitioning between wood and foliage

In Figure 1A, it was shown that the proportion of the above-ground dry matter increment allocated to wood, as opposed to foliage, varied greatly

among forest stands. Some of this variation will be due to environmental, management and exploitable genetic variation, although, as discussed below, we know surprisingly little about how these factors influence wood/foilage partitioning.

Wood/foilage partitioning is important, partly because it influences wood yield, but also because it influences the parameters in equation (2). New woody tissues have a lower nutrient content than foliage, so increased partitioning to wood decreases the average nutrient content of new dry matter increment ( $f_m$ ). This decreased nutrient demand should lessen the proportion of assimilates taken by roots (Fig. 5A), and increase the amount of new dry matter that can be produced per unit of nutrient.

Let us consider some of the factors that might influence wood/foilage partitioning.

### 1. *Variation with latitude*

Jordan (1971) postulated that trees adapted to low light intensities at high latitudes might devote more carbon to structural tissues, and less to foliage, than trees adapted to more equatorial conditions. He reasoned that, at low light intensities, there would be a greater selective pressure to produce stemwood, in order to overtop competitors, than at high light intensities. In support of this contention, he reported a decrease in the ratio of annual wood production to annual litterfall with increase in total possible incident solar radiation during the growing season, using data for 26 forest stands spanning cold temperate to tropical regions. In other words, proportionately more carbon was allocated to wood at high latitudes. This was not clearly the case among the 28 forest stands studied in the International Biological Programme (O'Neill & DeAngelis 1981), but the 204 broadleaved forest stands in the 'forest production data set' (Fig. 1; Cannell 1982) showed a significant, although weak, positive relationship between the percentage of the current above-ground dry matter increment allocated to wood and latitude ( $r = 0.28$ ). No such relationship existed for the 303 conifer stands, because no values existed for stands at latitudes less than 31°N or S.

### 2. *Relationship with 'vigour'*

Several authors have suggested that the cambium has a lesser priority for assimilates than the fine roots or foliage, so that the proportion of carbon allocated to wood might increase with increase in net photosynthesis or total net dry matter production per tree or per hectare (eg Gordon & Larson 1968; Rangnekar & Forward 1973; Waring *et al.* 1980). In support of this argument, the 'forest production data set' revealed a significant trend towards greater allocation to wood with increase in total dry matter production, accounting for 14% and 18% of the variation in percentage allocation to wood among the 204 broadleaved and 303 coniferous stands, respectively (Fig. 11). The IBP woodland data set revealed a similar trend, expressed by O'Neill and DeAngelis (1981) as an increase in current annual wood increment per unit of annual litterfall with increase in total above-ground dry matter production.

Among the studies in the 'forest production data set' there were four in which current net dry matter production had been estimated for comparable

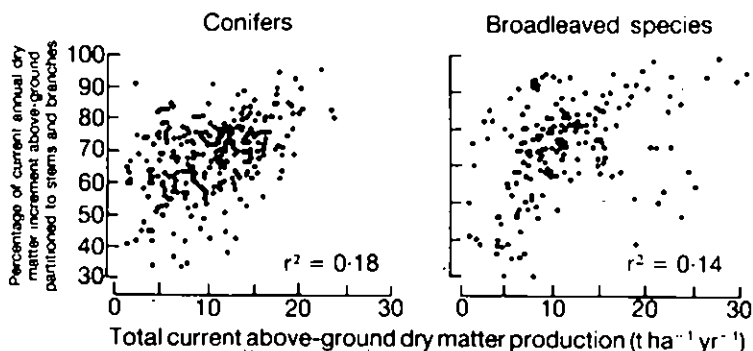


FIGURE 11. Percentage of the current annual dry matter increment above-ground taken by the woody parts (stems and branches, and including cones and fruits) in stands of conifers and broadleaved forest trees, as a function of their total current annual above-ground dry matter production.

Data are for forest stands of all types, ages, planting densities, etc. at various sites throughout the world, from Cannell (1982), as in Fig. 1A. Outlying values in the bottom-right of the graphs probably indicate failure to fully account for woody litterfall and/or tree mortality.

forests growing on neighbouring infertile and fertile sites. In all four studies, a smaller proportion of the above-ground dry matter increment was allocated to wood on infertile sites than on fertile sites, but only by a few per cent (Table III, average difference 5.5%; see also Satoo & Madgwick 1982, their p. 106). No consistent difference in wood/foilage partitioning existed between stands with and without fertilizers (Table III). The Swedish experiment, illustrated in Figure 7, on the effects of applying a nutrient solution to mature *Pinus sylvestris*, showed only a small effect on wood/foilage partitioning. Thus, on untreated trees, the  $4.74\ t\ ha^{-1}\ yr^{-1}$  ( $3.28 + 1.46$ ) of above-ground dry matter increment was partitioned 30.8% to foliage and 69.2% to wood, whereas in treated trees the  $15.32\ t\ ha^{-1}\ yr^{-1}$  ( $10.92 + 4.40$ ) of above-ground dry matter increment was partitioned 28.7% to foliage and 71.3% to wood (Fig. 7; see also Waring 1983; Linder & Rook 1984). Further support for slightly increased partitioning to wood with increase in nutrient supply comes from Ingestad's studies on *Betula verrucosa* seedlings illustrated in Figure 5B. However, the abundant evidence that fertilization increases ring widths, wood production and wood production per unit leaf area does not, of itself, provide any information on wood/foilage partitioning (cf Waring 1980).

Overall, the evidence strongly supports the conclusions that foliage and wood production are closely coupled, and that any effects of fertilization on increasing wood/foilage partitioning are much less important than its effects on increasing shoot/root partitioning.

### 3. Effect of tree age and size

Within the 'forest production data set', stand age accounted for only 6% and 3% of the variation in percentage of current net above-ground dry matter increment partitioned to wood in broadleaved and coniferous forest stands,



TABLE III. Effects of site 'quality' and fertilizer application on the proportion of the current net dry matter increment above-ground allocated to wood (stems and branches) as opposed to foliage (data from Cannell 1982)

Species	Country	Net dry matter increment above-ground (incl. litterfall) allocated to wood (%)		Reference	Page number in Cannell (1982)
		Infertile sites	Fertile sites		
<i>Picea abies</i>	Japan	70	73	Satou 1971	169
<i>Pinus banksiana</i>	Canada	65	70	Doucet <i>et al.</i> 1976	48-49
<i>Populus grandidentata</i>	USA	67	78	Koerper & Richardson 1980	268
<i>Pseudotsuga menziesii</i>	USA	73	76	Keyes & Grier 1981	333
<i>Pinus nigra</i>	Scotland	No fertilizer	Fertilizer applied <sup>1</sup>	Miller & Miller 1976	246
<i>Pinus sylvestris</i>	Finland	68	66	Paavilainen 1980	64
<i>Eucalyptus globulus</i>	Australia	80	77	Cromer <i>et al.</i> 1980	10
		60	64		

<sup>1</sup> Means of all fertilizer treatments.

respectively. Closer examination of particular studies showed that partitioning to wood was usually constant, or declined, with age after canopy closure, but in some studies there was an increase in partitioning to wood during the years before canopy closure (Fig. 12). It is tempting to conclude that, in young trees, the proportion of dry matter taken by the cambium is limited by the size of the cambial sink. If this is so, then the greatest *H.Incr.* of wood will be obtained when the trees are allowed to grow moderately tall. There is some suggestion of this in the literature on mini-rotation forestry (Cannell & Smith 1980; Heilman & Peabody 1981). Conversely, the greatest *H.Incr.* of foliage will be obtained when the trees are kept small, by pruning or coppicing, and

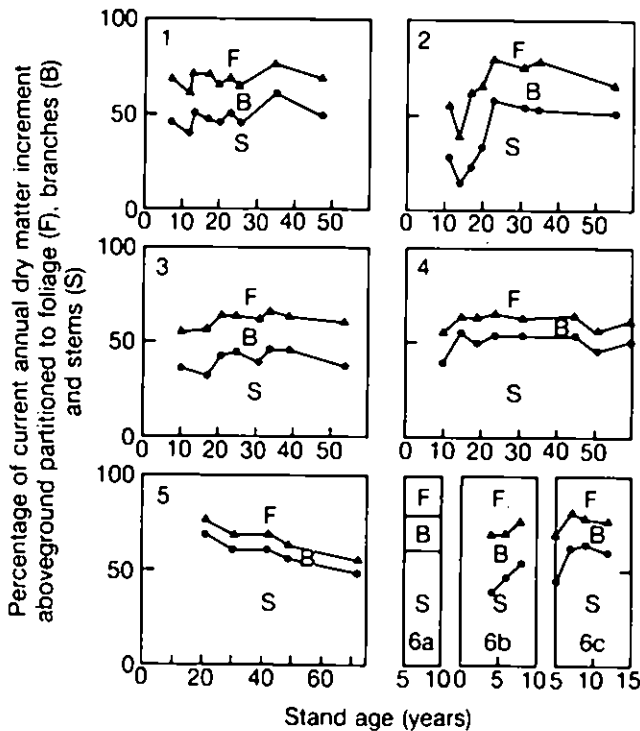


FIGURE 12. Age trends in the percentage distribution of annual above-ground dry matter increment in coniferous forest stands (including litterfall). F = foliage; B = branches and cones; S = stems.

1. *Pinus densiflora*, Japan (quoted by Satoo & Madgwick 1982).
2. *Pinus sylvestris*, England (Ovington 1957).
3. *Cryptomeria japonica*, Japan, Obi, at wide spacings (435 trees  $ha^{-1}$  at age 45) (Ando *et al.* 1968, see Cannell 1982).
4. As above, at close spacings (1,557 trees  $ha^{-1}$  at age 45).
5. *Pseudotsuga menziesii*, Washington, USA; averages have been taken of duplicate estimates for ages 30 and 42 years (Turner & Long 1975).
6. *Pinus radiata*. (a) Closely planted in New Zealand (Madgwick 1981); (b) New Zealand (Madgwick *et al.* 1977); (c) Australia (Forrest & Ovington 1970).

there is some evidence for this in the study on plucked and unplucked tea bushes (Fig. 10A).

However, in most forests, the size of the cambial sink, expressed as stem surface area, cannot be said to be limiting wood production, or partitioning to wood, for most of the rotation. This fact is self-evident when one realizes that the annual activity of the cambium, in terms of wood volume produced per unit surface area of cambium, is manifestly equal to the width of an annual ring (Duff & Nolan 1957), and, as forests increase in size beyond canopy closure, stem surface area (cambial sink size) increases, while mean ring width (cambial sink activity) decreases. At their maximum, mean ring widths in unthinned stands are below their potential value, as shown by the increase in ring width when forests are thinned. Even in thinned forests, which may have an almost constant stem surface area, there is a decrease in mean ring width with increase in tree size.

#### 4. *Other factors*

Many factors affect cambial activity, as expressed in mean annual ring widths and variation in ring widths along tree boles, but, on this evidence alone, it cannot be said that these factors affect dry matter partitioning. Thus, improved nutrition greatly increases ring widths, but, as we have seen, it may have only a small effect on wood/foilage partitioning. Similarly, thinning increases ring widths, but this increase occurs overwhelmingly because the total dry matter partitioned to wood within the stand is spread over a smaller cambial surface area, without necessarily any change in assimilate partitioning. This point may be illustrated by plotting mean ring widths against total cambial surface area for stands subjected to different degrees of thinning. There is invariably a strong inverse relationship, and, when one considers that there are accompanying changes in stem/branch ratio and mean wood density, it is impossible to conclude from any non-linearity in the relationship that thinning has any effect on wood/foilage partitioning (Hamilton 1976).

Mitchell (1975) was able to model the volume growth of thinned and unthinned forest stands on the assumption that the total wood increment of each tree was a simple function of its foliar volume. Furthermore, changes in ring width and stem basal area could be simulated on the assumption that the annual wood increment was disposed along each bole so as to maintain a constant cross-sectional area increment from the base of the crown to ground level (Pressler's Law, Larson 1963). Inevitably, ring widths decreased (a) from the base of the crown to ground level, with increase in bole circumference, (b) with increase in tree size, and (c) with decrease in crown size, as shown in other studies (Larson 1963; Denne 1979). In other words, variation in ring widths (cambial activity) results from geometrical factors and differences in assimilate supply, and against this background it is difficult to detect effects of management or the environment on the 'sink-strength' of the cambium itself.

Mechanical stress, in the form of bending, wind sway or stem rubbing, is known to stimulate cambial activity, and these treatments can alter the disposition of cambial activity around the bole, and can increase the ratio of radial/height growth. Several studies have shown that total plant dry matter

production is decreased, but there seems to be no quantitative evidence for a change in dry matter partitioning (Jacobs 1954; Larson 1965; Jaffe 1976; Mitchell *et al.* 1977; Rees & Grace 1980; and see Pressman *et al.* 1983).

### C. Partitioning between stems and branches

Numerous estimates have been made of the proportion of stems to branches in the standing woody biomass of forests, but relatively few estimates have been made of the distribution of current net dry matter increment, much less of the allocation of carbon, between stems and branches. Within the 'forest production data set', there were only 44 broadleaved and 47 coniferous stands in which reasonable estimates had been made of branch increments and woody litterfall from stems and branches. Whereas the stems formed, on average, about 79% of the above-ground woody biomass, they took only 57% and 68% of the current above-ground woody increment in the broadleaved and

TABLE IV. Distribution of (a) above-ground woody increment and (b) above-ground standing woody biomass, in broadleaved and coniferous forest stands

	44 broadleaved forests (%±SD)	47 coniferous forests (%±SD)
Age in years	73±37.0	56±56.2
(a) Percentage of above-ground woody increment taken by stems	57±14.9	68±13.4
(b) Percentage of above-ground standing woody biomass in stems	78±9.8	79±10.2

Means of all stands in Cannell (1982) for which estimates existed for woody biomass, increment and litterfall, partitioned to stems and branches. The woody biomass and stem biomass values include bark.

coniferous stands, respectively (Table IV; cf Fig. 1 which gives percentages of the total increment including foliage). However, the estimates of woody litterfall were highly variable, and no significant relationship could be found between the percentage of above-ground woody increment taken by stems and stand age, basal area, height, or total wood increment per hectare.

The carbon budget of Linder and Axelsson (1982) for 20-year-old *Pinus sylvestris* in Sweden (Fig. 7) suggested that the stems (excluding the branches) took only about 40% of the net, and about 28% of the gross (including respiration) carbon allocated to above-ground woody parts, irrespective of treatment. (Stems on untreated and treated trees increased by 0.88 and 3.16 t ha<sup>-1</sup> yr<sup>-1</sup>, respectively.)

It is often assumed that, because inter-tree competition suppresses branch growth, there is a corresponding increase in carbon partitioning to stems. However, the evidence for this fact in widely spaced or conventionally thinned forest stands is rather weak (see age trends in Fig. 12). The clearest evidence

comes from studies on very closely planted stands. Thus, in studies on closely spaced poplars, it was shown that the proportion of above-ground woody increment taken by stems increased with increasing population density, and this proportion increased with increasing inter-tree competition from the first

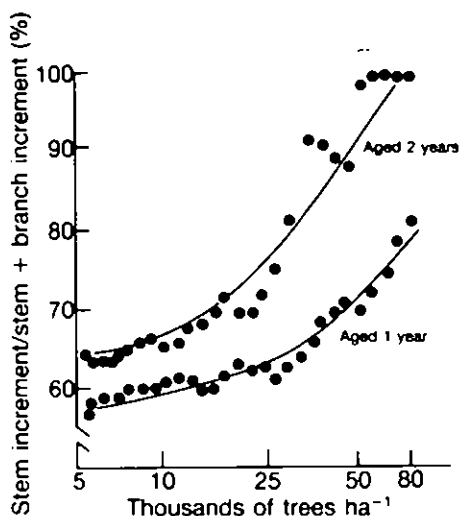


FIGURE 13. Percentage of the net above-ground woody biomass increment allocated to stems (as opposed to branches) in *Populus trichocarpa* grown at a range of close spacings (Cannell 1980).

to the second year of growth (Fig. 13). Satoo and Madgwick (1982) reported increased partitioning to stems in stands of *Pinus densiflora* with over 2,500 stems ha<sup>-1</sup>, and Madgwick (1981) found that more dry matter was allocated to stems in *Pinus radiata* planted with over 6,000 trees ha<sup>-1</sup>, compared with stands at wider spacing (2,500 trees ha<sup>-1</sup>, Madgwick *et al.* 1977; 1,500 trees ha<sup>-1</sup>, Forrest & Ovington 1970; see Fig. 12).

Genetic differences in branchiness are well known, and there are now several studies in which they have been quantified in terms of the proportion of stem- to branchwood in the standing biomass. In young or small trees, which have not yet shed branches, these proportions may satisfactorily reflect differences in dry matter partitioning (Fig. 14A), but in larger trees these proportions may be confounded with differences in branch retention (Fig. 14B). Nevertheless, there are clearly very large differences in stem/branch partitioning within species, which could be exploited to greatly increase stemwood production per unit of foliage on young trees (Cannell *et al.* 1984; Ford, Kärki & Tigerstedt, and Dickmann, this volume).

## VII. CONCLUSIONS

The purpose of this review was to highlight the opportunities to increase tree crop yields by altering dry matter partitioning. In trees yielding vegetative

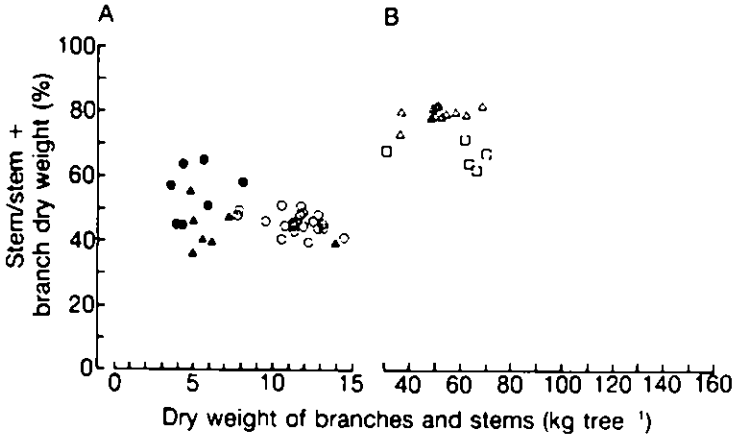


FIGURE 14. Genetic variation within pine species in the proportion of standing woody biomass in the stems (with bark), expressed as a percentage of the total above-ground woody biomass (stems and branches with bark).

- *Picea sitchensis* clones, aged 8 (Cannell *et al.* 1984).
- ▲ *Pinus contorta* clones, aged 8 (Cannell *et al.* 1984).
- *Pinus virginiana* half-sib families, aged 8 (Matthews *et al.* 1975).
- △ *Pinus taeda* half-sib families, aged 14 (van Buijtenen 1979).
- *Pinus elliotii* clones, aged 7-11 (van Buijtenen 1979).

products, the main opportunities seem to be to increase (a) the proportion of dry matter defined as yield, (b) the long-term foliage/fine root equilibrium, by altering the parameters in Equation 2, and (c) stem/branch partitioning in timber trees. There would seem to be less opportunity to substantially alter wood/foilage partitioning, although we know very little about what controls this, or how to lessen the high cost of the removal of vegetative parts. In fruit trees which are capable of a high fruit set every year, yields seem to be limited ultimately by root growth and nutrient supply.

It became clear, while writing this review, that our thinking on partitioning in tree crops could be very misleading if it is restricted to the ideas of harvest index and harvest increment of above-ground parts. In both management and genetic studies, we need more information on the total integrated carbon and nutrient budgets of whole trees over time.

## REFERENCES

- Agren, G. I., Axelsson, B., Flower-Ellis, J. G. K., Linder, S., Persson, H., Staaf, H. & Troeng, E. (1980). Annual carbon budget for a young Scots pine. In: *Structure and function of northern coniferous forests*, edited by T. Persson, 307-313. (Ecological bulletin no. 32). Stockholm: Swedish Natural Science Research Council.
- Alexander, D. McE. & Maggs, D. H. (1971). Growth responses of sweet orange seedlings to shoot and root pruning. *Ann. Bot.*, 35, 109-115.
- Ando, T., Hatai, K., Doi, K., Kataoka, H., Kato, Y. & Sakaguchi, K. (1968). Studies on the system of density control of Sugi (*Cryptomeria japonica*) stand. *Bull. Govt Forest Exp. Stn. Meguro*, 209, 1-76.

- Austin, R. B., Bingham, J., Blackwell, R. D., Evans, L. T., Ford, M. A., Morgan, C. L. & Taylor, M. (1980). Genetic improvements in winter wheat yields since 1900 and associated physiological changes. *J. Agric. Sci., Camb.*, **94**, 675-689.
- Avery, D. J. (1969). Comparisons of fruiting and deblossomed maiden apple trees, and of non-fruiting trees on a dwarfing and an invigorating rootstock. *New Phytol.*, **68**, 323-336.
- Avery, D. J. (1970). Effects of fruiting on the growth of apple trees on four rootstock varieties. *New Phytol.*, **69**, 19-30.
- Biscoe, P. V. & Gallagher, J. N. (1977). Weather, dry matter production and yield. In: *Environmental effects on crop physiology*, edited by J. J. Landsberg and C. V. Cutting, 75-100. London: Academic Press.
- Borchert, R. (1973). Simulation of rhythmic tree growth under constant conditions. *Physiologia Pl.*, **29**, 173-180.
- Borchert, R. (1976). Feedback control and age-related changes of shoot growth in seasonal and non-seasonal climates. In: *Tropical trees as living systems*, edited by P. B. Tomlinson and M. H. Zimmermann, 497-515. Cambridge: Cambridge University Press.
- Breure, C. J. & Corley, R. H. V. (1983). Selection of oil palms for high density planting. *Euphytica*, **32**, 177-186.
- Brix, H. & Ebell, L. F. (1969). Effects of nitrogen fertilization on growth, leaf area, and photosynthesis rate in Douglas fir. *Forest Sci.*, **15**, 189-196.
- Brouwer, R. (1962). Distribution of dry matter in the plant. *Neth. J. agric. Sci.*, **10**, 361-376.
- Buijtencan, J. P. van. (1979). Genetic differences in dry matter distribution within stems, branches and foliage in loblolly and slash pine. *Proc. North American Forest Biology Workshop, 5th*, edited by C. A. Hollis and A. E. Squillace, 235-241. Gainesville, FLA: University of Florida, School of Forest Resources.
- Butler, D. R. & Landsberg, J. J. (1981). Respiration rates of apple trees, estimated by CO<sub>2</sub>-efflux measurements. *Plant, Cell Environ.*, **4**, 153-159.
- Cannell, M. G. R. (1971). Production and distribution of dry matter in trees of *Coffea arabica* L. in Kenya as affected by seasonal climatic differences and the presence of fruits. *Ann. appl. Biol.*, **67**, 99-120.
- Cannell, M. G. R. (1974). Factors affecting Arabica coffee bean size in Kenya. *J. hort. Sci.*, **49**, 65-76.
- Cannell, M. G. R. (1980). Productivity of closely-spaced young poplar on agricultural soils in Britain. *Forestry*, **53**, 1-21.
- Cannell, M. G. R. (1982). *World forest biomass and primary production data*. London: Academic Press.
- Cannell, M. G. R. (1983). Plant management in agroforestry: manipulation of trees, population densities and mixtures of trees and herbaceous crops. In: *Plant research and agroforestry*, edited by P. A. Huxley, 455-487. Nairobi: International Council for Research in Agroforestry.
- Cannell, M. G. R. & Kimeu, B. S. (1971). Uptake and distribution of macro-nutrients in trees of *Coffea arabica* L. in Kenya as affected by seasonal climatic differences and the presence of fruits. *Ann. appl. Biol.*, **68**, 213-230.
- Cannell, M. G. R. & Smith R. I. (1980). Yields of mini-rotation, closely spaced hardwoods in temperate regions: review and appraisal. *Forest Sci.*, **26**, 415-428.
- Cannell, M. G. R. & Willett, S. C. (1976). Shoot growth phenology, dry matter distribution and root: shoot ratios of provenances of *Populus trichocarpa*, *Picea sitchensis* and *Pinus contorta* growing in Scotland. *Silvae Genet.*, **25**, 49-58.
- Cannell, M. G. R., Sheppard, L. J., Ford, E. D. & Wilson, R. H. F. (1984). Clonal differences in dry matter distribution, wood specific gravity and foliage 'efficiency' in *Picea sitchensis* and *Pinus contorta*. *Silvae Genet.*, **32**, 195-202.
- Chalmers, D. J. & Ende, B. van den. (1975). Productivity of peach trees: factors affecting dry weight distribution during tree growth. *Ann. Bot.*, **39**, 423-432.
- Charles-Edwards, D. A. (1976). Shoot and root activities during steady-state plant growth. *Ann. Bot.*, **40**, 767-772.
- Charles-Edwards, D. A. (1981). *The mathematics of photosynthesis and productivity*. London: Academic Press.
- Charles-Edwards, D. A. (1982). *Physiological determinants of crop growth*. London: Academic Press.
- Corley, R. H. V. (1973). Effects of planting density on growth and yield of oil palm. *Exp. Agric.*, **9**, 169-180.

- Corley, R. H. V., Gray, B. S. & Kee, Ng S. (1971a). Productivity of the oil palm (*Elaeis guineensis* Jacq.) in Malaysia. *Exp. Agric.*, **7**, 129-136.
- Corley, R. H. V., Hardon, J. J. & Tan, G. Y. (1971b). Analysis of growth of the oil palm (*Elaeis guineensis* Jacq.). 1. Estimation of growth parameters and application in breeding. *Euphytica*, **20**, 304-315.
- Cripps, J. E. L. (1971). The influence of soil moisture on apple root growth and root:shoot ratio. *J. hort. Sci.*, **46**, 121-130.
- Cromer, R. N., Williams, E. & Tompkins, D. (1980). Biomass and nutrient uptake in fertilized *E. globulus*. *Proc. IUFRO Symp. and Workshop on Genetic Improvement and Productivity of Fast-growing Trees*. Sao Pedro, Sao Paulo, Brazil.
- Daailow, D. (1953). Einfluss der Samenerzeugung auf die Struktur der Jahrringe. *Allg. Forstz.*, **8**, 454-455.
- Davidson, R. L. (1969). Effect of root/leaf temperature on root/shoot ratios in some pasture grasses and clover. *Ann. Bot.*, **33**, 561-569.
- Denne, M. P. (1979). Wood structure and production within the trunk and branches of *Picea sitchensis* in relation to canopy formation. *Can. J. For. Res.*, **9**, 406-427.
- Donald, C. M. & Hamblin, J. (1976). Biological yield and harvest index of cereals as agronomic and plant breeding criteria. *Adv. Agron.*, **28**, 361-405.
- Doucet, R., Berglund, J. V. & Farnsworth, C. E. (1976). Dry matter production in 40-year-old *Pinus banksiana* stands in Quebec. *Can. J. For. Res.*, **6**, 357-367.
- Drew, A. P. (1982). Shoot-root plasticity and episodic growth in red pine seedlings. *Ann. Bot.*, **49**, 347-357.
- Drew, A. P. & Ledig, F. T. (1980). Episodic growth and relative shoot:root balance in loblolly pine seedlings. *Ann. Bot.*, **45**, 143-148.
- Duff, G. H. & Nolan, N. J. (1957). Growth and morphogenesis in the Canadian forest species. II. Specific increments and their relation to the quantity and activity of growth in *Pinus resinosa* Ait. *Can. J. Bot.*, **35**, 527-572.
- Edwards, N. T., Shugart, H. H., McLaughlin, S. B., Harris, W. F. & Reichle, D. E. (1981). Carbon metabolism in terrestrial ecosystems. In: *Dynamic properties of forest ecosystems*, edited by D. E. Reichle, 499-536. Cambridge: Cambridge University Press.
- Eis, S., Garman, E. H. & Ebell, L. F. (1965). Relation between cone production and diameter increment in Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Dougl.) Lindl.), and western white pine (*Picea monticola* Dougl.). *Can. J. Bot.*, **43**, 1553-1559.
- Evans, L. T. (1975). *Crop physiology*. Cambridge: Cambridge University Press.
- Evans, L. T. (1976). Physiological adaptation to performance as crop plants. *Phil. Trans. R. Soc.*, **275B**, 71-83.
- Evans, L. T. (1980). The natural history of crop yield. *Am. Scient.*, **68**, 388-397.
- Fielding, J. M. (1960). Branching and flowering characteristics of Monterey pine. *Bull. Commonwealth For. Timb. Bur. Aust.*, no. 37.
- Forrest, W. G. & Ovington, J. D. (1970). Organic matter changes in an age series of *Pinus radiata* plantations. *J. appl. Ecol.*, **7**, 177-186.
- Gales, K. (1979). Effects of water supply on partitioning of dry matter between roots and shoots in *Lolium perenne*. *J. appl. Ecol.*, **16**, 863-877.
- Gifford, R. M. & Evans, L. T. (1981). Photosynthesis, carbon partitioning, and yield. *A. Rev. Pl. Physiol.*, **32**, 485-509.
- Gordon, J. C. & Larson, P. R. (1968). Seasonal course of photosynthesis, respiration, and distribution of <sup>14</sup>C in young *Pinus resinosa* trees as related to wood formation. *Pl. Physiol., Lancaster*, **43**, 1617-1624.
- Graat, M. C. & Mitton, J. D. (1979). Elevational gradients in adult sex ratios and sexual differentiation in vegetative growth rate of *Populus tremuloides* Michx. *Evolution, Lancaster, Pa.*, **33**, 914-918.
- Gross, K. L. & Soule, J. D. (1981). Differences in biomass allocation to reproductive and vegetative structures of male and female plants of a dioecious perennial herb, *Silene alba* (Miller) Krause. *Am. J. Bot.*, **68**, 801-807.
- Hamilton, G. J. (1976). The Bowmont Norway spruce thinning experiment 1930-1974. *Forestry*, **49**, 109-121.
- Hansen, P. (1971a). The effect of cropping on the distribution of growth in apple trees. *Tidsskr. Plavl.*, **75**, 119-127.



- Hansen, P. (1971b). The effects of cropping on uptake, content, and distribution of nutrients in apple trees. *Tidsskr. PLAVt.*, 75, 615-625.
- Hansen, P. (1977). The relative importance of fruits and leaves for cultivar-specific growth rates of apple fruits. *J. hort. Sci.*, 52, 501-508.
- Harper, J. L. (1977). *Population biology of plants*. London: Academic Press.
- Head, G. C. (1969). The effects of fruiting and defoliation on seasonal trends in new root production on apple trees. *J. hort. Sci.*, 44, 175-181.
- Heilman, P. & Peabody, D. V. (1981). Effect of harvest cycle and spacing on productivity of black cottonwood in intensive culture. *Can. J. For. Res.*, 11, 118-123.
- Heim, G., Landsberg, J. J., Watson, R. L. & Brain, P. (1979). Eco-physiology of apple trees: dry matter production and partitioning by young Golden Delicious trees in France and England. *J. appl. Ecol.*, 16, 179-194.
- Hesketh, J. D. & Jones, J. W. (1976). Some comments on computer simulators for plant growth - 1975. *Ecol. Modell.*, 2, 235-247.
- Ingestad, T. (1979). Nitrogen stress in birch seedlings. II. N, K, P, Ca and Mg nutrition. *Physiologia Pl.*, 45, 149-157.
- Ingestad, T. & Lund, A. B. (1979). Nitrogen stress in birch seedlings. I. Growth technique and growth. *Physiologia Pl.*, 45, 137-148.
- Isebrands, I. & Nelson, N. D. (1983). Distribution of <sup>14</sup>C-labelled photosynthates within intensively cultured *Populus* clones during the establishment year. *Physiologia Pl.*, 59, 9-18.
- Jacobs, M. R. (1954). The effect of wind sway on the form and development of *Pinus radiata* D. Don. *Aust. J. Bot.*, 2, 35-51.
- Jaffe, M. J. (1976). Thigmomorphogenesis: a detailed characterization of the response of beans (*Phaseolus vulgaris* L.) to mechanical stimulation. *Z. Pflanzenphysiol.*, 77, 437-453.
- Jarvis, P. G. & Leverenz, J. W. (1983). Productivity of temperate, deciduous and evergreen forests. In: *Physiological plant ecology 4*, edited by O. L. Lange, P. S. Nobel, C. B. Osmond and H. Ziegler, 233-280. (Encyclopedia of plant physiology, vol. 121D). Berlin: Springer.
- Jordan, C. F. (1971). A world pattern in plant energetics. *Am. Scient.*, 59, 425-433.
- Keays, J. L. (1971). *Complete tree utilization. An analysis of the literature*, vols I-V. Vancouver. Canadian Forestry Service, Forest Products Laboratory.
- Keyes, M. R. & Grier, C. C. (1981). Above- and below-ground net production in 40-year-old Douglas fir stands on low and high productivity sites. *Can. J. For. Res.*, 11, 599-605.
- Kinerson, R. S., Ralston, C. W. & Wells, C. G. (1977). Carbon cycling in a loblolly pine plantation. *Oecologia*, 29, 1-10.
- King, D. & Roughgarden, J. (1983). Energy allocation patterns of the California grassland annuals *Plantago erecta* and *Clarkia rubicunda*. *Ecology*, 64, 16-24.
- Kira, T. & Yabuki, K. (1978). Primary production rates in the minamata forest. In: *Biological production in a warm-temperate evergreen oak forest of Japan*, edited by T. Kira, Y. Ono and T. Hosokawa, 131-139. (JIBP Synthesis vol. 18). Tokyo: University of Tokyo Press.
- Koerper, G. J. & Richardson, C. J. (1980). Biomass and net primary production regressions for *Populus grandidentata* on three sites in northern lower Michigan. *Can. J. For. Res.*, 10, 92-101.
- Larson, P. R. (1963). Stem form development in forest trees. *Forest Sci. Monogr.*, no. 5.
- Larson, P. R. (1965). Stem form of young *Larix* as influenced by wind and pruning. *Forest Sci.*, 11, 412-424.
- Ledig, F. T. (1983). The influence of genotype and environment on dry matter distribution in plants. In: *Plant research and agroforestry*, edited by P. A. Huxley, 427-454. Nairobi: International Council for Research in Agroforestry.
- Lenz, F. (1979). Fruit effects on photosynthesis, light- and dark-respiration. In: *Photosynthesis and plant development*, edited by R. Marcelle, H. Clijsters and M. van Poucke, 271-281. The Hague: Junk.
- Linder, S. & Axelsson, B. (1982). Changes in carbon uptake and allocation patterns as a result of irrigation and fertilization in a young *Pinus sylvestris* stand. In: *Carbon uptake and allocation in sub-alpine ecosystems as a key to management*, edited by R. H. Waring, 38-44. Corvallis, OR: Oregon State University, Forest Research Laboratory.
- Linder, S. & Rook, D. A. (1984). Effects of mineral nutrition on the carbon dioxide exchange of trees. In: *Nutrition of forest trees in plantations*, edited by G. D. Bowen and E. K. S. Nambiar, 211-236. London: Academic Press.
- Linder, S. & Troeng, E. (1981). The seasonal course of respiration and photosynthesis in strobili of Scots pine. *Forest Sci.*, 27, 267-276.

- Lloyd, D. G. (1980). Sexual strategies in plants. I. An hypothesis of serial adjustment of maternal investment during one reproductive season. *New Phytol.*, **86**, 69-79.
- Loomis, R. S., Rabbinge, R. & Ng, E. (1979). Explanatory models in crop physiology. *A. Rev. Pl. Physiol.*, **30**, 339-367.
- McLaughlin, S. B., McConathy, R. K. & Bate, B. (1979). Seasonal changes in within-canopy allocation of  $^{14}\text{C}$ -photosynthate by white oak. *Forest Sci.*, **25**, 361-370.
- McMurtrie, R. & Wolf, L. (1983). Above- and below-ground growth of forest stands: a carbon budget model. *Ann. Bot.*, **52**, 437-448.
- Madgwick, H. A. I. (1981). Above-ground dry matter content of a young close-spaced *Pinus radiata* stand. *N.Z. J. For. Sci.*, **11**, 203-209.
- Madgwick, H. A. I., Jackson, D. S. & Knight, P. J. (1977). Above-ground dry matter, energy and nutrient contents of trees in an age series of *Pinus radiata* plantations. *N.Z. J. For. Sci.*, **7**, 445-468.
- Magambo, M. J. S. & Cannell, M. G. R. (1981). Dry matter production and partition in relation to yield of tea. *Exp. Agric.*, **17**, 33-38.
- Mags, D. H. (1961). Changes in the amount and distribution of increment induced by contrasting watering, nitrogen and environmental regimes. *Ann. Bot.*, **25**, 353-361.
- Mags, D. H. (1963). The reduction in growth of apple trees brought about by fruiting. *J. hort. Sci.*, **38**, 119-128.
- Mags, D. H. (1965). Growth rates in relation to assimilate supply and demand. II. The effect of particular leaves and growing regions in determining the dry matter distribution in young apple trees. *J. exp. Bot.*, **16**, 387-404.
- Martinez-Carrasco, R. & Thorne, G. N. (1979). Physiological factors limiting grain size in wheat. *J. exp. Bot.*, **30**, 669-679.
- Matthews, J. D. (1963). Factors affecting the production of seed by forest trees. *For. Abstr.*, **24**, 1-13.
- Matthews, J. A., Feret, P. P., Madgwick, H. A. I. & Bramlett, D. C. (1975). Genetic control of dry matter distribution in twenty half-sib families of Virginia pine. In: *Proc. Southern Forest Tree Improvement Conference, 13th, Raleigh, NC*, 234-241. Macon, GA: Eastern Tree Seed Laboratory.
- Miller, H. G. & Miller, J. D. (1976). Effect of nitrogen supply on net primary production in Corsican pine. *J. appl. Ecol.*, **13**, 249-256.
- Mitchell, K. J. (1975). Dynamics and simulated yield of Douglas fir. *Forest Sci. Monogr.*, no. 17.
- Mitchell, C. A., Dostal, H. C. & Seipal, T. M. (1977). Dry weight reduction in mechanically dwarfed tomato plants. *J. Am. Soc. hort. Sci.*, **102**, 605-608.
- Mooney, H. A., Ferrar, P. J. & Slatyer, R. O. (1978). Photosynthetic capacity and carbon allocation patterns in diverse growth forms of *Eucalyptus*. *Oecologia*, **36**, 103-111.
- Moorby, J. (1977). Integration and regulation of translocation within the whole plant. In: *Integration of activity in the higher plant*, 425-454. (Symp. Soc. Exp. Biol. 31). Cambridge: Cambridge University Press.
- O'Neill, R. V. & DeAngelis, D. L. (1981). Comparative productivity and biomass relations of forest ecosystems. In: *Dynamic properties of forest ecosystems*, edited by D. E. Reichle, 411-449. Cambridge: Cambridge University Press.
- Orians, G. H. & Solbrig, O. J. (1977). A cost-income model of leaves and roots with special reference to arid and semi-arid areas. *Am. Nat.*, **111**, 677-690.
- Ovington, J. D. (1957). Dry matter production of *Pinus sylvestris* L. *Ann. Bot.*, **21**, 287-316.
- Paavilainen, E. (1980). Effect of fertilization on plant biomass and nutrient cycle on a drained dwarf shrub pine swamp. *Commun. Inst. for. fenn.*, no. 98.
- Parry, M. S. (1974). The control of biennial bearing of Laxton's Superb apple trees. *J. hort. Sci.*, **49**, 123-130.
- Penning de Vries, F. W. T. & Laar, H. H. van, eds. (1982). *Simulation of plant growth and crop production*. Wageningen: Centre for Agricultural Publishing and Documentation.
- Perrson, H. (1980). Fine-root dynamics in a Scots pine stand with and without near-optimum nutrient regimes. *Acta phytogeogr. suec.*, **68**, 101-110.
- Pressman, E., Huberman, M., Aloni, B. & Jaffe, M. J. (1983). Thigmomorphogenesis. the effect of mechanical perturbation and ethrel on stem pithiness in tomato (*Lycopersicon esculentum* (Mill.)) plants. *Ann. Bot.*, **52**, 93-100.
- Pritts, M. P. & Hancock, J. F. (1983). Seasonal and lifetime allocation patterns of the woody golden rod, *Solidago pauciflosculosa* Michaux (Compositae). *Am. J. Bot.*, **70**, 216-221.

- Quinlan, J. D. & Preston, A. P. (1971). The influence of shoot competition on fruit retention and cropping of apple trees. *J. hort. Sci.*, **46**, 525-534.
- Rangnekar, P. V. & Forward, D. F. (1973). Foliar nutrition and wood growth in red pine: effects of darkening and defoliation on the distribution of  $^{14}\text{C}$ -photosynthate in young trees. *Can. J. Bot.*, **51**, 103-108.
- Rauner, J. L. (1976). Deciduous forests. In: *Vegetation and the atmosphere*, vol. 2, edited by J. L. Monteith, 241-264. London: Academic Press.
- Rees, D. J. & Grace, J. (1980). The effects of shaking on the extension growth of *Pinus contorta* Dougl. *Forestry*, **53**, 154-166.
- Rees, A. R. & Tinker, P. B. H. (1963). Dry-matter production and nutrient content of plantation oil palms in Nigeria. I. Growth and dry-matter production. *Pl. Soil*, **19**, 19-32.
- Reich, P. B., Teskey, R. O., Johnson, P. S. & Hinckley, T. M. (1980). Periodic root and shoot growth in oak. *Forest Sci.*, **26**, 590-598.
- Reynolds, J. F. & Thornley, J. H. M. (1982). A shoot:root partitioning model. *Ann. Bot.*, **49**, 585-597.
- Richards, D. & Rowe, R. N. (1977). Effects of root restriction, root pruning and 6-benzlamino-purine on the growth of peach seedlings. *Ann. Bot.*, **41**, 729-740.
- Richards, D., Goubran, F. H. & Collins, K. E. (1979). Root-shoot equilibria in fruiting tomato plants. *Ann. Bot.*, **43**, 401-404.
- Satoo, T. (1971). Materials for the studies of growth in stands. VIII. Primary production relations in plantations of Norway spruce in Japan. *Bull. Tokyo Univ. Forests*, **65**, 125-142.
- Satoo T. & Madgwick, H. A. I. (1982). *Forest biomass*. The Hague; London: Martinus Nijhoff/Junk.
- Schulze, E.-D. (1970). Der  $\text{CO}_2$ -Gaswechsel der Buche (*Fagus sylvatica* L.) in Abhängigkeit von den Klimafaktoren im Freiland. *Flora, Jena*, **159**, 177-232.
- Schulze, E.-D., Fuchs, M. I. & Fuch, M. (1977). Spatial distribution of photosynthetic capacity and performance in a mountain spruce forest of northern Germany. I. Biomass distribution and daily  $\text{CO}_2$  uptake in different crown layers. *Oecologia*, **29**, 43-61.
- Simmonds, N. W. (1982). Some ideas on botanical research on rubber. *Trop. Agric., Trin.*, **59**, 2-8.
- Singh, I. D. & Stoskopf, N. C. (1971). Harvest index of cereals. *Agron. J.*, **63**, 224-226.
- Swank, J. C., Below, F. E., Lambert, R. J. & Hageman, R. H. (1982). Interaction of carbon and nitrogen metabolism in the productivity of maize. *Pl. Physiol., Lancaster*, **70**, 1185-1190.
- Tanton, T. W. (1979). Some factors limiting yields of tea (*Camellia sinensis*). *Exp. Agric.*, **15**, 187-191.
- Templeton, J. K. (1969). Partition of assimilates. *J. Rubb. Res. Inst. Malaya*, **21**, 259-263.
- Thompson, K. & Stewart, A. J. A. (1981). The measurement and meaning of reproductive effort in plants. *Am. Nat.*, **117**, 205-211.
- Thornley, J. H. M. (1976). *Mathematical models in plant physiology*. London: Academic Press.
- Thornley, J. H. M. (1977). Root:shoot interactions. In: *Integration of activity in the higher plants*, edited by D. M. Jennings, 367-389. Cambridge: Cambridge University Press.
- Thorpe, M. R., Lang, A. & Michin, P. E. H. (1983). Short-term interactions between flows of photosynthate. *J. exp. Bot.*, **34**, 10-19.
- Tuomi, J., Niemela, P. & Mannila, R. (1982). Resource allocation on dwarf shoots of birch (*Betula pendula*): reproduction and leaf growth. *New Phytol.*, **91**, 483-487.
- Turner, J. & Long, J. N. (1975). Accumulation of organic matter in a series of Douglas fir stands. *Can. J. For. Res.*, **5**, 681-690.
- Wareing, P. F. & Patrick, J. (1975). Source-sink relations and the partition of assimilates in the plant. In: *Photosynthesis and productivity in different environments*, edited by J. P. Cooper, 481-499. Cambridge: Cambridge University Press.
- Wareing, R. H. (1983). Estimating forest growth and efficiency in relation to canopy leaf area. *Adv. ecol. Res.*, **13**, 327-353.
- Wareing, R. H., Thies, W. G. & Muscato, D. (1980). Stem growth per unit of leaf area: a measure of tree vigor. *Forest Sci.*, **26**, 112-117.
- Warren-Wilson, J. (1972). Control of crop processes. In: *Crop processes in controlled environments*, edited by A. R. Rees, K. E. Cockshull, D. W. Hand and R. G. Hurd, 7-30. London: Academic Press.
- Watson, B. T. (1980). The effect of cooling on the rate of phloem translocation in the stems of two angiosperms, *Picea sitchensis* and *Abies procera*. *Ann. Bot.*, **45**, 219-223.