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PRINCIPLES AND PROCESSES OF CARBON SEQUESTRATION BY TREES

By *G. L. Unwin and
P. E. Kriedemann*



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RESEARCH AND DEVELOPMENT DIVISION
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S U M M A R Y

This paper defines carbon sequestration by trees and briefly reviews the physiology of carbon assimilation and likely carbon dynamics of future plantation forests. Although maximum rate of carbon assimilation usually occurs early in the new plantation, mature forests continue to store carbon in significant amounts for the effective life of the forest (and forest products). Along with increasing controls on emissions of greenhouse gases, effective management of additional forest plantations for carbon sequestration provides one of the few low-cost, low-energy alternatives for amelioration of greenhouse effects. New plantation forests therefore offer Australian industry an attractive, environmentally favourable basis for gaining carbon credits to offset continuing emissions in the short to medium term. The paper underlines the physiological processes and biological limitations on which carbon sequestration is based and discusses management imperatives for State Forests' continuing development of new softwood and hardwood plantations for this purpose.

Forests are capable of effective sequestration and storage of atmospheric carbon in above-ground and below-ground biomass by way of processes of photosynthesis and tree growth. Rate of biomass increase and hence rate of carbon sequestration vary through rotation of a new plantation as an integration of genetic, environmental and silvicultural determinants. It follows from the physiological basis to carbon sequestration that efficiency and energy cost of carbon uptake and carbon storage in plantations are profoundly influenced by site and stand management factors and by genetic factors associated with managed, even-aged tree populations.

Conversion of atmospheric carbon to assimilated carbohydrate (*eg* providing the cellulose content of new wood) is limited by quantum requirements for photosynthesis and by diminished efficiencies in strong sunlight. Both of these factors are intrinsic to green plants and neither is amenable to forest improvement. Hence future gains in carbon sequestration by trees will come elsewhere, especially from site improvement, improved silvicultural strategy and targeted genotype selection.

As a result of metabolic costs of carbon assimilation and maintenance requirements for tree growth, maximum carbon sequestration by plantation forests will be favoured on improved sites. These will be stocked with low lignin genotypes adapted to deliver optimal growth rates in response to increasing atmospheric CO₂ and high soil nutrient inputs. This is not to discount the important role of tree breeding and site amelioration towards improved environmental management of trees for carbon gain (and other essential benefits) on poor sites (*eg* in drier regions or for rehabilitation purposes).

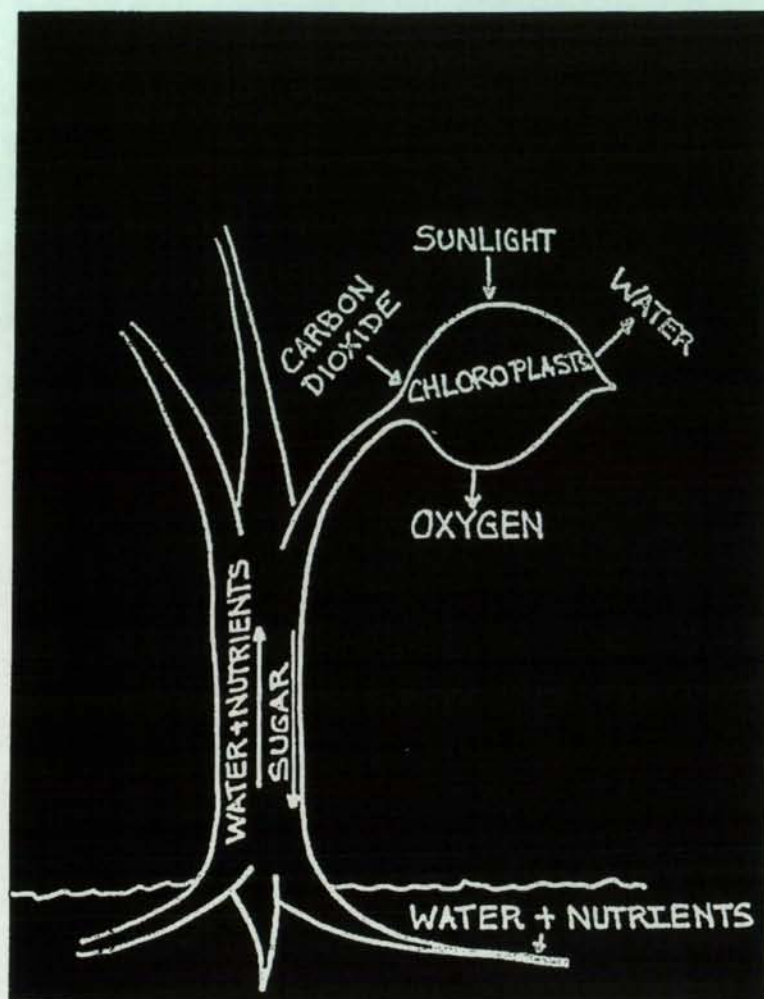


Figure 1. Carbon sequestration by trees: assimilation of atmospheric CO_2 , transport of carbohydrate and partitioning of carbon in tree biomass. Not shown is respiratory return of carbon to the soil and atmosphere.

INTRODUCTION - WHAT IS CARBON SEQUESTRATION?

Global emissions of carbon have been increasing for about 140 years since the beginning of the Industrial Revolution. The sharpest increase is observed during the most recent 50 years (Kaufman and Franz 1993), principally from accelerated use of fossil fuels. Concentration of carbon dioxide (CO₂) in the atmosphere has increased by about 25% from pre-industrial levels and will approach 360 ppm by end of year 2000. It is estimated that future doubling of atmospheric CO₂ concentration to about 700 ppm will risk an accompanying greenhouse rise of approximately 1.5 – 4.0°C in mean global surface temperature (Atwell *et al.* 1999).

Forests are capable of effective sequestration and storage of atmospheric carbon in above-ground and below-ground biomass by way of processes of photosynthesis and tree growth. Carbon is absorbed and assimilated by tree foliage and is stored as carbon-rich organic compounds such as cellulose and hemicelluloses, lignin, starch, lipid and waxes, mostly in secondary woody tissues in tree boles and in large roots, as well as in foliage, branches and fine roots.

Establishing forest plantations on presently non-forested land provides an energy-conscious world with a clean, efficient means of absorbing some of the excess in atmospheric CO₂ (Borough *et al.* 1998). Such absorption offers a significant offset against continuing greenhouse gas emissions and may be combined with other benefits such as timber production, environmental protection, added biodiversity and land rehabilitation.

Three major components (or sets of processes) together constitute net sequestration of carbon in forest trees (Figure 1):

1. **Carbon uptake and assimilation**, including immediate respiratory losses which detract from previously 'fixed' carbon in photosynthetic plant cells;
2. **Carbon transport, allocation and partitioning** of carbon for storage, structural and metabolic use in above-ground and below-ground parts of the tree; and
3. **Return of forest carbon to the atmosphere** via oxidative pathways, notably via the food chain, biological decay and combustion of forest biomass and forest products.

Forest cover accounts for approximately 40% (5.1 billion ha) of the land area of the earth's surface (FAO 1995). In global terms, forests are a major carbon store and account for about 80% of all above ground biomass, and about 40% of below ground carbon (Kirschbaum *et al.* 1996). Kirschbaum (1998) provides a comprehensive summary of global carbon pools and fluxes (Figure 2). Forests and woodlands accommodate about 331 Gt of organic carbon in biomass, and forest soils another 656 Gt. These are significant portions of the global carbon pool in relation to the atmosphere (750 Gt), though orders of magnitude less than estimates of the large global reservoirs in the oceans (40,000 Gt) and fossil fuels (>20,000 Gt). By comparison, forests and woodlands in Australia represent about 0.3% of the global total forest area and forests in New South Wales represent 13.4% of our national estate (ABARE 1998).

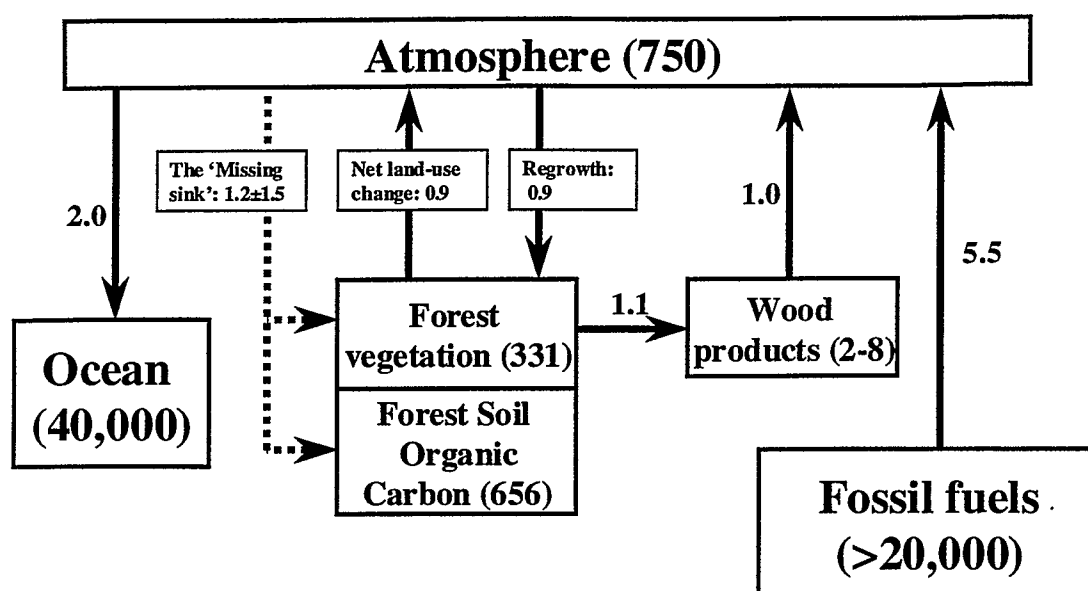


Figure 2. Estimated pools and fluxes in the global carbon cycle of relevance to forestry (Kirschbaum 1998). Pool sizes are given in GtC. Numbers next to arrows give estimated net fluxes in GtC yr⁻¹. Arrows drawn in solid type are based on direct estimates, whereas the 'missing sink' is calculated from the difference unaccounted by other fluxes. (Note that cold temperate boreal forests of the northern hemisphere may account for a higher proportion of the soil carbon pool, relative to area of land occupied, than do Australian forests in mild temperate or tropical conditions.)

All forests are sustained by sunlight and draw resources from both the atmosphere (carbon dioxide) and soil (water and nutrients). Tree genetics set a potential for resource conversion into biomass and thus limit the maximum efficiency of carbon sequestration. However, site factors commonly inhibit the expression of inherent biological efficiency. Net storage of carbon is thus an outcome of species genotype x environment interactions. Both aspects are amenable to limited intervention and improvement by research and appropriate forest operations (*eg* tree breeding programmes and practices of plantation management, including site selection, silviculture and choice of rotation length).

Figure 3 (adapted from BTCE 1996) provides a generalised view of tree growth and yield pattern for a simplified (monospecific, unthinned) tree plantation. Such curves are useful to illustrate relevant concepts, terminology and growth phases on which more complex growth and yield models are based. Attributes of tree species and site conditions (site quality, climate, soils, past and present management histories and disturbance regimes) are combined mathematically with prescriptions of silvicultural regime and stand management practices using appropriate growth functions. Silvicultural prescriptions (*eg* stand density, thinning and pruning) may include options for rotation length, product mix, pricing policy and harvesting strategy. The conventional objective has been to create predictive models of tree growth and yield of wood products appropriate to prevailing forest management criteria and market opportunities. With appropriate conversion and calibration for above- and below-ground carbon content across the range of expected species, site conditions and silvicultural options, such models can be adapted for preliminary accounting of carbon gain.

Although maximum rate of growth (and hence rate of carbon assimilation) usually occurs early in the life of a new plantation (soon after canopy closure), mature forests continue to store carbon in significant amounts for the effective life of the forest (Figure 3). Along with increasing controls on emissions of greenhouse gases (principally carbon dioxide, methane and nitrous oxide), effective management of additional forest plantations for carbon sequestration provides one of the few low-cost, low-energy

alternatives for amelioration of greenhouse effects. New plantation forests therefore offer intrinsic value to Australian industry as a basis for gaining carbon credits to offset against continuing greenhouse emissions. State Forests of New South Wales is at the forefront of developing new softwood and hardwood plantations for this purpose.

This paper outlines the functional and biological basis on which successful management of carbon forestry depends – providing an introduction to the physiology, bioenergetics and measurement of carbon sequestration by trees. Management implications for achievement of commercial and environmental objectives of carbon trading in plantation forestry are also discussed.

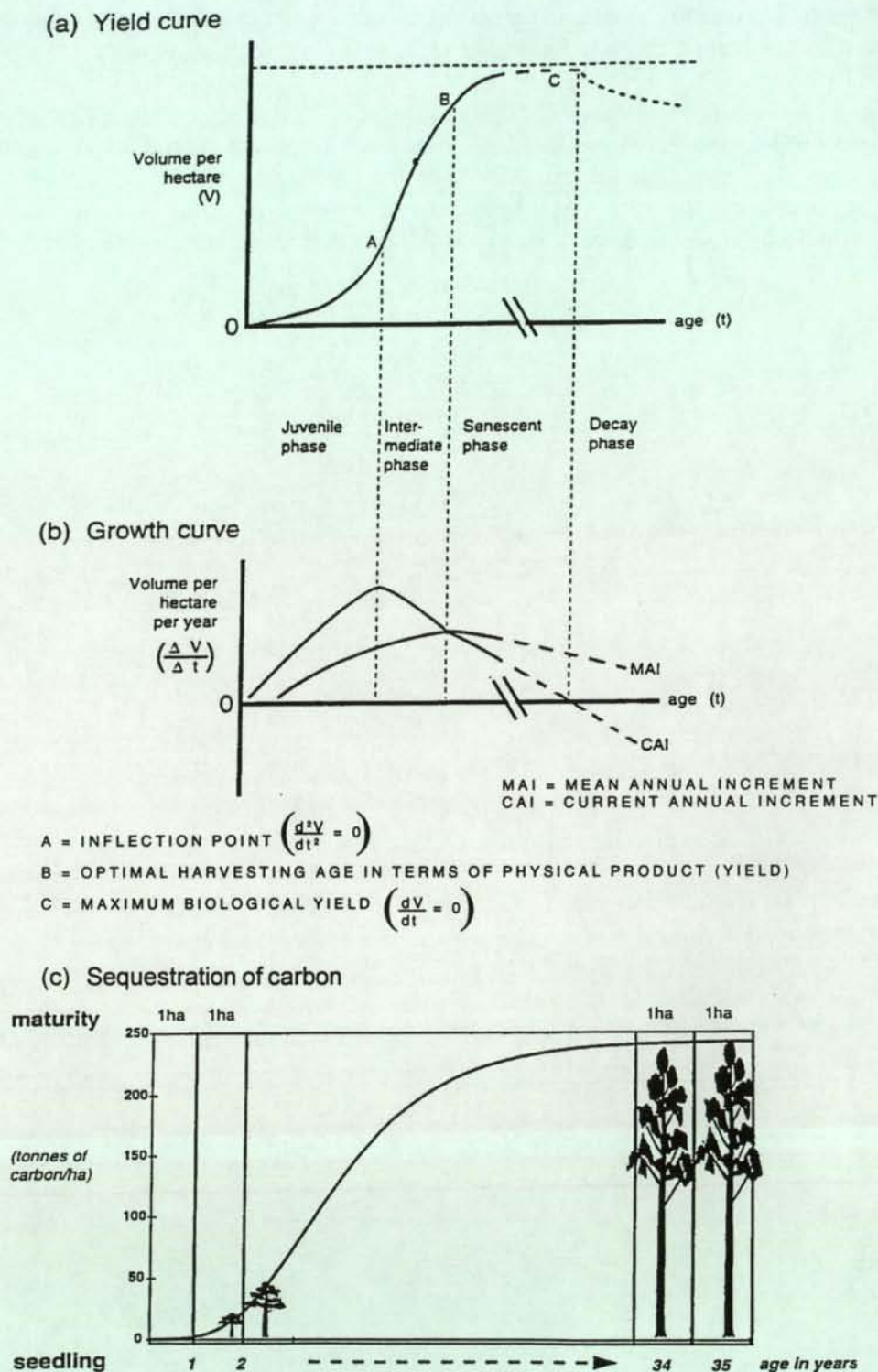


Figure 3. Generalised growth and yield pattern for a monospecific unthinned tree plantation: (a) standing tree volume curve, (b) volume growth curve and (c) notional sequestration of carbon stored in a continuous cycle of (1 ha) annual plantation establishment with a 35-year rotation. (Adapted from BTCE 1996.)

PHYSIOLOGY OF CARBON ASSIMILATION

1. NET CARBON SEQUESTRATION

Sunlight striking leaves of trees generates chemical reducing power within the chloroplasts of mesophyll cells (M in Figure 4) enabling reduction of CO_2 into carbohydrate. This energy demanding process leads to formation of photoassimilates (mostly in the form of sugars and starch) within the foliage. The disaccharide sucrose is then loaded into vascular elements (V in Figure 4) and transported enormous distances from tree crowns to growing regions such as stems and roots. Photoassimilate is subsequently partitioned into stem and root growth as more complex organic (carbon-based) compounds are incorporated into new wood by the vascular cambium (W and VC in Figure 5).

Leaf loading of photoassimilate into minor veins, transport in major veins and eventual utilisation for wood formation, all consume metabolic energy. Cell respiration furnishes that energy from oxidation of surrounding cellular carbohydrates (sugars). A significant portion of assimilated carbon is thus consumed prior to sequestration. As much as 50% of carbon assimilated by a tree canopy can be dissipated via respiratory CO_2 (Figure 6). Losses are especially high on poor sites where a greater proportion of a tree's carbon-based energy is needed to capture sparse resources such as water and nutrients.

2. WATER USE

Carbon dioxide enters via stomata (pores) in leaves of tree canopies (ST in Figure 4). The uptake of CO_2 is accompanied by substantial transpirational loss via exit of water vapour through those same stomata. Vascular plants typically transpire between 100 and 1000 g of water per g dry mass of plant material formed (less under humid conditions; more under dry conditions). This translates to an equivalent range of water use of 100–1000 kilolitres per tonne of dry mass produced. This large cost in water for such a meagre amount of carbon fixation is a direct consequence of a huge reduction in water vapour partial pressure of outside air compared to saturated or near-saturated conditions inside leaves (a difference of up to 35,000 μbars on a hot day). By contrast, the CO_2 concentration gradient between the near atmosphere and inside the leaf is much smaller. Carbon dioxide molecules diffusing into leaves or foliage needles (in the case of *Pinus*) have further to go in reaching chloroplasts within mesophyll cells (M in Figure 4), and are responding to a much more modest difference in CO_2 partial pressure, typically 355 μbars outside (late 1990s level) compared with 250 μbars inside. [In physiological terms, this inward flux of CO_2 molecules during canopy photosynthesis usually reaches around 20–40 $\mu\text{mol m}^{-2}\text{s}^{-1}$ whereas the corresponding outward flux of water molecules will be about 2,000–3,000 $\mu\text{mol m}^{-2}\text{s}^{-1}$!] Trees are thus bedevilled by an intrinsically low water-use efficiency *ie* a low efficiency for carbon gained per unit of water consumed.

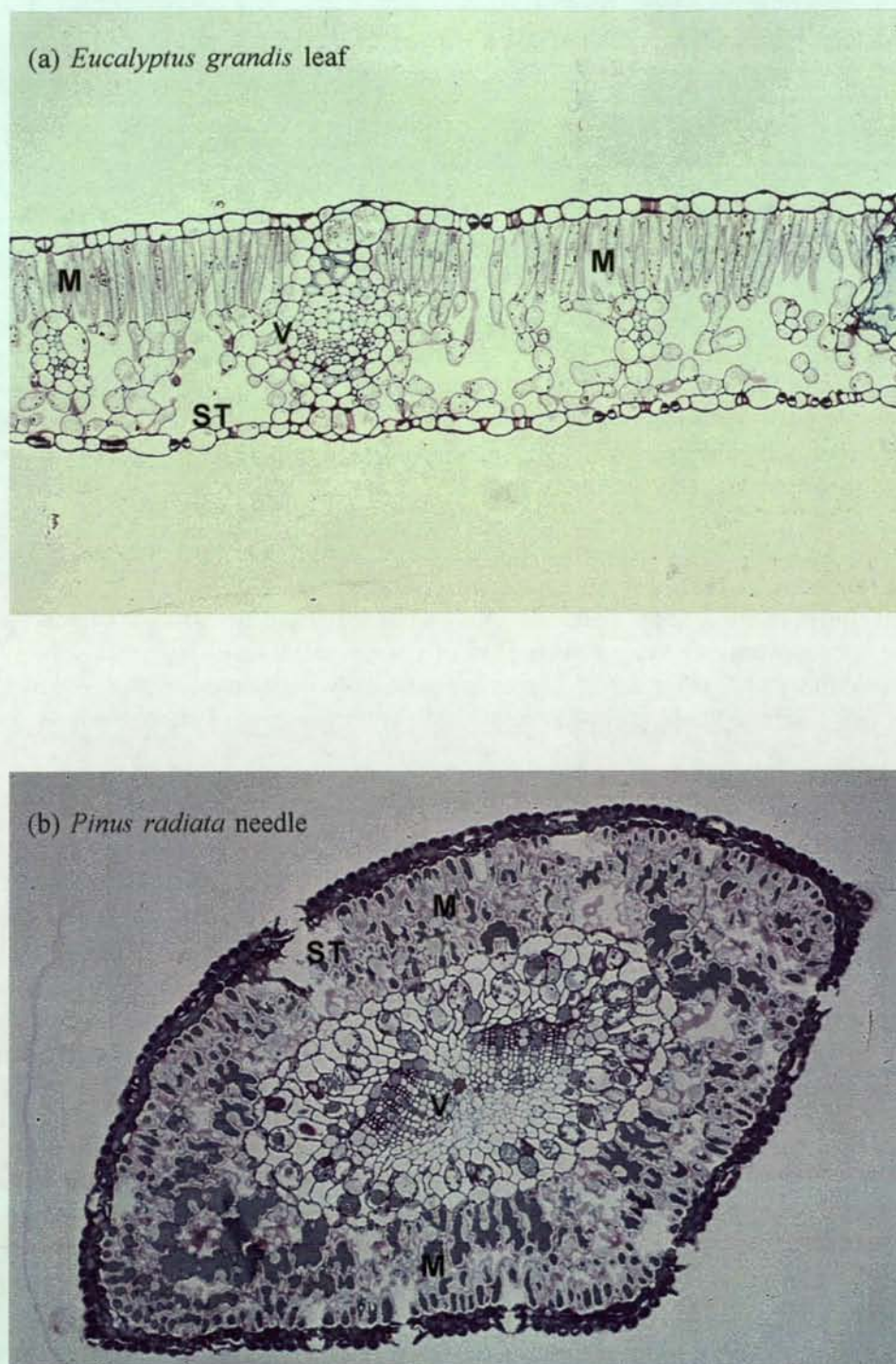


Figure 4. Transverse sections from (a) *Eucalyptus grandis* leaf and (b) *Pinus radiata* needle showing mesophyll tissue (M), vascular elements (V) and stomatal pores (ST). Photomicrographics courtesy Ian Craig, Forestry and Forest Products, CSIRO.

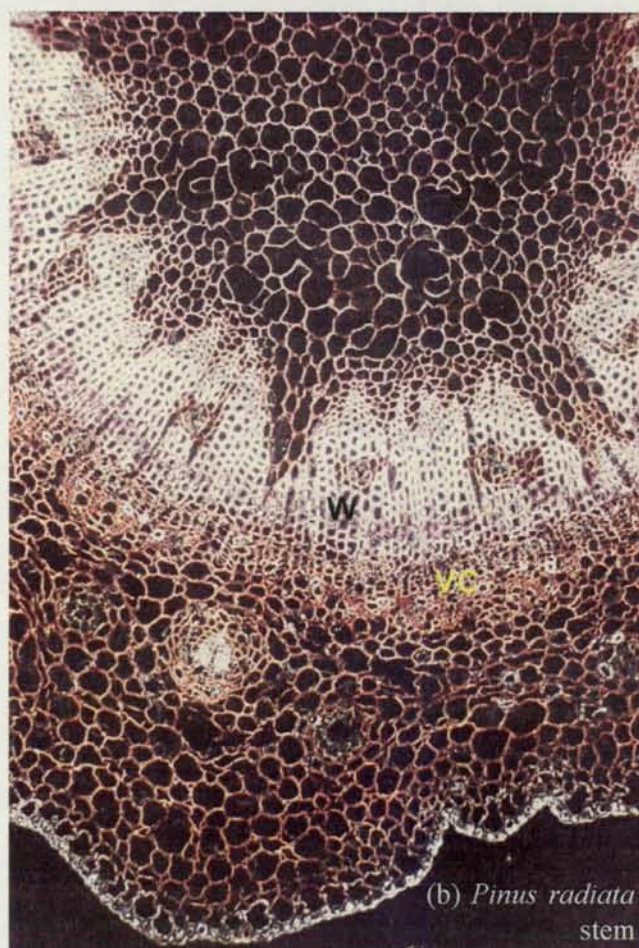
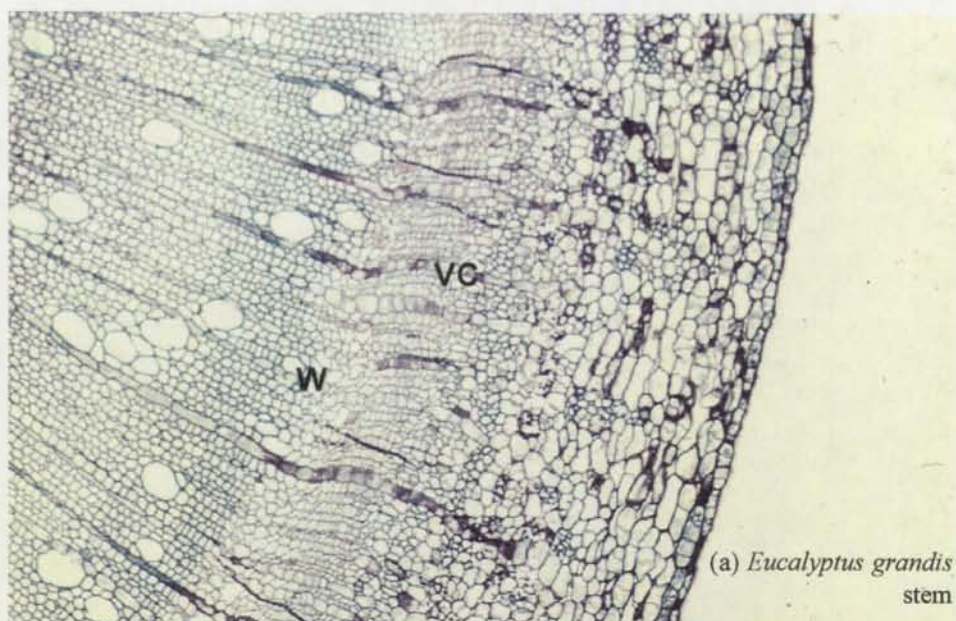


Figure 5. Stem anatomy of (a) *Eucalyptus grandis* and (b) *Pinus radiata* showing formation of young secondary xylem (new wood W) and phloem vascular tissues either side of a cambial layer (VC). Photomicrographics courtesy (a) I.Craig Forestry and Forest Products, CSIRO, and (b) K.Bamber & R.Colley, State Forests of New South Wales.

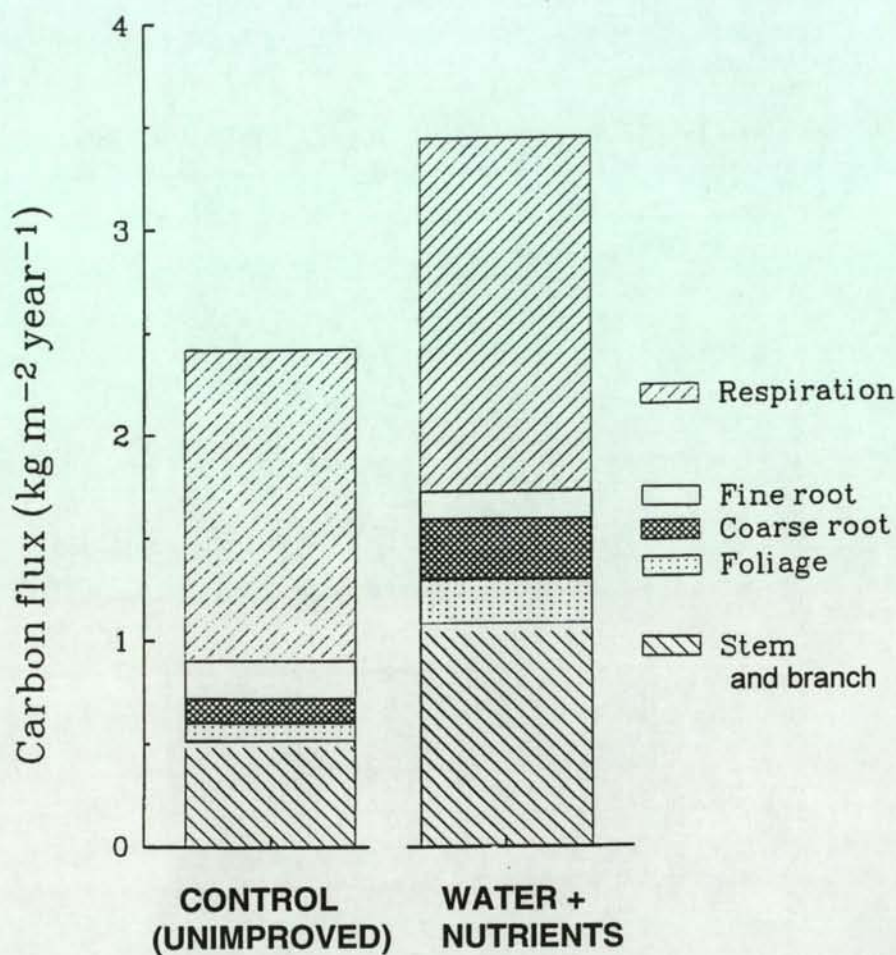


Figure 6. Measured annual carbon fluxes for *Pinus radiata*, age 20 years, growing near Canberra ACT on either a low quality control site (natural rainfall and no additional nutrients) or an improved site (irrigated with nutrients in solution). Carbon stored in stem and branch, foliage, coarse root and fine root is higher on the improved site but carbon loss due to tree respiration is a much smaller proportion of total carbon flux. (Based on Ryan *et al.* 1996.) See also Snowden and Benson 1992 for relative allocation at age 10 years.

FUTURE CARBON DYNAMICS

1. ELEVATED CO₂ AND WATER USE

Ironically, global change and increasing CO₂ levels in the atmosphere could have a beneficial impact on capacity of forest trees to sequester carbon. Contemporary research in tree response to increasing atmospheric carbon levels has certainly provided a timely boost to scientific understanding of carbon – nutrient – water relations and tree growth. All else being equal, immediate water use of present-day plants decreases as atmospheric CO₂ rises, whereas carbon assimilation is enhanced. Thus, in the presence of elevated CO₂, a given rate of carbon assimilation is accompanied by slower transpiration, and water-use efficiency improves.

Partial stomatal closure under elevated CO₂ is largely responsible for improved experimental performance and carbon uptake in present day trees. As atmospheric CO₂ concentration continues to rise, future trees will develop leaves with a lower stomatal density and such leaves can be expected to transpire more slowly. For example, in investigation of tropical species such as *Eucalyptus tetradonta* (Eamus *et al.* 1995), photosynthetic capacity increased by more than 50% at forecast 2030 CO₂ levels while stomatal conductance decreased by more than 45% (relative to present CO₂). Under these conditions, where other inputs such as water and nutrients were ideal for growth, instantaneous water use efficiency was improved by a factor of about three. In nature, elevated CO₂ of coming decades will be accompanied by generally warmer conditions and a change in rainfall seasonality, so that direct CO₂ effects on carbon gain may lose force with time, however some improvement in water use efficiency should still apply.

2. CARBON AND NUTRIENT INTERACTIONS

Carbon assimilation and direct effects of elevated CO₂ on tree growth and biomass accumulation are compounded by soil nutrient input and foliar nutrition (*eg* availability of N and/or P). Interactive nutrient effects with elevated CO₂ levels have been demonstrated experimentally, in early growth of tree seedlings, *eg* in *Eucalyptus grandis* (Conroy 1992), *E. camaldulensis* and *E. cypellocarpa* (Wong *et al.* 1992) and *Pinus radiata* and *P. caribaea* var. *hondurensis* (Conroy *et al.* 1990a, 1990b). Positive interactions between CO₂ and nitrogen or phosphorous input on whole plant biomass were significant, highlighting expected CO₂ x N and/or CO₂ x P effects. For example, CO₂ enrichment with low nitrogen supply enhanced growth by a factor of 1.75 in *Eucalyptus camaldulensis* (Figure 7) and 1.85 in *Eucalyptus cypellocarpa*; CO₂ enrichment on high nitrogen supply enhanced growth by factors of 2.66 and 3.10 respectively. Experimentally, a strong positive interaction between elevated CO₂ and high N on carbon sequestration and growth of young trees can be attributed to compounding effects of increased leaf expansion and faster carbon assimilation on a leaf area basis. In *E. grandis* (Conroy *et al.* 1992), absolute dry weight response to elevated CO₂ (660 ppm) was largest when both N and P availability was high but relative increase in dry weight was maximised at low P availability.

While favourable growing conditions allow (*eg* adequate supply of water, nitrogen and phosphorus), tree canopies can be expected to respond favourably to enhanced CO₂, especially among fast-growing plantation species such as those being considered. On a nutrient-rich site with adequate moisture, the time course of leaf area index (canopy leaf area relative to ground area) will accelerate in response to elevated CO₂, reaching a ceiling value earlier than at present-day levels. Provided weed control is effective, 'Site capture' will be assured earlier, and once canopies close, elevated CO₂ should also sustain carbon gain in a more water-efficient manner.

On nutrient-poor sites, representative of drier inland native forests or exposed rehabilitation sites, effects of global change in atmospheric carbon are less clear. In terms of regeneration, tree establishment and growth dynamics, strongly limiting site resources (such as water, P and/or N) could be expected to restrict seedling response to elevated CO_2 . Depending on degree and complexity of growth limitation, there is commonly an interactive effect of co-limiting resources, based on relative availability of environmental inputs (Conroy 1999). If one component such as CO_2 is enhanced, plant nutrients such as P, which may already be in short supply, will become even more limiting to growth. In two-year-old greenhouse specimens of *P. radiata*, CO_2 enrichment increased whole-plant dry matter production, irrespective of water availability, but only when P supply was adequate (Conroy *et al.* 1990a). Accordingly, there may also be reduced foliar demand on other, less-limiting growth factors, such as N, as a result of stronger limitation by P.

Opposing the co-limiting trend, however, on dry sites, stomatal response to elevated CO_2 may lead to improved plant water relations and reduced plant water deficits, eg in *Maranthes corymbosa* (monsoon vine forest) and *E. tetradonta* (tropical woodland and savanna) in northern Australia (Eamus *et al.* 1995), and in a variety of other tree species elsewhere (Reekie and Bazzaz 1989). In field conditions, net response of whole-tree water use in CO_2 -enriched but moisture-limited environments will therefore vary among species and sites, as two or more opposing physiological responses are involved. Widely observed reduction in stomatal density, conductance and transpiration rate per unit leaf area may be countered by increased leaf area per plant, in response to elevated CO_2 , thus it is possible that actual demand on soil water can be similar for ambient and CO_2 -enriched growing stock. In mildly N-deficient soils, particularly in water-stressed environments, however, relative growth response to elevated CO_2 may exceed relative response in more favoured environments, as a consequence of improved water or nutrient use efficiency.

In adaptive terms, species which are endemic to drier or nutrient-poor regions commonly show a lower intrinsic vigour as seedlings, presumably because fast growth would have had no selective advantage in those original habitats. Where future rainfall and moisture retention allow, rehabilitation forests based on non-endemic planting stock with higher growth potential would be expected to pay a growth dividend on costly site investments and nutrient additions.

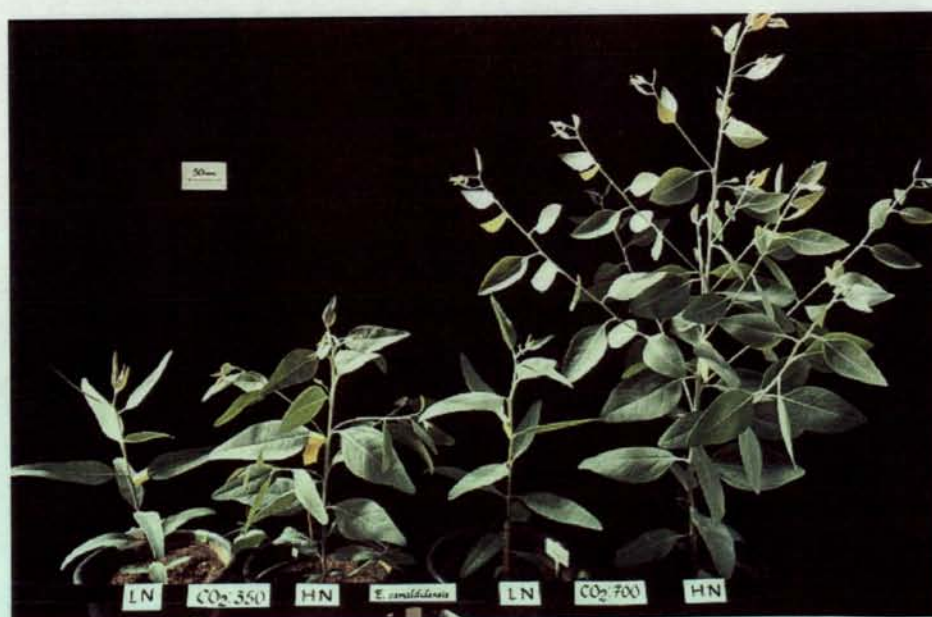


Figure 7. Experimental growth response in seedlings of *Eucalyptus camaldulensis* to factorial combination of nitrogen x carbon dioxide supply viz. 1.2 and 6.0 mM N x 350 and 700 ppm CO_2 respectively. LN = low N, HN = high N treatments. (Details in Wong *et al.* 1992.) Photograph P.E. Kriedemann

BIOENERGETICS OF CARBON SEQUESTRATION HOW MUCH DOES IT COST?

Sequestration of carbon from the atmosphere depends upon interception and utilisation of sunlight, but subsequent use necessitates expenditure of metabolic energy. Fixed carbon meets this need, so that costs associated with growth and maintenance of trees can be represented by biomass equivalents. Notional values for dry matter utilisation show that respiratory demand is substantial. Commonly one-fifth to one-third and, under stressful conditions, as much as two-thirds of a tree's daily fixed CO_2 can be respired over that same period (Figure 6).

Biological energy derived from respiration sustains both maintenance and growth. Maintenance respiration corresponds to CO_2 release associated with (i) production of energy for maintenance of chemical and electrochemical gradients across membranes (ii) turnover of cellular constituents such as proteins and (iii) physiological costs of acclimation to harsh environments. Growth respiration covers synthesis of new biomass from photoassimilate and nutrients. Such construction costs will vary according to the chemical composition of plant material, and by implication, the amount of energy embedded in these molecules.

Compounds with a high carbon concentration demand more energy for their synthesis. Biomass stored as lipid (oils, waxes *etc.*) represents an investment of almost three times as much energy as would be required for storage of the same amount of nonstructural carbohydrate (*eg* sucrose). Similarly, tree species that form wood with a high lignin content would require about twice as much energy as needed to store an equivalent mass of pure cellulose.

Construction cost, and thus growth respiration, also vary according to the chemical form of available nitrogen (*eg* N_2 , NO_3^- or NH_4^+) and sites of N assimilation (leaves or roots). Nitrogen reduction for plant use is energetically expensive. As a general rule, most respiratory energy generated by trees is devoted to root physiology and nutrient acquisition. Any intrinsic differences in respiratory efficiency become more important when trees are exposed to unfavourable site conditions. Poor sites invariably lead to increased allocation of energy resources to fine root turnover and maintenance of new root tissue. Indeed, variation between locations in overall efficiency of sunlight utilisation for wood formation by conifers has been attributed to this source of carbon loss.

Light requirements for photosynthesis set a limit on sunlight energy conversion and photosynthetic efficiency declines with increasing sunlight, reducing conversion efficiency to about 2.7% at light saturation. More than half of the energy assimilated is used in maintenance respiration and metabolic costs of new shoot and root growth. Combining the effects of light saturation, respiratory losses and allocation of carbon below ground, sunlight utilisation efficiency (ϵ) is reduced to about 1.3 g dry mass per MJ sunlight energy on optimal sites (a value comparable to *P. radiata* on high quality sites in ACT or NZ). Assuming a carbon content of 0.50 g g^{-1} , this maximum conversion value may be expressed as approximately 0.65 g carbon sequestered per MJ sunlight absorbed.

Efficiency of carbon sequestration will be much reduced if forests are nutrient, water or temperature limited. Conversion efficiencies, or productivities of conifer stands (g biomass accumulated per MJ of light energy absorbed) thus range between about 1.4 (New Zealand) and 0.27 (Wisconsin). Rainfed plantations in southern New South Wales are expected to vary between say 1.25 and 0.65 (g MJ^{-1}). Converting these published values to a similar gramme carbon basis, reduction in ϵ at Wisconsin ($\epsilon = 0.13 \text{ g C MJ}^{-1}$) is due to harsh winters and hot dry summers; Sweden ($\epsilon = 0.33$) with extremely cold winters, is equal to a control stand in ACT ($\epsilon = 0.33$) where effective growing season was reduced by summer drought and extreme water stress.

MEASUREMENT OF CARBON SEQUESTRATION

1. CARBON MEASUREMENT IN FORESTS

Complexity of carbon processes in forests is to some degree overcome or avoided by approaching carbon measurement along proven lines of forest assessment. Accurate and reliable methods of tree mensuration and timber resource inventory are available. The starting point of carbon audit in forests is therefore quite simple, although there are questions in common with sampling, estimation, error prediction *etc.* Established inventory methods and inventory data used to estimate tree growth rates, volume and wood yield can be applied and refined using appropriate expansion factors (of lesser-known accuracy and reliability) to account for expected content and storage of carbon across the predicted forest estate. Measurement of carbon sequestration in forests therefore borrows considerably from conventional approaches to forest assessment and inventory, including:

1. Estimation, through stratification and suitable sampling of a limited number of measures across a selected range of variables and sample sites (depending on scale of the forest or plantation enterprise and known or suspected variability);
2. Approximation, with predetermined or assessable levels of precision and risk of error, as a trade-off against cost;
3. Conservative use of default parameters to delimit or define first estimates of poorly documented or unmeasurable items, based on best available evidence or argument.

Improved carbon audit will need to focus on refined estimates of carbon allocation in wood produced by forests and species of particular age, site and management specification. Most promising research in carbon measurement is therefore aimed at the reliability with which carbon contents can be derived from estimates of known or expected wood product. Prediction and validation of present and future carbon values will be based on (a) empirical and/or process modelling of carbon yield (either directly or via estimates of wood production), and (b) improved use of allometric (growth-related) equations which include reliable conversion estimates and carbon surrogates *ie* closely related variables that are readily measured or accessible, where sequestered carbon is not readily measured (*eg* carbon allocated to roots).

Carbon estimation can thus benefit by research results and methodology which already surround measurement and prediction of growth, productivity, biomass, wood yield and carbon relations of forests for a range of plantation species and forest types. (For examples, see Attiwill 1979, Baker and Attiwill 1985, Bengtsson *et al.* 1994, Raison and Myers 1992, Turner and Lambert 1983 and 1986, and numerous other studies cited in the Greenhouse Challenge Vegetation Sinks Workbook (Australian Greenhouse Office, 1998).

The Greenhouse Office compiled the workbook of techniques for estimating carbon sequestration in vegetation management projects. The following outline of carbon estimation in plantations follows methodology presented therein. The Workbook defines carbon sequestration in terms of CO₂ 'sinks' (removals from the atmosphere) and 'stores' (carbon storage held in biomass). The Workbook is itself generally consistent with the previous Reference Manual prepared internationally by IPCC (1996).

2. CARBON POOLS AND FLUXES

Carbon stored or moving through components of forest ecosystems (e.g. trees, shrubs, animals, litter *etc.*) is usefully considered in terms of Pools (which represent reservoirs of stored carbon, either transient or persistent) and Fluxes (representing transfer of carbon from one part of the carbon cycle, or pool, to another). Kirschbaum (1998) portrays carbon pools and fluxes on an estimated global scale (Figure 2). Similar accounts may be prepared regionally or for individual forests and plantations (*eg* using the workbook cited above).

There are two broad approaches to quantification of carbon sequestration in plantations. The first is a mechanistic or reductionist approach to analysis and measurement of the many carbon processes and fluxes, in effect an ecophysiological derivation of forest carbon sequestration (Landsberg 1986; Landsberg and Waring 1997). This approach, though theoretically sound, is likely to be found in research of principles and processes, is highly scale-dependent and is often limited by site specific observations and inputs. The reductionist approach is fragmented by nature, is expensive and in practical management terms is dependent on the capacity to rebuild component processes and their outcomes (at many different scales) into a comprehensive estimate or model of gross carbon differences over time. The inherent value of such analysis is in description and enumeration of processes and principles on which real gains in broad understanding of carbon sequestration are based.

Process-based models are being developed by State Forests of New South Wales for initial prediction of carbon sequestration in new hardwood plantations. In this instance, process models find a useful management application in predicting carbon outcomes for new species and new sites where particular site/species performance data are not available for construction of empirical models.

By comparison, the more pragmatic, empirical approach takes an holistic view, based on repeated measurement or estimation of size and status of the more important carbon pools, the magnitude and direction of gross changes recorded periodically, in relation to 'baseline' or previously reported conditions. Empirical methods focus on size (mass or volume) and carbon content of various, significant pools and their changes, as measured or estimated over the life of plantations, (including, where harvesting occurs, their wood products). This approach avoids many detailed problems associated with quantification and resolution of opposing fluxes and differing time scales and spatial attributes encountered in some process models. For example, net carbon gain through assimilation and storage of carbon by trees is derived through periodic measures or estimates of carbon content inferred by changes in tree biomass. Comparison is made with previous biomass estimates to determine change in carbon stored. An audit of carbon accounts can then be expressed either in periodic or cumulative terms (*eg* annually, five-yearly or on rotation-to-date basis) or, in terms of average carbon gain sequestered, during a whole rotation or predicted over many successive rotations. Carbon costs (losses to the atmosphere) may be included in such an audit, accounting for CO₂ equivalence in biological decay, in emissions due to forest operations, transport services, materials (*eg* fertilizers) and equipment, and in harvesting and wood product usage, depending on ownership arrangements and agreed boundaries of responsibility.

Problems with the second (empirical) approach focus on relevant and accurate partitioning of carbon pools; advance identification of the most significant and sensitive (or changeable) pools; development of suitable allometric functions for estimation of important carbon pools which are beyond immediate reach (*eg* woody roots); and comparable accounting of above- and below-ground components of biomass.

3. ESTIMATING CARBON POOLS AND SEQUESTRATION

The empirical approach to carbon accounting is based on a plan of repeated sampling and measurement (eg at five-yearly intervals), providing estimates of carbon content in respective forest components (carbon pools). Pools which are included are those which are deemed to be significant, usually because of their size, in relation to the total carbon budget (eg trees, tree roots and soil), and/or because of their sensitivity, or propensity for rapid change during the life of a plantation (eg litter, above- and below-ground biomass, including tree stems, foliage and roots).

Net carbon stored or emitted during a particular interval (I) is given by the following two equations (Australian Greenhouse Office, 1998):

$$\begin{aligned}\Delta C_I &= C_I - C_{I-1} \text{ and} \\ C_I &= TR_I + L_I + V_I + S_I + WP_I\end{aligned}$$

Terms and abbreviations are defined as follows:

ΔC_I	Net carbon sequestration increment or emission in interval I, (t C)
C_I	Total cumulative carbon stored at end of interval I, (t C)
TR_I	Carbon in Trees and Roots Pool at end of interval I, (t C)
L_I	Carbon in Litter Pool at end of interval I, (t C)
V_I	Carbon in Other Vegetation Pool at end of interval I, (t C)
S_I	Carbon in Soil Pool at end of interval I, (t C)
WP_I	Carbon in Wood products harvested or unsold during interval I, (t C)
(t C)	Tonnes carbon

For estimation of above-ground pools (eg wood, branches, foliage), variables which often correlate well with biomass include stocking density, basal diameter or basal area of trees and tree height, stem volume, crown projection of trees and shrubs (eg foliage projective cover, FPC), Leaf Area Index (LAI) *etc.* Some of these measures, eg tree diameter and height, also correlate well with total tree biomass and therefore make suitable surrogates in allometric equations designed to estimate root biomass, for example. Alternatively, Root/Shoot biomass ratios may be used, however, preliminary sampling of additional material will often be required to establish such ratios unless previously determined values are shown to apply. Carbon content of tree biomass (including stem and root wood), plant litter and other vegetation is derived using a suitable dry matter to carbon conversion ratio, commonly equated to 0.5. This factor is reported to vary (eg through range 0.40 – 0.57) according to source of the derivation, to chemical composition of biomass, to age and condition of plant material, (including wood properties, lignification), species, site and growth rate, *etc.* (eg see BTCE 1996).

Biological breakdown of plantation debris (above- and below-ground) may be included as an emission from the Trees and Roots Pool according to estimated rates of litterfall and decay, especially if these estimates can be established by complementary studies or sampling (eg within a subset of permanent growth plots). Alternatively, where plant debris is identified with particular silvicultural operations (eg weed control, pruning, thinning, harvesting), litter may be quantified by appropriate subsampling and measurement during or soon after the event. Carbon losses are then amortised by linear or other decay functions (eg during a subsequent 10-year period).

Where growth models or yield tables for merchantable volume already exist and can be shown to apply to species and site(s) in question, sequestered carbon in the Trees and Roots Pool may be estimated directly using the following equation (Australian Greenhouse Office, 1998):

$$\Delta C_t = CAI_t * D_t / 1000 * (1 + R_t) * 1 / HI_t * 0.50$$

where terms are defined thus:

ΔC_t	Annual carbon increment for year _t (t C ha ⁻¹ yr ⁻¹)
CAI_t	Annual volume increment in year _t (m ³ ha ⁻¹ yr ⁻¹) obtained from growth model, yield table or sample plot measure
D_t	Basic density of Trees and Roots in year _t (kg m ⁻³) (division by 10 ³ to convert kilograms to tonnes)
R_t	Ratio of root to total above-ground tree mass in year _t (eg 0.2 – 0.35)
HI_t	Harvest index: ratio of stemwood to above-ground biomass
0.50	Appropriate dry mass to carbon conversion factor.

Default values for basic density, root to shoot ratio and harvest index are reported for a range of pine and plantation eucalypt species, however caution should be exercised as such values are sensitive both to site condition and silvicultural regime (hence history of tree growth environment) (Beets and Pollock 1987, Wilkes 1989).

Conventional techniques of forest sampling and inventory are readily adapted to produce biomass (hence carbon) estimates for major tree pools, at least for common plantation species. An appropriate, preferably permanent, sampling design is required, usually with prior stratification of new plantation sites and random location of sufficient sample plots within strata. (State Forests Permanent Growth Plots in plantations are ideal if re-measured regularly at five-year intervals, if adequately representative of the range and variability of plantation sites and, if applicable, to species and genotypes.) Appropriate experimental relationships to determine biomass ratios or to validate allometric functions need to be available or must be developed (through more intensive sampling and analysis) to estimate Root and Litter pools for species and range of sites in question. Unless previously established in relevant growth/yield functions (eg West and Mattay 1993), parameters used in allometric equations should be validated by species and site using follow-up measurements spanning the first rotation and confirmed during subsequent rotations, as growth/age related functions will change from establishment to maturity.

Accuracy and precision of carbon measurements from permanent sample plots need to be such that an estimate of sequestration (ΔC_t) during any periodic interval (I) can be determined with (usually 95%) confidence by statistically valid comparison of successive measures (Australian Greenhouse Office, 1998). (The error of the difference between estimates is the sum of errors of the estimates.)

With success of applying international standards in other aspects of plantation practice, eg Pruned Stand Certification, there is an opportunity to develop certified monitoring and validation systems for carbon sequestration. Such standards would provide commercial assurance of carbon audits and verification of carbon sequestered by new plantations. This strategy however, will depend on effective measuring and monitoring of carbon pools if they are to form the basis of commercial trading in sequestration of carbon eg Carbon Credits.

IMPLICATIONS FOR FOREST MANAGEMENT AND PROSPECTS FOR CARBON FORESTRY

Establishment and care of forest trees for carbon sequestration (among other benefits) provide new questions and new opportunities for forest management. The concept of silvicultural intervention and management of tree growth principally for sequestration of atmospheric CO₂ is yet innovative and will benefit by further scientific definition.

Tree growth, rate of biomass increase and hence the rate of carbon sequestration vary through rotation of a new plantation as an integration of genetic, environmental and silvicultural determinants. It follows from the physiological basis to carbon sequestration (above) that efficiency of carbon uptake and carbon storage in plantations is profoundly influenced by site and stand management factors and by genetic factors intrinsic to plantation species and their growth behaviour as managed, even-aged tree populations.

Under ideal conditions, solar energy conversion by a tree canopy in full sun is only about 2.7% (based on energy stored compared to light energy absorbed). This low value is set by quantum requirements for photosynthesis, and diminished efficiencies in strong light. Both are intrinsic to plants and neither is amenable to forest improvement. Future gains therefore will come elsewhere, especially from site improvement, silvicultural strategy and genotype selection.

As observed, carbon losses associated with stemwood formation and root physiology reduce that 2.7% value even further, so that a pine plantation on a high quality site produces wood at a net conversion efficiency of about 1%. On poor quality sites, this value drops even further due to reduced canopy development and a greater allocation of carbon to root growth and maintenance in response to water stress and sparse nutrients. By implication, there is much room for improvement, even within constraints set by basic biology and conventional plantation management. Interactions between genotype and site factors on tree growth will be largely responsible for that improvement, so that selection for genotypes with an inherent capacity for greater vigour on improved sites should pay dividends.

With global change, and especially increased partial pressure of atmospheric CO₂, energy conversion efficiency will increase, especially on high quality sites. A positive interaction between CO₂ and nutrient supply on biomass gain is now well documented for small trees, and will likely accelerate canopy development in future plantations. The time course of increasing volume increments (eg CAI, Figure 3(b)) should then become truncated, so that well nourished stands will achieve slightly higher maximum growth rates earlier in their life cycles, and rotations for optimal carbon sequestration may be shortened by present standards for timber production. Whether early gains can be sustained over the life of a plantation remains untested.

Photosynthetic acclimation to elevated CO₂ will likely constrain tree response of present day genotypes to increased atmospheric CO₂ of coming decades, especially where soil conditions limit canopy development. As with any environmental factor, altered CO₂ supply becomes a selection pressure, and in locations where faster assimilation offers a selection advantage, existing genotypes will be replaced in nature by better adapted variants. Tree breeders should be able to apply such selection more intensively to produce new genotypes which are better equipped to sequester elevated CO₂ in future plantations.

Regardless of photosynthetic adaptation, water use efficiency will be improved by elevated CO₂ due to a more favourable diffusion gradient from ambient air to fixation sites within leaves. Site moisture will thus be used more effectively for wood formation and, where other factors allow, locations now regarded as marginal with respect to soil moisture supply might qualify for plantation forestry in future.

Carbon fixation by tree canopies is thus influenced by genetic factors, but bioenergetics of photoassimilate formation and transport are set by basic physiology, and probably show little genetic variation. However, energy costs of wood formation do vary with genotype and in accordance with chemical composition. Although rich in carbon content, high lignin timber is energy intensive, whereas low lignin timber is a more economic carbon store (meaning that more carbon will be stored for equal or less carbon loss). Each gramme of lignin requires about 2.12 g of glucose energy for synthesis (releasing CO₂), whereas pure cellulose requires only 1.22 g of glucose. Commensurate with retention of essential structural properties, tree selection for fast-growing, low lignin timber would be conducive to more energy efficient carbon storage.

Optimal conversion of basic environmental resources and inputs (such as light, water, carbon dioxide and inorganic plant nutrients) to maximise both added and average stored carbon (as opposed to imperatives of wood or wood fibre production alone) therefore requires a new focus on several key aspects of plantation management, including the following:

- ◆ Land availability, land condition, tenure and cost
- ◆ Species/genotype selection and improvement
- ◆ Site selection and site management, including management of nutrient and water relations for improved carbon uptake and storage
- ◆ Silvicultural strategies for stand management, specifically to maximise carbon assimilation and storage and to minimise carbon return to the atmosphere by either biological (decomposition) or physical (combustion) processes
- ◆ Growth, biomass and volume prediction for selected species, sites and rotations
- ◆ Wood to carbon conversion factors and carbon yield modelling
- ◆ Carbon dynamics of plantation forests, including above and below ground partitioning of stored carbon, ageing, senescence and biomass decay and/or combustion
- ◆ Harvest strategy, product utilisation and product life, particularly to maximise longevity of carbon stored.

With suitable revision, tree growth and timber yield models may be modified and dedicated to the purpose of predictive carbon accounting in new plantations. To be effective in this function, revised models need to include aspects of carbon cycle dynamics which are sensitive to forest management. Biomass or forest product decay functions are important, as are carbon balance equations which include time course of both carbon losses and carbon gains over successive rotations (to define persistence and magnitude of the stored carbon pool). Future carbon models will require suitably refined and verified biomass to carbon conversion factors as these will differ according to carbon composition of biomass components, species, age and lignification of woody tissues *etc.* As in conventional growth and yield models, carbon sequestration models may be verified against past and present growth measurements and yield records, in this case augmented by contemporary analyses (or certification) of carbon content, thereby enabling suitable validation and improvement.

Added emphasis on the difficult area of below-ground carbon accounting requires improved understanding of soil-root relations and dynamics of below-ground carbon pools in both tree biomass and soils. Attention is also required to range and variation in site conditions due to nature of new land which is likely to be available (eg enriched ex-pasture sites or effluent disposal sites, exposed mine rehabilitation sites or drier, less productive rangeland). Maximum carbon sequestration by plantation forests should be favoured on improved sites that are stocked with low lignin genotypes adapted to high CO₂ x nutrient inputs. This is not to discount the important role of tree breeding and site amelioration towards improved management of trees for carbon gain (and other environmental benefits) on poor sites.

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REFERENCES

- ABARE (1998). National Forest Inventory 1997. *Australian Forest Products Statistics*, March quarter 1998. ABARE, Canberra.
- Attiwill, P.M. (1979). Nutrient cycling in a *Eucalyptus obliqua* (L'Herit.) forest. III. Growth, biomass and net primary productivity. *Aust. J. Bot.* 27: 439-458.
- Atwell, B.J., Kriedemann, P.E. and Turnbull, C.G.N. (Eds) (1999). *Plants in Action*. ASPP/MacMillan, South Yarra. 664 pp.
- Australian Greenhouse Office (1998). *Greenhouse Challenge Vegetation Sinks Workbook – Quantifying Carbon Sequestration in Vegetation Management Projects*, Vers. 1.0, December 1998. Australian Greenhouse Office, Canberra.
- Baker, T.G. and Attiwill, P.M. (1985). Above-ground nutrient distribution and cycling in *Pinus radiata* D. Don and *Eucalyptus obliqua* (L'Herit.) forests in south-eastern Australia. *For. Ecol. & Manage.* 13: 41-52.
- Beets, P.N. and Pollock, D.S. (1987). Accumulation and partitioning of dry matter in *Pinus radiata* as related to stand age and thinning. *N.Z. J. For. Sci.* 17(2/3): 246-271.
- Bengtsson, J., Wikstrom, F. and Smith, C.T. (Dyck, W.J. ed.) (1994). Effects of whole-tree harvesting on the amount of soil carbon: model results. *N.Z. J. For. Sci.* 23(3): 380-389.
- Borough, C., Bourke, M. and Bennett, D. (1998). Forests as CO₂ sinks – an opportunity for forest growers? *Australian Forest Grower* 21(1): Liftout Section 43: 1-6.
- BTCE (1996). *Trees and greenhouse: costs of sequestering Australian transport emissions*. Working Paper 23. Australian Bureau of Transport and Communications Economics, Canberra.
- Conroy, J.P., Milham P.J., Mazur, M. and Barlow, E.W.R. (1990a). Growth, dry weight partitioning and wood properties of *Pinus radiata* D. Don after two years of CO₂ enrichment. *Plant, Cell & Environ.* 13: 329-337.
- Conroy, J.P., Milham P.J., Reed, M.L. and Barlow, E.W. (1990b). Increases in phosphorus requirements for CO₂-enriched pine species. *Plant Physiology* 92: 977-982.
- Conroy, J.P., Milham P.J. and Barlow, E.W.R. (1992). Effect of nitrogen and phosphorus availability on the growth response of *Eucalyptus grandis* to high CO₂. *Plant, Cell & Environ.* 15: 843-847.
- Conroy, J.P. (1999). Factor interaction and CO₂ enrichment. In: B.J. Atwell, P.E. Kriedemann and C.G.N. Turnbull (eds). *Plants in Action*. Ch.13.3, pp. 422-428. ASPP/MacMillan, South Yarra.
- Eamus, D., Berryman, C.A. and Duff, G. (1995). The impact of CO₂ enrichment on water relations of *Maranthus corymbosa* and *Eucalyptus tetrodonta*. *Aust. J. Bot.* 43: 273-282.

- FAO (1995). Forests and land cover, Forest Resources Assessment 1990: global synthesis. Food and Agricultural Organization, Rome.
- IPCC (1996). Land-use change in forestry. In: *Guidelines for National Greenhouse Gas Inventories: Reference Manual*. Ch. 5. Intergovernmental Panel on Climate Change. WMO/UNEP.
- Kaufman, D.G. and Franz, C.M. (1993). Biosphere 2000. Protecting our global environment. pp. 257-261. Harper Collins: New York.
- Kirschbaum, M.U.F., Fischlin, A., Cannell, M.G.R., Cruz, R.V. Galinski, W. and Cramer, W.A. (1996). Climate change impacts on forests. In: R.T. Watson, M.C. Zinyowera and R.H. Moss (eds.). *Climate Change 1995: Impacts, Adaptations and Mitigation of Climate Change: Scientific-Technical Analyses. Contribution of Working Group II to the Second Assessment Report of the Intergovernmental Panel on Climate Change*. pp. 131-158. Cambridge University Press, Cambridge and New York.
- Kirschbaum, M.U.F. (1998). The role of forests in the global carbon cycle. *Proc. Int. Conf. on Indicators for Sustainable Forest Management*, August 1998. pp. 58. IUFRO/CFTT, Vic. Dept. of Natural Resources and Environment, Melbourne.
- Landsberg, J.J. (1986). Physiological ecology of forest production. Academic Press, London.
- Landsberg, J.J. and Waring, R.H. (1997). A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *For. Ecol. & Manage.* 95: 209-228.
- Raison, R.J. and Myers, B.J. (1992). The biology of forest growth experiment: linking water and nitrogen availability to the growth of *Pinus radiata*. *For. Ecol. & Manage.* 52: 279-308.
- Reekie, E.G. and Bazzaz, F.A. (1989). Competition and patterns of resource use among seedlings of five tropical trees grown at ambient and elevated CO₂. *Oecologia* 79: 212-222.
- Ryan, M.G., Hubbard, R.M., Pongracic, S., Raison, R.J. and McMurtrie, R.E. (1996). Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nitrogen status. *Tree Phys.* 16: 333-343.
- Snowdon, P. and Benson, M.L. (1992). Effects of combinations of irrigation and fertilization on the growth and above-ground biomass production of *Pinus radiata*. *For. Ecol. & Manage.* 52: 87-116.
- Turner, J. and Lambert, M.J. (1983). Nutrient cycling within a 25-year old *Eucalyptus grandis* plantation in New South Wales. *For. Ecol. & Manage.* 6: 155-168.
- Turner, J. and Lambert, M.J. (1986). Effects of forest harvesting and nutrient removals on soil nutrient reserves. *Oecologia* 70: 140-148.
- West, P.M. and Mattay, J.P. (1993). Yield prediction models and comparative growth rates for six eucalypt species. *Aust. For.* 56: 211-225.
- Wilkes, J. (1989). Variation in wood density of *Pinus radiata* in New South Wales, Australia. *Can. J. For. Res.* 19: 289-294.
- Wong, S.C., Kriedemann, P.E. and Farquhar, G.D. (1992) CO₂ x nitrogen interaction on seedling growth of four species of eucalypt. *Aust. J. Bot.* 40: 457-472.

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