

Why don't our stands grow even faster? Control of production and carbon cycling in eucalypt plantations

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The growth of *Eucalyptus* stands varies several fold across sites, under the influence of resource availability, stand age and stand structure. We describe a series of related studies that aim to understand the mechanisms that drive this great range in stand growth rates. In a seven-year study in Hawaii of *Eucalyptus saligna* at a site that was not water limited, we showed that nutrient availability differences led to a two-fold difference in stand wood production. Increasing nutrient supply in mid-rotation raised productivity to the level attained in continuously fertilised plots. Fertility affected the age-related decline in wood and foliage production; production in the intensive fertility treatments declined more slowly than in the minimal fertility treatments. The decline in stem production was driven largely by a decline in canopy photosynthesis. Over time, the fraction of canopy photosynthesis partitioned to below-ground allocation increased, as did foliar respiration, further reducing wood production. The reason for the decline in photosynthesis was uncertain, but it was not caused by nutrient limitation, a decline in leaf area or in photosynthetic capacity, or by hydraulic limitation. Most of the increase in carbon stored from conversion of the sugarcane plantation to *Eucalyptus* plantation was in the above-ground woody biomass. Soil carbon showed no net change. This study and other studies on carbon allocation showed that resource availability changes the fraction of annual photosynthesis used below-ground and for wood production. High resources (nutrition or water) decrease the partitioning below-ground and increase partitioning to wood production. Annual foliage and wood respiration and foliage production as a fraction of annual photosynthesis was remarkably constant across a wide range of fertility treatments and forest age. In the Brazil *Eucalyptus* Productivity Project, stand structure was manipulated by planting clonal *Eucalyptus* all at once or in three groups at three-monthly intervals, producing a stand where trees did not segregate into dominants and one that had strong dominance. The uneven stand structure reduced production 10–15% throughout the rotation.

Keywords: age-related productivity decline, carbon allocation, forest production ecology, nutrition

Introduction

Why do stands differ in wood growth (Figure 1)? This central question has been addressed using a variety of approaches, but most approaches offer only approximate answers that are not easily generalised. For example, we know that productivity will vary with climate, 'site index' or site quality and sites with taller mature trees are more productive than sites with shorter mature trees. We know that tree growth declines with tree age. We know that applying fertiliser often, but not always, increases growth. We know that improved 'genetics' can increase growth. In all of these cases, we know some factor that relates to the differences in growth that we observe. However, from the point of view of ecophysiological processes, we still do not completely know why these patterns occur, nor can we easily predict productivity for different conditions (different site, longer rotation, different climate, different fertility, etc.).

Researchers have progressed to being able to quantify and simply predict productivity for different climates (Landsberg and Waring, 1997) and the response of productivity to fluctuations in weather. These advances have come

from a fundamental understanding of how climate controls photosynthesis and plant growth, and recognise a strong interaction between climate and the amount and function of vegetation at any site. From a climate perspective, most of the controls are quite simple. Radiation and leaf area control the amount of radiation available for photosynthesis, and temperature, humidity and soil water control the opening of stomata to admit or limit CO₂ through the stomata to realise photosynthesis.

The non-biophysical component of growth or productivity is less known. We have only an incomplete knowledge of carbon allocation and the interaction of carbon sinks with photosynthesis. We do not understand the cause of age-related growth decline, a phenomenon that controls the economics of forestry and the process of carbon storage in forests. We cannot predict the response of a given site to fertiliser application, how long it will last and its final location within the ecosystem. We do not know the mechanism responsible for the better performance of 'genetically superior' trees and we cannot predict the effects of climate

disturbances that will be more common in the future (such as drought, more extreme storms and temperatures) on survival and productivity.

In this paper, we will describe our experimental approach for understanding the mechanisms causing differences in productivity with age, resource availability, and genetics. We will also present published and unpublished key findings from studies of *Eucalyptus* in Hawaii for age and nutrition, from the literature on carbon allocation, and from studies of *Eucalyptus* in Brazil (the ongoing Brazil *Eucalyptus* Productivity Project [BEPP] study).

Experimental approach

Our experimental approach (Giardina *et al.*, 2003, 2004; Ryan *et al.*, 2004; Stape *et al.*, 2008) used experimental manipulations of resources (water and nutrients) similar to studies in Sweden (SWECON), Australia (BFG) and North Carolina USA (SETREES). To these pioneering experimental designs, we added a component that aims to untangle the contribution of differences in genetics from that of differences in stand structure. To do this, we compared the carbon budgets of: (1) plants started from seed, (2) clonal *Eucalyptus* with portions of the stand planted at different times and (3) clonal *Eucalyptus* planted at the same time. For processes that change with tree age and size, we used common measurements throughout a typical rotation of 6–7 years. This approach has fewer problems than chronosequence studies, because the trees are under the same environment for all experiments, except for the factors that are experimentally manipulated.

Above-ground wood production represents a small fraction of the annual carbon balance of a forest, and varies 8–31% (Figure 2, Litton *et al.*, 2007). Because this component is small and variable, we measured most or all of the annual flows of carbon to the largest sinks, and estimated gross primary production (GPP) as a sum of these flows (Figure 2). Knowing all of the major fluxes allowed us to determine how the experimental manipulations change both

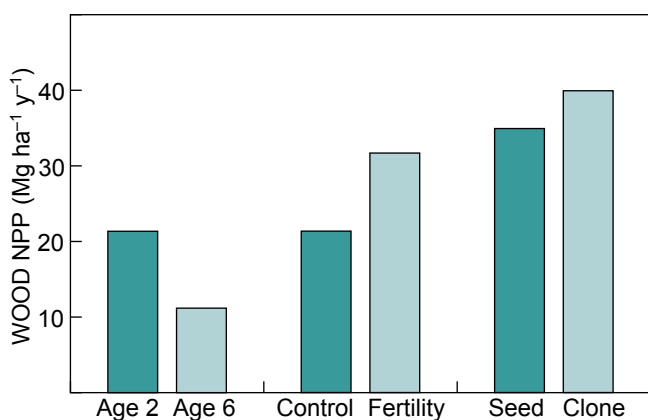


Figure 1: Differences in wood net primary productivity (NPP) between pairs of stands in response to age, fertility and ‘genetics’. Age and fertility data are from *Eucalyptus* in Hawaii (Ryan *et al.*, 2004), and seed vs clone data are from Brazil (JLS *et al.*, unpubl. data)

canopy carbon gain and carbon allocation, which are keys to furthering a mechanistic understanding and generalisation.

We measured above-ground net wood production by measuring stem diameter or stem diameter and height and used allometric equations to estimate biomass and carbon content. Foliage production was estimated using litter fall (collected monthly and corrected for decomposition in the litter traps), leaf area from light interception or LiCor LAI-2000 measurements and corrected for clumping by comparison with harvest data, and leaf mass per area of foliage collected during periodic harvests. The largest component of the carbon outflow is to below-ground sinks, such as fine root production, fine root respiration, mycorrhizae production and respiration, and root exudation. To measure this component, we used a carbon balance approach by measuring the above-ground inputs (litterfall), outputs (soil respiration), and any change in storage in the soil carbon and large roots (Giardina and Ryan, 2002).

For the study in Hawaii, we measured above-ground foliage and wood respiration, components whose annual flux can be similar to that of above-ground wood production (Litton *et al.*, 2007). A literature survey showed that this component was tightly linked to production for these fast-growing trees (Litton *et al.*, 2007), and this component is expensive and difficult to measure routinely. For the BEPP study, we measured these respiration components for a chronosequence at one site and where all clones were grown in a common garden, and use these measurements for our estimates.

Results

Stand age

In Hawaii, wood production declined with stand age. By age six, above-ground wood production was 26–52% of the peak at age two (Figure 3). Overall, fertility affected

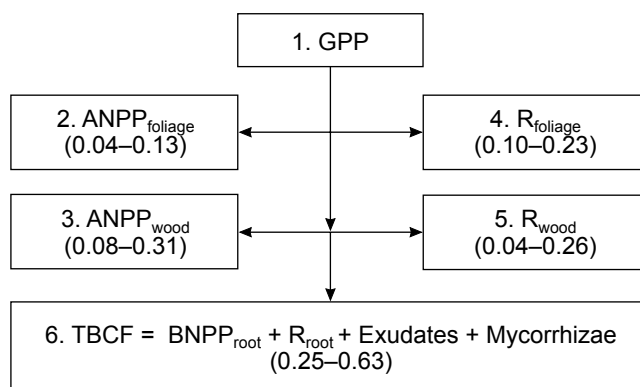


Figure 2: Major carbon flows summed to estimate gross primary production (GPP), and the range in annual GPP flow to each component found in a literature survey (from Litton *et al.*, 2007). GPP equals the total of above-ground net primary productivity of foliage (ANPP_{foliage}) and wood (ANPP_{wood}), respiration of foliage (R_{foliage}) and wood (R_{wood}), and total below-ground carbon flux (TBCF) consisting of below-ground net primary production of roots (BNPP_{root}), root respiration (R_{root}), root exudates (Exudates) and mycorrhizal growth and respiration (Mycorrhizae)

the rate of decline in wood and foliage production; production in the intensive fertility treatments declined more slowly (47% at age six relative to the peak) than in the minimal fertility (control) treatments (39% at age six relative to the peak). A decline in canopy photosynthesis was largely responsible for the decline in production, and the fraction of canopy photosynthesis partitioned to below-ground allocation and foliar respiration increased with stand age and contributed to the decline in above-ground wood production (Figure 4). The decline in photosynthesis was not caused by nutrient limitation, a decline in leaf area or in photosynthetic capacity, or by hydraulic limitation. In fact, we do not know what caused the decline in canopy photosynthesis. Recent work has suggested that hydraulic limitation—stomatal closure forced by overcoming gravity and a longer path for water flow in taller trees—lowers photosynthesis in older,

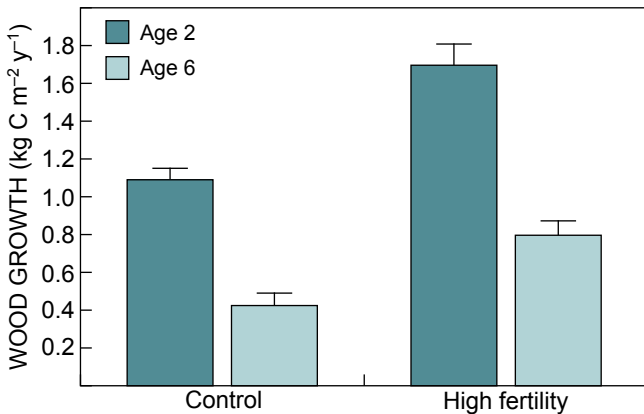


Figure 3: Wood production at ages two and six for minimally fertilised (control) and intensively fertilised (high fertility) treatments (data from Ryan *et al.*, 2004; Hawaii, USA)

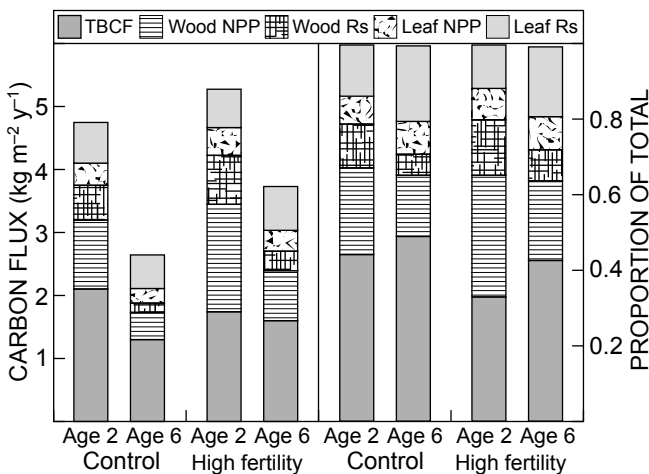


Figure 4: Gross primary production and annual carbon partitioning for minimally fertilised and intensively fertilised treatments at age two (peak production) and age six (data from Ryan *et al.*, 2004; Hawaii, USA). TBCF = total below-ground carbon flux, NPP = net primary production, Rs = respiration

taller trees, but is not sufficient to explain the much larger decline in photosynthesis in larger, older trees (Barnard and Ryan, 2003; Ryan *et al.*, 2006). Other work points to a potential sink limitation as the cause of lower photosynthesis in older, taller trees (Ryan *et al.*, 2006). A sink limitation would work through a signal of starch or sugar buildup in sink-limited cells that would signal a feedback to lower photosynthesis. Chronic lower turgor pressure resulting from the lower leaf water potential caused by gravity in taller trees could limit cell expansion and trigger such a sink limitation (Woodruff *et al.*, 2004). This potential mechanism needs much further explanation and a link to the complete carbon budget of a stand to be tested.

In Brazil, above-ground wood production declined with stand age at the five sites with a record sufficiently long to evaluate this (Figure 5). The decline varied by site and treatment from 39 to 96% at ages three to five years compared to the peak at age two. For two of the five sites, production declined more rapidly for the drier, rain-fed treatments, compared to the irrigated treatments. The large differences among sites, and for some sites among treatments, suggests that the BEPP study will soon provide further information about the mechanism of age-related productivity decline.

Carbon storage in plantations (net ecosystem production)

Fast-growth plantations may promote carbon storage on the landscape if they replace non-wood vegetation such as pasture. In Hawaii, the increase in carbon stored from conversion of sugarcane plantation to *Eucalyptus* plantation was in the above- and below-ground woody biomass. Soil carbon showed no net change (Figure 6). The gain in carbon stored after conversion is very rapid (about 1.5 kg C m⁻² y⁻¹ or 55 tonnes CO₂ ha⁻¹ y⁻¹). After conversion, however, the total amount of carbon that can be stored is about 130 tonnes CO₂ ha⁻¹, the average amount of carbon on the landscape at any one time for a working forest with a 6–7 year rotation. Gains in carbon storage from conversion of pasture to plantation forests need to be balanced against greater water use by the faster-growing trees (Jackson *et al.*, 2005), a change in the

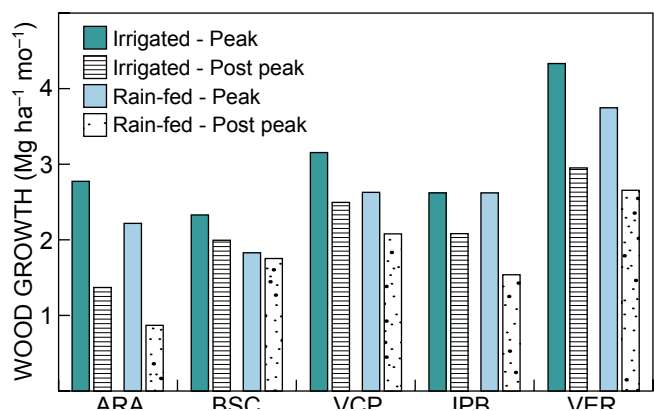


Figure 5: Above-ground wood production for irrigated and rain-fed treatments for peak and post-peak periods at five sites in Brazil (data from the Brazil *Eucalyptus* Productivity Project)

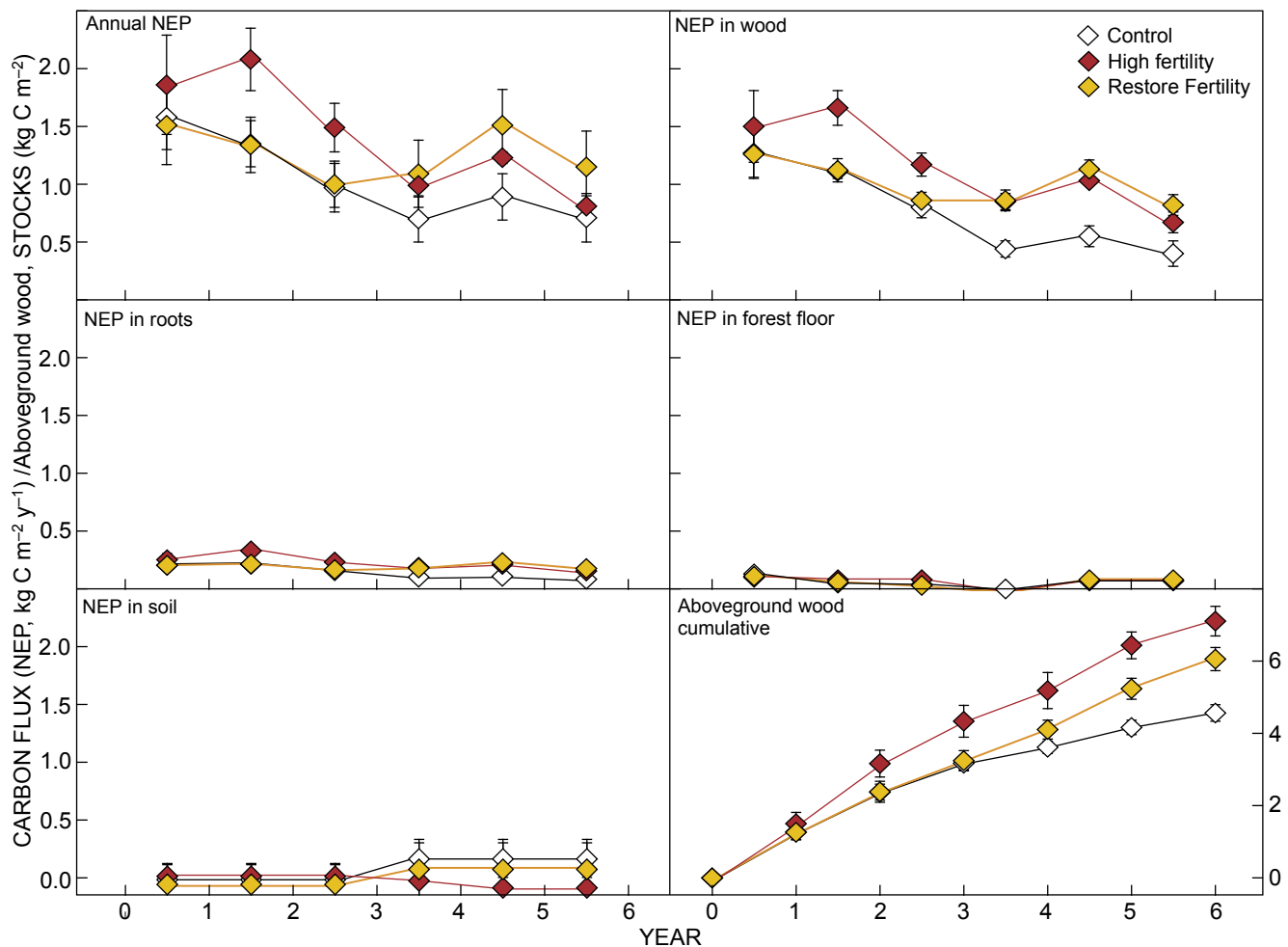


Figure 6: Annual net carbon storage (NEP) in different components and total carbon storage in wood in a eucalypt plantation in Hawaii (data from Ryan *et al.*, 2004)

albedo (forests are darker and absorb more radiation than do pastures, which negates some of the benefit of removing CO₂ from the atmosphere), and radiatively active gasses produced in forest management, such as isoprene (Funk *et al.*, 2006) and nitrogen oxides.

Fertility

In Hawaii, above-ground wood production increased up to two-fold with nutrient availability (Figure 3). The increase in wood production resulted from two separate mechanisms. First, GPP increased in the heavily fertilised treatments (Figure 4), because of an increase in leaf area and an increase in photosynthetic capacity of the foliage. Second, annual partitioning to below-ground fluxes decreased as a proportion of GPP, even though the flux was similar (Figures 4 and 7). These two mechanisms seem to be a common feature of a response to increased resources (Litton *et al.*, 2007). In Brazil, GPP increased in an irrigated treatment compared to the rain-fed treatment, and the fraction of GPP used annually below-ground decreased, leading to an increase in above-ground wood production (Stape *et al.*, 2008).

In *Eucalyptus*, the response to fertility occurred in one year, as assessed with the Hawaii 'restore fertility' treatment. These results suggest that where nutrients limit growth, gains in wood production can occur even in mid-rotation stands.

Genetics

Stem growth in stands containing genetically identical trees developed by cloning techniques often grow more wood than genetically diverse stands derived from seeds. The difference in growth rates are often 5–10%. But why do clonal stands often grow better? An answer of 'better genetics' does not help us understand the physiological reasons. In the BEPP project, we tested whether the higher growth rate of clonal stands was due to better genetics than in seed-derived stands. In one location (International Paper of Brazil, Mogi Guacu, Brazil), we found that clonal plots accumulated 6.4% more wood than seed-origin plots, even with heavy fertilisation and irrigation (Figure 8). Clonal stands show lower variation in tree sizes within stands than seed-origin stands; could the difference in growth rates result from uniformity of tree sizes rather than genetics *per se*? One treatment established trees from the same clone with planting dates spread out over three

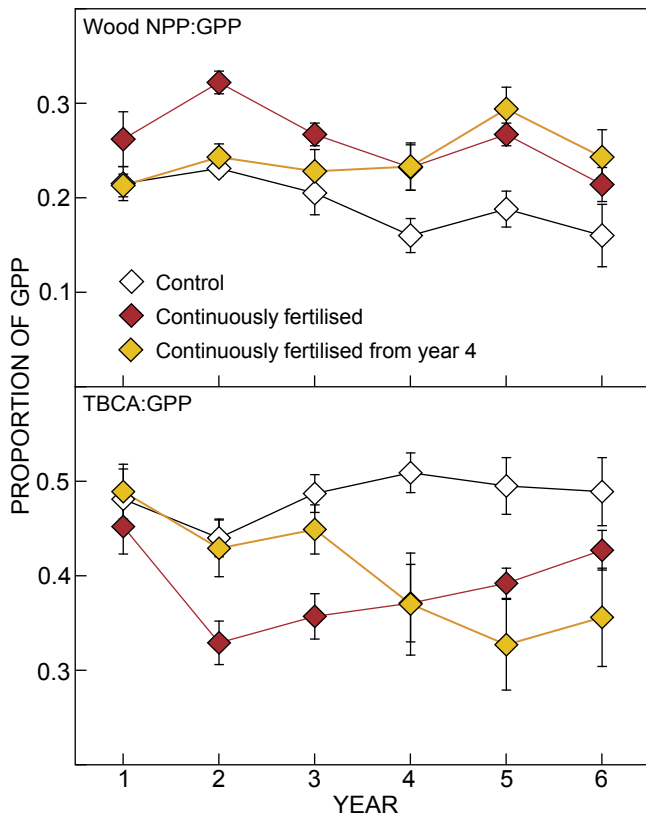


Figure 7: The response of carbon partitioning to above-ground wood production and to below-ground varies with fertility and is extremely rapid (data from Ryan *et al.*, 2004; Hawaii, USA)

months. This delayed-planting scheme led to higher variation in tree sizes within plots, matching the variation in seed-origin stands. The uneven sizes of clonal trees reduced the growth rate by 7.5%, erasing the difference commonly found between clonal and seed-origin stands. The higher growth of clonal stands probably depends as much on greater uniformity of tree sizes than on better physiology from better genes. But why does stand uniformity lead to higher growth rates? We hope to have the answers in time for the IUFRO conference sponsored by the Institute of Forest Research Studies at the University of Sao Paulo in November 2008.

Discussion

We have outlined a powerful approach for understanding the mechanisms underlying differences in wood growth. One of the most powerful features of the approach is that it can identify both differences in overall productivity (GPP) and differences in annual carbon partitioning. Knowing how resources, stand age and climate alter both factors will lead to more general and robust models of forest production. These models will be especially useful when moving to new sites, where plantations have not previously been planted, and for assessing performance in potentially altered climates in the future.

From our work in Hawaii and Brazil, we have learned that the upper limit for annual partitioning to above-ground wood

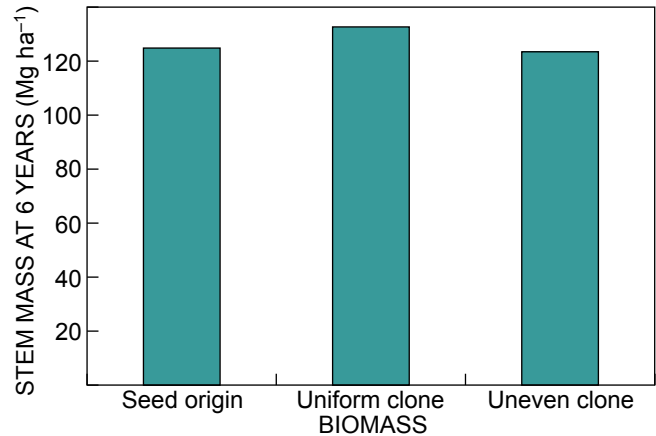


Figure 8: Biomass of seed-origin plantings, clonal planted at the same time, and one-third of the clones planted every three months (data from BEPP study, Brazil)

production is about 35% of GPP for ‘genetically superior’ clones and under minimal resource limitation. We suspect that further increases in partitioning to wood are possible and recommend that genetics trials incorporate at least some portion of the carbon balance approach to further understand the target mechanism.

While declining photosynthesis is a proximate cause for age-related declines in productivity, we still do not know the ultimate reason. Does photosynthesis decline because of a sink limitation? To evaluate this mechanism, we need to link photosynthesis to sink limitation at the whole-plant and stand level. If a sink limitation does reduce photosynthesis, can we uncover a mechanism to increase sinks, especially to wood? Our results do show that traditional indices of GPP, such as light interception, foliar N or photosynthetic capacity, would currently overestimate photosynthesis in older stands.

One finding that we have yet to explore is the tremendous variability in production, age-related growth decline and response to resources among sites. Use of replicated experiments in Brazil has been a very powerful tool for identifying variability among sites and we have the information to discern differences because of photosynthesis and differences caused by carbon allocation. One fact we have learned is that sites chosen for the replicated BEPP experiments are not ‘typical’ for the forest estate where they occur; they are more fertile and responded less to nutrition than we had expected. We learned this fact through an approach that has broad utility for understanding patterns at the landscape scale, i.e. a twin-plot approach (Stape *et al.*, 2006). This approach establishes many sets of paired plots (paired to determine that no pretreatment differences exist and to provide a control). Productivity and light interception can be measured and then a treatment imposed (for example, fertilisation). If these plots are randomly located on the landscape (or stratified according to soil type, climate and stand age), they provide a very solid answer about the treatment response (Stape *et al.*, 2006). If the treatment can be implemented simply and the plots are part of the normal inventory network, the addition of the ‘twin plots’ is

simple and yields much information. In Brazil over 700 'twin plots' have been established over many forest estates, and companies are using this approach to decide when and how much to fertilise.

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