

Thinking about Efficiency of Resource Use in Forests

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Abstract. The growth of forests can be described as a function of the supply of resources, the proportion of these resources captured by trees, and the efficiency with which trees use these resources to fix carbon dioxide. This function can be modified to explain wood production by subtracting the allocation of carbon (C) to respiration and other tissues. At the scale of leaves and seconds, rates of net photosynthesis typically show declining marginal gains in carbon (C) with increasing rates of light absorption, water transpiration, and sometimes nitrogen (N) concentration. However, these trends may not represent the trends that occur at the scale of forests and years, owing to more complete C accounting (including costs of synthesis and maintenance of tissues), and interactions among resources. Patterns in the growth of forests, across environmental gradients or silvicultural treatments, demonstrate substantial variation in efficiency of resource use at the scale of forests and years, including increasing efficiency of resource use as rates of resource use increase. Case studies from *Eucalyptus* plantations indicate that more productive sites tend to have higher efficiency of resource use than less productive sites, and within-site increases in production from silvicultural treatments may result in part from increased efficiencies in resource use. The questions raised here apply to all forests, but the level of confidence in our general conclusions remains limited by the number of studies available with complete estimates of rates of resource use and production.

Introduction

Forest production depends on trees obtaining resources from the environment and using these resources to fix atmospheric CO₂ into biomass. The production of wood also depends on the pattern of biomass allocation in trees; wood biomass commonly accounts for 10 to 30% of the total production of trees. This verbal model can be stated in a quantitative form that provides some powerful insights into patterns in forest growth across species, environmental gradients, and stand age:

Gross Primary Production (GPP) =

Resource Supply x Proportion of Resource Supply
Captured x Efficiency of Resource Use

(based on Montieth 1977). This equation can be modified to define the production of woody biomass as the same function, minus allocation to other tissues and respiration. Several authors have used versions of this equation to explain patterns in forest growth (cf. Cannell

1989, Binkley et al. 1990, Landsberg 1997, Ryan et al. 1997, McMurtrie et al. 1997), but wider use of this approach would be useful. One forest may produce more wood than another as a result of higher resource supply, by capturing a greater proportion of available resources, by using resources more efficiently, or by allocating a greater proportion of biomass to wood. Foresters commonly expect higher rates of wood production from sites with greater supplies of resources such as water and nutrients, and forest scientists have quantified the rates of resource use for many forests around the world. Expectations about patterns of resource use efficiency have been clouded by incomplete production budgets, confusion over scales and definitions of terms, and poor definitions of economic analogies. In this paper, we briefly highlight the utility of the production ecology

equation, and focus on ways of thinking about the efficiency of resource use.

The production ecology equation

An application of the production ecology equation (Figure 1) details the components of the increase in production from irrigation of a clonal *Eucalyptus* stand in Brazil. Irrigation increased GPP from $6.2 \text{ kg m}^{-2} \text{ yr}^{-1}$ to $11.3 \text{ kg m}^{-2} \text{ yr}^{-1}$. Irrigation did not alter the supply of incoming light, but the percentage of light intercepted by the canopy increased from 63% to 71%. This increase in light capture is notably smaller than the increase in GPP, indicating a substantial increase in the efficiency of converting captured light into biomass. Irrigation increased the annual supply of water from $1.21 \text{ m}^3/\text{m}^2$ to $2.17 \text{ m}^3/\text{m}^2$, but the percentage of the water supply actually used by the trees declined from 74% to 58%, giving an actual annual water use of $0.90 \text{ m}^3/\text{m}^2$ for the rainfed stand and $1.25 \text{ m}^3/\text{m}^2$ for the irrigated stand. The difference in water use was again smaller than the relative increase in GPP, indicating a substantial increase in the efficiency of water use by the irrigated stand (rising from 6.9 kg/m^3 to 9.0 kg/m^3).

Irrigation more than doubled wood production from $1.44 \text{ kg m}^{-2} \text{ yr}^{-1}$ to $3.46 \text{ kg m}^{-2} \text{ yr}^{-1}$, a larger proportional increase than the increase in GPP (Figure 1), and a greater increase in the efficiency of wood production per unit of resource used.

Patterns of Resource Use Efficiency

The example above showed that the efficiency of using light and water increased as the amount of light and water used by the forest increased. This may seem counter-intuitive; many ecologists expect “declining marginal returns” of carbon gain per unit of resource used as the supply of a resource increases. This may be a logical expectation for some situations, but this pattern may not describe forest resource use at annual time scales. We briefly discuss prior work on resource use efficiency, and then explore present specific case studies. Discussions of efficiency are often clouded by differences in terminology; Table 1 provides a definition of terms commonly used in discussions of forest production and resource use.

The expectation of declining marginal returns is widespread in biology and chemistry, such as the Michaelis-Menton equation for the kinetics of enzyme reactions. Indeed, Pastor and Bridgam’s (1999) discussion of resource use efficiency uses the word “law” when referring to expectations of declining marginal returns. As we elaborate below, this

expectation may describe resource use efficiency very well at the scale of leaves and seconds (where reactions are most analogous with simple chemical reactions), but may not encompass the ecosystem-scale processes that determine efficiency of resource use at the scale of forests and years. This discrepancy across scales may derive from a broader accounting of the production budget (including costs of generating leaves and roots), and from interactions among the supplies and efficiency of use for several resources.

This classic expectation can be illustrated at the scale of leaves at the time scale of one second (Figure 2). At very low rates of resource use, leaves do not show positive rates of net photosynthesis; this is the classic “compensation point” from plant physiology, or R_{\min} in the terminology of Pastor and Bridgham (1999, which provides thorough coverage of the theoretical implications of resource efficiencies). When the resource use level is above this minimum, net photosynthesis increases rapidly with increases in resource use, the rate of increase typically slows as resource use rates become very high. The slope of the curve of resource use efficiency with increasing resource use is steep when resource use is close to the R_{\min} , and then declines as resource use moves far beyond the R_{\min} . These general expectations are illustrated at the scale of leaves and seconds for 5-year-old *Eucalyptus saligna* in a plantation in Hawaii (Figure 2). This general pattern indicates that the efficiency of using water and light (defined in units of production per unit of resource used) must initially increase as the rate of resource use increases, then decline. The efficiency of N use (at the scale of seconds) differs conceptually from that of light and water, as the N acts as a catalyst (not consumed in the reaction of photosynthesis) rather than as a resource; in this case, the light-saturated rate of photosynthesis increased linearly with increasing N concentration in leaves, with a Y-intercept of 0, indicating a constant rate of N use efficiency across levels of N concentration.

Moving from the scale of a leaf to the scale of a forest and a year, the key issues in resource-use efficiency center on two conditions:

- 1) whether the X intercept is positive (= negative Y intercept, or a positive R_{\min}), in the relationship between production and resource use, and

- 2) whether resource use efficiency increases with the rate of resource use rises to the point where

efficiency declines (as illustrated at the scale of leaves and seconds in Fig. 2).

We expect condition #1 to be universal, because forests are not observed to occur in environments with extremely low rates of resource supply (and hence use), and because the production and maintenance of tree-sized tissues represents a very large “investment” that must be covered by obtaining a large minimum supply of resources. The instantaneous light compensation point for a leaf is always much lower than the “compensation point” that would provide for the C invested in constructing the leaf. Net growth of trees would occur only after construction and maintenance costs have been covered.

We think condition #2 remains remarkably under-investigated for forests. Too few estimates have been developed for complete C budgets and resource use at the scale of hectares and years. In the absence of evidence at this scale, ecologists and foresters often assume strong declines in the marginal gain of C for marginal increases in resource use, much like the pattern that has been observed routinely at the scale of leaves and seconds. The limited information we have examined suggests that in fact forests often remain in the range of production and resource use where efficiency of resource use continues to increase. As noted by Pastor and Brigham (1999), a positive X-intercept must give a positive slope for the relationship between growth/resource use and resource use for at least some levels of low rates of resource use. Below we provide evidence supporting this assertion from field-based estimates of production and resource use in *Eucalyptus* plantations, and from the emergent patterns in the 3-PG model of Landsberg and Waring (1997)

Evidence for increasing resource use efficiency as forests increase rates of resource use

Interest in resource use efficiency among ecologists was stimulated by Vitousek's (1982) examination of nitrogen use efficiency as a function of nitrogen supply. Information on the N content of annual litterfall was available for many forests, and Vitousek (1982) used the mass of litterfall as an index of total forest growth, and the N content of litterfall as an index of N supply (nitrogen use efficiency = litterfall mass/litterfall N content). He plotted the ratio of litterfall mass:N as a function of N content of litterfall, and found that the efficiency of N use appeared to decline markedly as the supply of N increased. This approach could suffer from autocorrelation of the two axes (as the N content of litterfall appears in both), but Vitousek showed that the

decline in N use efficiency differed somewhat from the trend that would result from autocorrelation alone (see also Pastor and Bridgman's theoretical consideration of this trend).

This approach would not work if litterfall mass was not a constant proportion of ecosystem production as ecosystem production increases, which may be the case for *Eucalyptus* plantations (and other forests?). The 14-site rainfall gradient examined by Stape et al. (2003a, this volume) showed the litterfall mass/N uptake pattern followed the declining efficiency pattern, whereas the actual trend in ANPP/N uptake showed the opposite (increasing) trend because of the striking decline of litterfall mass as a proportion of ANPP as ANPP increased (Figure 3). Goncalves et al. (1997) examined the pattern between annual aboveground increments of biomass and N, and found a linear increase ($N \text{ uptake in kg ha}^{-1} \text{ yr}^{-1} = 1.87 + 3.1 \text{ times biomass increment in Mg ha}^{-1} \text{ yr}^{-1}$, $r^2 = 0.84$). The near-zero intercept and linear trend yielded a constant rate of wood production per unit of N in wood. Across gradients of forest production, wood production tends to increase more than leaf production, so we suspect this constant rate of wood production/N in wood may have resulted from an actual increase in the overall efficiency of production/N use by the trees. These studies clearly indicate that we should not necessarily expect the efficiency of N use to decline as N supply increases.

Why would forests remain on the linear part of the slope of production versus resource use, rather than proceed farther into a region of declining marginal gains from marginal increases in resource use? The short answer might be that plants are integrated systems where investments in tissues (leaves and roots) to obtain resources (light, water, nutrients) are balanced to a greater or lesser degree, and “luxury” consumption of resources may not be not widespread in forests. In addition, changes in the rate of use of one resource is often associated with changes in the rate of use of other resources, and the efficiency of use of these other resources. Trees with greater access to water may demonstrate greater efficiencies of use for light and nitrogen than trees that are more drought-stressed.

Some economic analogies have been developed by ecologists to gain insights on likely patterns of biomass allocation and nutrient use efficiencies (Bloom et al. 1985, Chapin et al. 2002). A full review of these ideas is beyond this paper, but we

note that the definitions of economic analogs by Bloom et al. (1985) reduced the insights they could obtain from economic analogies (as described by Hof et al. 1990). For example, Bloom et al. (1985) used resources as analogs of economic inputs, and biomass as an analog of both economic products and economic revenues. Hof et al. (1990) recommended using the carbon (C) invested in roots and leaves as inputs, the resources obtained by leaves and roots as analogs of products, and the C gain through the use of these resources as revenue. Hof et al. (1990) concluded that the efficiency of using a resource (GPP/resource used) such as water should increase as the amount of water captured increased, not as a result of more efficient photosynthesis, but as a result of reduced leaf area. For the given amount of available light, trees with more water required less investment in roots to meet the water loss associated with a CO₂ uptake, yielding an overall increase in net C gain per unit water used. As the inputs to a factory increase in availability, manufacturing becomes more efficient per unit of resource used because the inputs are cheaper to obtain; a direct analogy back to the discussion above of compensation points (or R_{min}).

Light use efficiency in wood production by *Eucalyptus nitens*

A case study with *Eucalyptus nitens* from Australia illustrates the increased efficiency of using light to produce wood (wood production/light used) as the amount light interception increases. Smethurst et al. (2002) examined the overall pattern between leaf area index (LAI) and stemwood production across a range of stand treatments for 4 sites (Figure 4). Wood production increased as LAI increased from 2 to 10, with the greatest increase in wood growth/LAI occurring at an LAI of about 4. This would seem to indicate a declining efficiency of resource use with LAI > 4, but resource use does not relate linearly with LAI. Light capture per unit of leaf area declines exponentially as LAI increases (the Beer-law pattern), and conversion of LAI to light interception showed a sustained increase in wood production per unit light interception, and increasing efficiency of light use. For this conversion, we assumed a Beer-law light extinction coefficient of -0.5 and an annual light supply (photosynthetically active radiation, PAR) of 2.5 GJ/m², but the overall trend of increasing efficiency is consistent for any reasonable choice of parameters. Referring back to the production ecology equation, this increased efficiency of light use to produce wood could result from an overall increase in

efficiency of light use, or from a shift in biomass allocation that covaries with overall forest growth. These two alternatives cannot be evaluated without more information, but the overall conclusion remains robust: wood production per unit of light intercepted increased with increasing light interception.

Resource use efficiency and GPP for a plantation of *Eucalyptus grandis* x *urophylla*

Stape et al. (2003a) found increases in ANPP per unit resource used in clonal stands of *Eucalyptus urophylla* x *grandis* as the rate of resource use increased across a rainfall gradient in Bahia, Brazil. This increase could have resulted from increased efficiency of production (GPP/resources) as a function of resource use, or it may have been an indirect result of high-rainfall sites experiencing lower vapor pressure deficit (which would increase rates of photosynthesis per unit of water transpired).

A stronger test of the direct role of resource use comes from an irrigation experiment in the same region, where the water supply varied by treatment without any substantial effect on VPD (Stape 2002). We use production data (Figure 1) from a single year (with a normal rainfall pattern that included a 3-month dry period) to illustrate how resource use efficiencies changed in response to irrigation (Figure 5). Production per unit of light used increased with irrigation, with the greatest increase in efficiency for wood production (wood production/light used), and the least for GPP (GPP/light used). The disproportionate increase in efficiency for wood production resulted from an increased allocation of GPP to wood production (and lower proportional allocation belowground) in irrigated plots. The same trend was apparent for the efficiency of water use, and for the efficiency of N use (with N use defined simply as the N content of the canopy). The effect of irrigation on water use efficiency was smaller (30% in GPP/water, 70% increase in wood/water) than the effect on light or N use efficiency (58% in GPP/light, 110% for wood/N). The simultaneous increase in efficiency of using all three of these resources in response to an increase in the supply of just one resource (water) illustrates the interacting nature of these calculations of efficiency; an improved supply of one resource commonly increases the efficiency of using other resources (Nambiar and Brown 1997), and

simulation models may be required for a full accounting of responses.

Patterns in Light and Water Use Efficiency in the 3-PG Model

Stape et al. (2003b, this volume) parameterized the 3-PG model for plantations of *Eucalyptus grandis* × *urophylla* in Bahia, Brazil. The parameterized version of the model provided good representations of leaf area, resource use, and biomass production and allocation. This model was designed to integrate resource use and forest production, but it does not have an a priori expectation about the efficiency of resource use. We took a base-case parameterization for 3-PG, representing the *Eucalyptus* stand from Stape et al. (2003b) for the non-irrigated treatment, and the normal year of precipitation (which included a 3-month dry period). We then changed the model parameterization to increase rainfall by up to 1000 mm/yr, with the additional rainfall spread evenly through the year. A second set of simulations allowed vapor pressure increase when rainfall was increased, based on an empirical relationship for this site. With increasing rainfall, GPP/water use was almost constant, within a 3% range across a 1000 mm gradient in rainfall (Figure 6). Allowing the VPD to decrease in response to increasing rainfall allowed water use efficiency to increase by 21%. The increased use of water drove substantial increases in the efficiency of light use; each 100 mm increment in annual rainfall increased the efficiency of light use by about 5% (for baseline VPD) or 8% (with VPD decreasing with rainfall increment). These simulations did not include the change in cloudiness that would be associated with increasing precipitation (likely to be less than 10% reduction in incoming light at this location). Overall, the changes in efficiency were smaller in these simulations than those actually observed in response to irrigation (Figures 1 and 5) or year-to-year variations in weather (Stape 2002), so more investigation of these patterns with case studies and models should be very productive.

Patterns in Light Use Efficiency for *Eucalyptus* Plantations around the World

Several studies have documented patterns of aboveground net primary production (ANPP) of *Eucalyptus* plantations in relation to intercepted light (Figure 6). All these studies showed increasing rates of ANPP with increasing light capture, and positive X-intercepts (=positive R_{\min} , and negative Y intercepts), which dictated that the ANPP/light intercepted must

increase with increasing light interception. We note that some of this increased efficiency probably resulted from shifts in allocation of GPP away from belowground production and into aboveground production, but for the two studies that estimated the entire GPP budget (Stape 2002, Ryan et al. 2003), the increase in efficiency was also true for GPP/light intercepted. It is possible that the apparent linear trends in Figure 7 could turn into curves that demonstrate declining marginal returns from light capture beyond 3 or 4 $\text{GJ m}^{-2} \text{yr}^{-1}$, but we have no observations from *Eucalyptus* plantations with such high rates.

Implications for Managing Forest Production

This view of the production ecology of forests has three main implications for how foresters and forest scientists think about forest growth. The first is that the basic production ecology equation can provide insight to any pattern of forest growth. Why is wood production higher on one soil type than another, or why did fertilization lead to a large growth response on one site but not another? The production ecology equation has heuristic value in structuring the possible answers to these (and related) questions. Second, a clear understanding of patterns of resource use efficiency across resource gradients is fundamental to explaining forest growth. Across a rainfall gradient in Brazil, the increase in ANPP with increasing rain resulted more from the effects of water supply and VPD on the efficiency of water use than on the simple increase of water use (Stape et al. 2003a, this volume). The third implication is that environmental issues about the impacts of forest management hinge in part on resource use and efficiency of use. The rate of wood growth per m^3 of water transpired by a forest varies greatly among sites; a given amount of water use can yield twice the wood increment on sites with higher water supplies and lower VPD.

We look forward to studies that examine the ideas presented here in more detail, with stronger empirical tests of the patterns that have begun to emerge from recent experiments. We expect the overall trend toward increasing efficiency of resource use with increasing resource use (at the scale of forests and years) will remain robust, but the details, magnitudes and interactions among resources and biomass partitioning require much more work to provide a general picture of trends and exceptions.

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Table 1. A glossary of commonly used terms in forest production and resource use (based in part on Berendse and Aerts 1987, Pastor and Bridgham 1999). Measures of production are commonly given in units of dry mass (or biomass), or in the mass of carbon alone.

Term	Definition
Aboveground net primary production (ANPP)	The quantity (or fraction) of net primary production allocated to aboveground tissues (=biomass produced in aboveground tissues)
Belowground production	Growth of roots, sometimes including carbohydrate consumed in respiration of roots (for synthesis and maintenance of tissues), and sometimes including carbohydrate used by mycorrhizal fungi
Compensation point	Level of resource supply where production matches respiration, yielding 0 net production; most commonly used as light intensity required for photosynthesis to match leaf respiration. Similar to R_{min}
Current annual increment	Annual rate of wood growth (or wood+bark), minus mortality in the same year.
Efficiency	In physics, work per unit of force applied. More broadly, the yield of a process per unit of resource.
Gross increment	Annual rate of biomass production (typically just stemwood)
Gross primary productivity (GPP)	The total quantity of biomass produced by photosynthesis (often omitting the C respired by leaves during photosynthetically active periods)
Mean annual increment	Annual average rate of wood growth (or wood+bark) for an entire rotation (= average of each year's current increment, minus mortality)
Mortality	Most commonly, the biomass resident in trees that die during a given period; sometimes used in reference to rate of tissue death from living trees, such as litterfall
Net ecosystem production	The quantity of biomass remaining after subtracting plant respiration and microbial respiration. This is the net change in ecosystem biomass content over a defined time period; also called net ecosystem flux.
Net increment	Annual rate of biomass (typically just stemwood) increase (=gross increment – mortality)
Net photosynthesis	The total quantity of carbon produced by photosynthesis, minus the C respired by leaves during photosynthetically active periods)
Net primary production (NPP)	The quantity of biomass remaining after subtracting plant respiration (for both synthesis of new tissues, and maintenance of tissues) is subtracted from GPP
Photosynthetically active radiation (PAR)	Light with wavelengths between 400 and 700 nm, commonly with units of photons ($\mu\text{mol of photons m}^{-2} \text{ s}^{-1}$), or units of energy ($\text{MJ m}^{-2} \text{ s}^{-1}$)
Resource	An element or form of energy used by plants in direct or indirect processes of production; in this paper, light (energy form), water (lost as a byproduct of CO ₂ uptake), and nutrients (catalysts for biochemical reactions, and components of cells) are the resources of interest
Resource availability	Quantity or rate of resources available in the environment (=resource supply)
Resource capture	The quantity of resources used by a plant at a defined scale of space of time; may be expressed as a proportion of the supply of the resource, or in units of quantity or rate (=resource use)
Resource capture efficiency	Proportion of available resources captured by plants (similar to resource capture, but as a proportion rather than a quantity or rate)
Resource response efficiency	Production per unit of resource used times the resource capture efficiency
Resource supply	Quantity or rate of resources available in the environment (=resource availability)
Resource supply efficiency	Production per unit of resource supply, regardless of proportion of supply actually obtained by plants

Resource use	The quantity of resources used by a plant at a defined scale of space of time (=resource capture)
Resource use efficiency	Production per unit of resource used, or resource available in the environment. A broad term needs to be defined clearly for any particular use, especially specifying if resource use is defined as supply in the environment or resources actually used by plants. In this paper, used as production measure per unit of resource used by plants
Respiration	The loss of biomass as carbon dioxide from metabolic processes associated with synthesis of biochemicals (also called construction respiration) and maintenance of cell structure and chemistry (called maintenance respiration)
R _{min}	The level of a resource required for production to match respiration (or other cost of production); similar to compensation point
Stem production	The growth of wood (sometimes wood + bark)
Total belowground carbon allocation (TBCA)	Total flux of carbon from photosynthesis to the belowground portion of the ecosystem, including net production of roots, root respiration, and mycorrhizae
Wood production	The growth of stems, sometimes including bark and branches

$$\text{GPP} = \text{Resource Supply} \times \text{Proportion of Resource Supply Captured} \times \text{Efficiency of Resource Use}$$

Light Control: $6.1 \text{ kg/m}^2 = 3.46 \text{ GJ/m}^2 \times 0.63 \times 2.8 \text{ kg/GJ}$
Irrigated: $11.3 \text{ kg/m}^2 = 3.46 \text{ GJ/m}^2 \times 0.71 \times 4.6 \text{ kg/GJ}$

Water Control: $6.1 \text{ kg/m}^2 = 1.21 \text{ m}^3/\text{m}^2 \times 0.74 \times 6.9 \text{ kg/m}^3$
Irrigated: $11.3 \text{ kg/m}^2 = 2.17 \text{ m}^3/\text{m}^2 \times 0.58 \times 9.0 \text{ kg/m}^3$

$$\text{Wood production} = \text{Resource Supply} \times \text{Proportion of Resource Supply Captured} \times \text{Efficiency of Resource Use} - \text{Allocation to respiration and other tissues}$$

Light Control: $1.4 \text{ kg/m}^2 = 3.65 \text{ GJ/m}^2 \times 0.66 \times 2.8 \text{ kg/GJ} - 4.7 \text{ kg/m}^2$
Irrigated: $3.5 \text{ kg/m}^2 = 3.65 \text{ GJ/m}^2 \times 0.74 \times 4.6 \text{ kg/GJ} - 7.8 \text{ kg/m}^2$

Water Control: $1.4 \text{ kg/m}^2 = 1.21 \text{ m}^3/\text{m}^2 \times 0.74 \times 6.9 \text{ kg/m}^3 - 4.7 \text{ kg/m}^2$
Irrigated: $3.4 \text{ kg/m}^2 = 2.17 \text{ m}^3/\text{m}^2 \times 0.58 \times 9.0 \text{ kg/m}^3 - 7.8 \text{ kg/m}^2$

Figure 1. Irrigation increased gross primary production (GPP) in a 4.5-year-old plantation of *Eucalyptus urophylla x grandis* in Bahia, Brazil. The production ecology equation (after Montieth 1977) showed the increase in GPP resulted in part from increased supply and capture of water, and slightly increased capture of light. The largest effects of increased water supply were on the efficiency of GPP/unit of resource used (from data in Stape 2002).

Figure 2. At the scale of leaves and seconds, *Eucalyptus saligna* in Hawaii show declining efficiency in using light (upper), water (middle), with increasing rates of use of these resources; efficiency of using nitrogen was constant. PAR = photosynthetically active radiation. Data come from measurements on leaves from five 5-year-old trees; for transpiration figure, rates were measured on leaves under a variety of light and VPD (most were PAR > 800 and VPD > 1 kPa). Solid lines represent average photosynthesis; dashed lines represent photosynthesis per unit of resource used (unpublished data from M.G. Ryan).

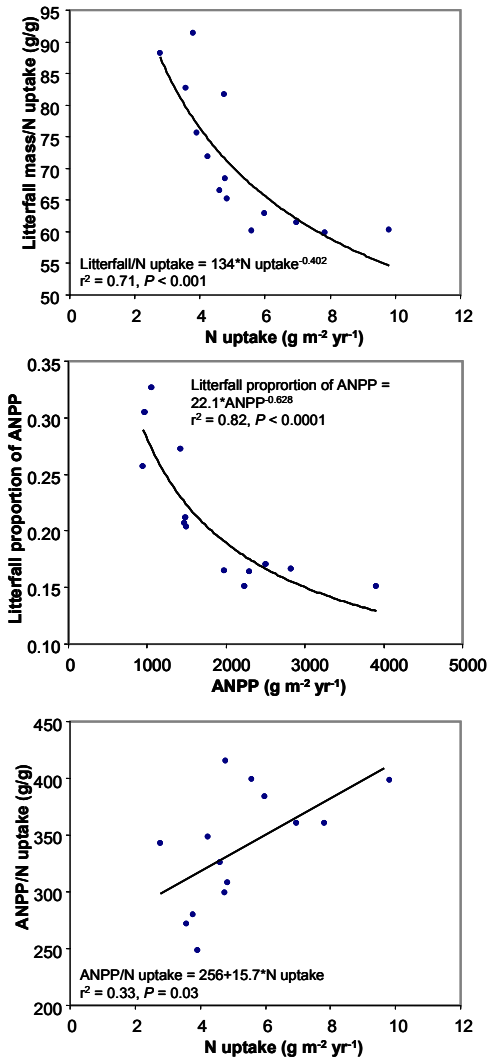
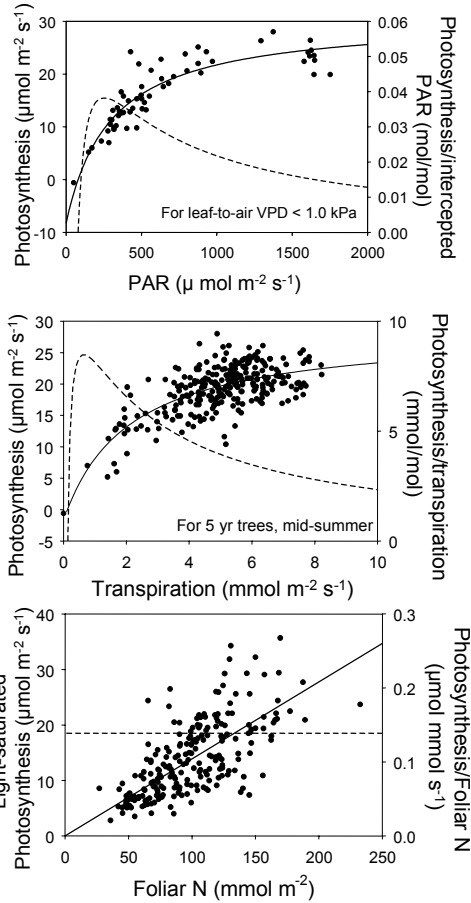


Figure 3. The efficiency of N use in clonal *Eucalyptus* plantations would appear to decline as N uptake increases across a rainfall gradient in Bahia, Brazil, if litterfall mass were used as a surrogate for ANPP (top graph). However, litterfall as a proportion of ANPP declines sharply as ANPP increases (middle graph), so the actual N use efficiency (defined as ANPP/N uptake) increased as N uptake increased (bottom graph; from data in Stape 2002).

Figure 4. Across 93 stands (with varying fertility treatments) at 4 sites, the stem growth of *Eucalyptus nitens* related strongly with stand leaf area ($r^2=0.84$, Smethurst et al. 2002). Stem growth per unit of leaf area peaked at a leaf area of about 4.5. Assuming a light extinction coefficient of -0.5 and an annual incoming photosynthetically active radiation of 2.5 GJ/m², stem growth tripled as light interception increased by 50% (bottom left). The greater increase in stem growth than light capture means the efficiency of converting light into wood increased with increasing light capture (bottom right). The slope and Y-intercept of the increase in efficiency depends on assumptions of the light extinction coefficient and the annual incoming PAR, but all reasonable estimates for these parameters yield a positive slope.

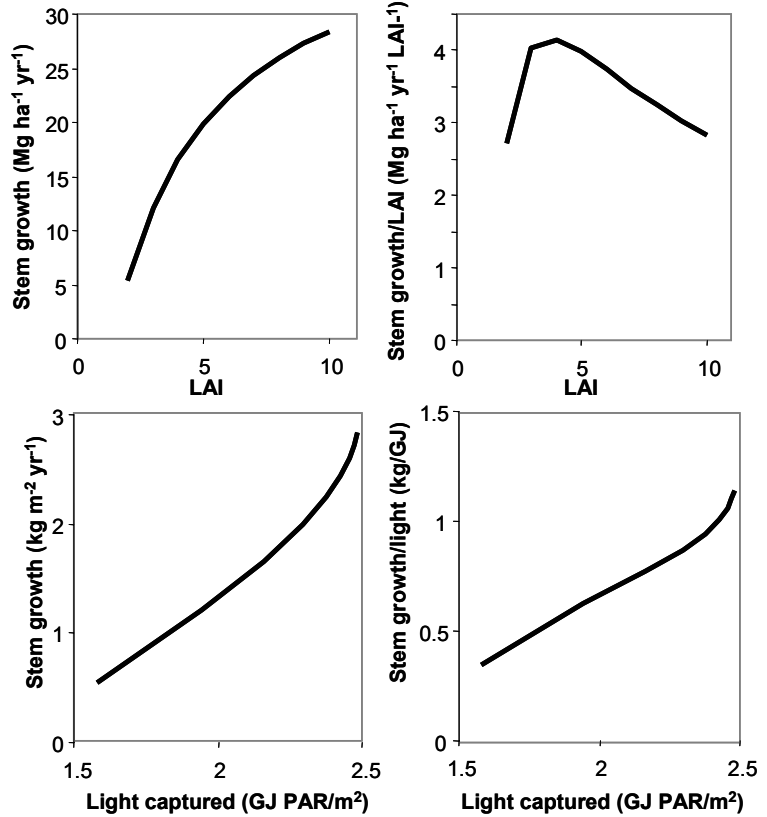
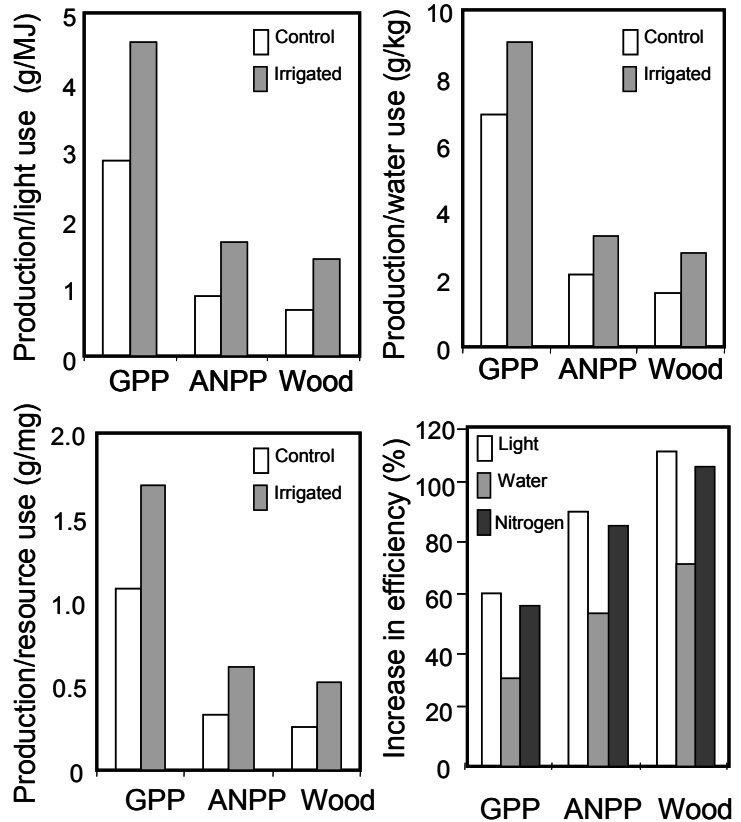


Figure 5. Irrigation increased gross primary production (GPP), aboveground net primary production (ANPP) and wood growth per unit of light, water, and nitrogen (=N content of canopy) used by a 4.5-year-old plantation of *Eucalyptus urophylla* x *grandis* in Bahia, Brazil (from data in Stape 2002). The increased in efficiency of production per unit of resource used (bottom right graph) ranged from 32% (for GPP/water used) to more than 100% (for wood growth per unit of light or nitrogen).



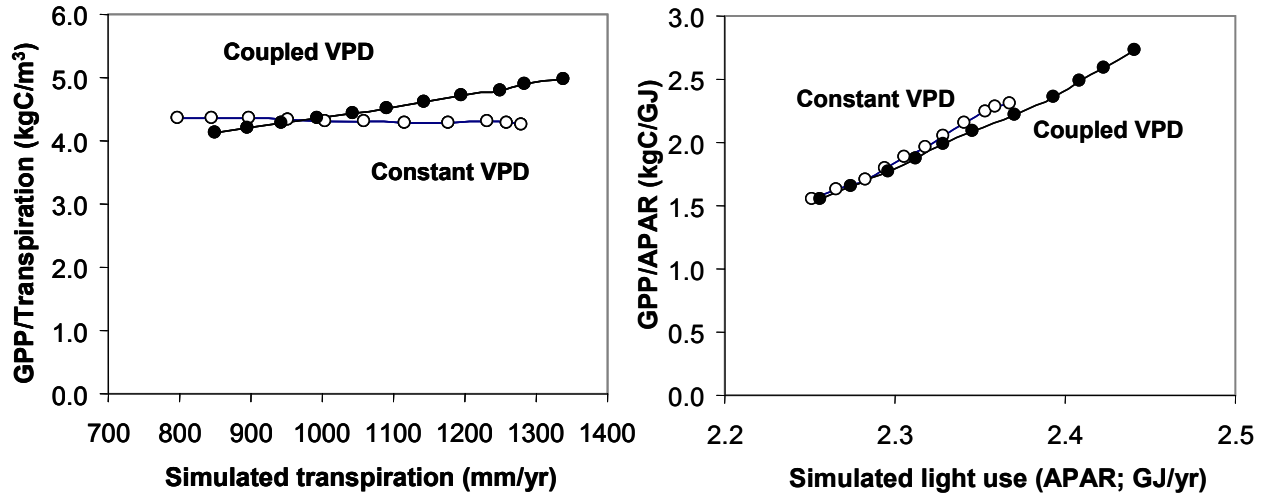


Figure 6. Simulations with the 3-PG model showed that increasing rainfall (each point represents 100 mm/yr increase in rainfall) led to increasing transpiration, but no change in the efficiency of water use (GPP/transpiration) if VPD was held constant at 1.2 kPa. Allowing VPD to vary with monthly precipitation (VPD range from 1.4 kPa to 0.9 kPa) demonstrated an increase in efficiency of water use as water use increased. Increasing simulated rainfall had little effect on leaf area and light interception (a 10-15% range), but a dramatic effect on the efficiency of light use (60% to 85% increase; simulations based on data from Stape et al. 2003b).

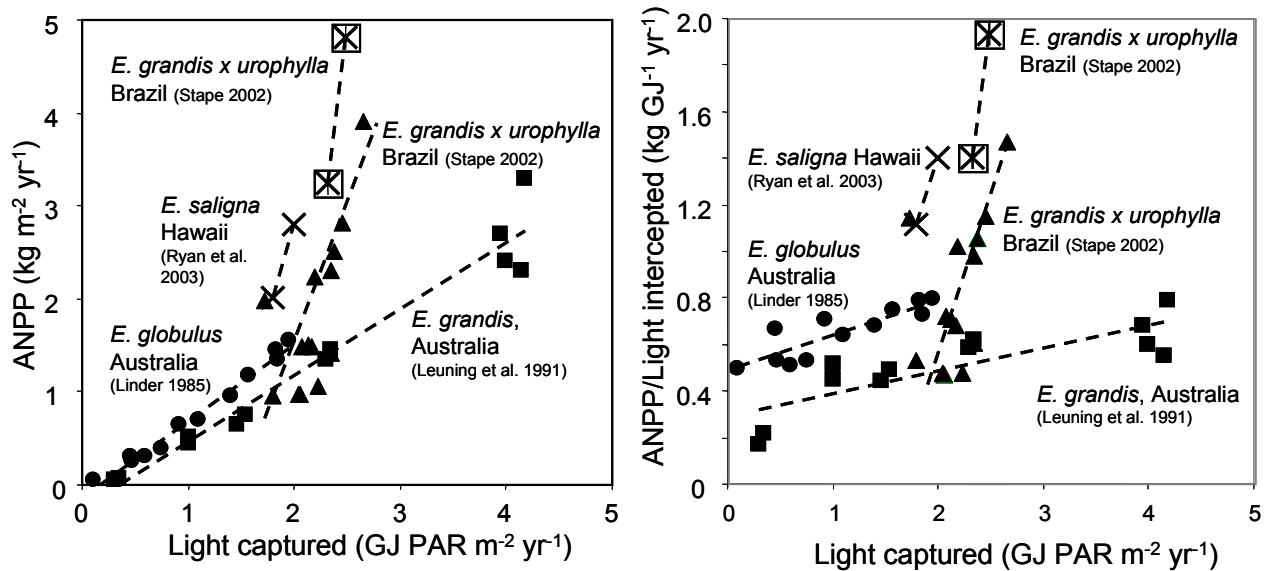


Figure 7. Estimates of aboveground net primary production (ANPP) and intercepted photosynthetically active radiation (PAR) vary substantially for *Eucalyptus* plantations around the world, but ANPP/light interception tends to increase with light interception in all cases.