



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 resources captured by trees, and the efficiency with which trees use resources to fix carbon dioxide. This function can be modified to explain wood production by subtracting the allocation of biomass to other tissues and to respiration. At the scale of leaves and seconds, rates of net photosynthesis typically show declining marginal gains with increasing rates of light absorption and transpiration. However, these trends may not represent those that occur at the scale of forests and years, owing to more complete biomass accounting (including costs of synthesis and maintenance of tissues), interactions among resources, and adaptation of biomass partitioning to optimize resource capture and use. Patterns in the growth of forests, across environmental gradients or silvicultural treatments, demonstrate that the efficiency of resource use at the scale of forests and years can increase with increasing rates of resource use. Case studies from *Eucalyptus* plantations indicate that more productive sites tend to have higher efficiency of resource use than less productive sites, and silvicultural treatments may increase both resource supplies and efficiency of resource use. The questions raised here apply to all forests, but the level of confidence in our general conclusions remains limited by the small number of studies available with complete estimates of rates of resource use and production.

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Keywords: *Eucalyptus* plantations; Forest light interception; Leaf area index; Resource-use efficiency

1. 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 partitioning (or allocation) in trees; woody biomass commonly accounts for 10–30% 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 (based on Monteith, 1977):

Gross primary production

= resource supply

× proportion of resource supply captured

× efficiency of resource use (1)

This equation, referred to as the production ecology 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., 1992; Landsberg, 1997; Ryan et al., 1997; McMurtrie et al.,

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1994), and 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. Expectations about patterns of resource-use efficiency have been clouded by incomplete production budgets, confusion over scales and definitions of terms (see reviews by Sheriff et al., 1995; Pastor and Bridgman, 1999), and poor definitions of economic analogies (discussed by Hof et al., 1990). In this paper, we highlight the utility of the production ecology equation, and focus on ways of thinking about the efficiency of resource use.

2. An illustration of the production ecology equation

An application of Eq. (1) shows why production increased with irrigation of a clonal *Eucalyptus* stand in Brazil (Table 1). Irrigation increased gross primary production (GPP) from 6.1 to 11.3 kg m⁻² per year. 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 was 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 to 2.17 m³ m⁻², but the percentage of the water supply used by the trees declined from 74 to 58%, giving an annual water use of 0.90 m³ m⁻² for the rainfed stand and 1.25 m³ 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 to 9.0 kg m⁻³). Irrigation more than doubled wood production from 1.4 to 3.5 kg m⁻² per year, a larger proportional increase than the increase in GPP, and a greater increase in the efficiency of wood production per unit of resource used.

Why should efficiency of resource use be higher in the irrigated stand? A leaf with an adequate supply of water can fix more CO₂ per unit of light intercepted than a water-stressed leaf with closed stomata; increased supplies of one limiting resource should logically increase the efficiency of use of other resources. More intriguingly, an increase in water use can also increase the efficiency of water use by increasing the “return on investment” of growing the canopy. A canopy that is well supplied with water will show more “profit” (net photosynthesis) than a similar canopy that has more frequent stomatal closure; greater

Table 1
Irrigation increased GPP in a 4.5-year-old plantation of *E. grandis* × *urophylla* in Bahia, Brazil (Stape, 2002)

Resource	Treatment	GPP ^a	Resource supply	Fraction used	Efficiency of use	
Light	Control	6.1	3.46	0.63	2.8	
	Irrigated	11.3	3.46	0.71	4.6	
Water	Control	6.1	1.21	0.74	6.9	
	Irrigated	11.3	2.17	0.58	9.0	
Resource	Treatment	Stem growth ^b	Resource supply	Fraction used	Efficiency of use	Partitioning to other pools
Light	Control	1.4	3.46	0.63	2.8	4.7
	Irrigated	3.5	3.46	0.71	4.6	7.8
Water	Control	1.4	1.21	0.74	6.9	4.7
	Irrigated	3.5	2.17	0.58	9.0	7.8

The production ecology equation (Eq. (1), after Monteith, 1977) showed that the increase in GPP (kg biomass m⁻² per year) 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 per unit resource used. The treatment effects on stem growth were accentuated by the differences in partitioning to leaves and below-ground biomass. Precipitation and incident light (photosynthetically active radiation, PAR) were measured; water use was estimated using the Penman-Monteith model, potential evapotranspiration and measured soil-water storage capacity. GPP was estimated by measurements of leaf and stem production, allocation of carbon to below-ground biomass, and estimates of leaf and stem respiration.

^a GPP = resource supply × fraction used × efficiency of use.

^b Stem growth = resource supply × fraction used × efficiency of use – partitioning to other pools.

net photosynthesis from the same investment in canopy biomass would increase the efficiency of water use.

3. 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. Expectations of declining marginal returns are logical for some situations, but this pattern may not describe forest resource-use at annual time scales. Discussions of efficiency are often clouded by differences in terminology, Table 2 defines some common terms used in forest production and resource use.

The expectation of declining marginal returns is widespread in biology and chemistry, such as the Michaelis–Menten 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. In classical Michaelis–Menten systems, the rate of a reaction depends on the supply of the substrate (resource), and the concentration of the enzyme that catalyzes the reaction. The rate of photosynthesis in a leaf depends on the simultaneous supplies of light, CO₂, and water, and the leaf’s concentration of photosynthetic enzymes, such as Rubisco. The net rate of photosynthesis per unit of light intensity is less than zero at low light intensities, owing to greater CO₂ loss in respiration than gain in photosynthesis. Above this compensation point, net photosynthesis increases with increasing light intensity, but the rate of increase declines. The decline results from either a constraining supply of other resources (e.g. CO₂ and water), or from a limited concentration of photosynthetic enzymes.

This classic expectation can be illustrated at the spatial scale of leaves at the time scale of one second. 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). These general

expectations are illustrated for 5-year-old *Eucalyptus saligna* in a plantation in Hawaii (Fig. 1). The efficiency of using water and light (defined in units of production per unit of resource used) initially increased as the rate of resource use increased, then declined. The second derivative of the two upper curves in Fig. 1 is negative throughout, indicating that the *marginal* gain per unit of resource used was indeed negative, even for the domain where the *average* efficiency increased with increasing use. Again, this results from the R_{\min} having a positive X-intercept (and negative Y-intercept).

The efficiency of nitrogen (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 *E. saligna* (Fig. 1), the light-saturated rate of photosynthesis increased linearly with increasing N concentration in leaves, with a Y-intercept of zero. The efficiency of N use remained constant across levels of N concentration.

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 Michaelis–Menten 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 several factors, including:

1. A negative Y-intercept in the relationship between production and resource use; the arithmetic requires that the efficiency of using resources must increase over some domain of resource supply before the average efficiency can decline;
2. Interactions among the supplies and efficiency of use for several resources; and
3. The longer term (weeks, months, years) adjustments in biomass partitioning (particularly production of leaves, roots, and mycorrhizae) as trees adapt to ambient environmental conditions and resource supplies.

How does the shape of the resource response-curves diverge from classic Michaelis–Menten patterns when the processes and patterns are scaled from leaves and seconds to stands over longer time periods? Few data are available at the scale of stands and seasons; one recent study (Turner et al., 2003) showed that GPP per

Table 2

A glossary of commonly used terms in forest production and resource use (based in part on Berendse and Aerts, 1987; Pastor and Bridgham, 1999)

Term	Definition
Above-ground net primary production (ANPP)	Above-ground dry-matter production per unit of ground area per unit of time (=biomass produced in above-ground tissues)
Absorbed photosynthetically active radiation (APAR)	Light intercepted by the canopy, with wavelengths between 400 and 700 nm, commonly with units of photons (μmol of photons $\text{m}^{-2} \text{s}^{-1}$), or units of energy ($\text{MJ m}^{-2} \text{s}^{-1}$)
Below-ground 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 ($=R_{\min}$)	Level of resource supply where production matches respiration, yielding zero net production; most commonly used as light intensity required for photosynthesis to match leaf respiration
Efficiency	In physics, work per unit of force applied. More broadly, the yield of a process per unit of resource. The definition of the process and the resource need to be identified carefully, particularly if resource refers to a supply in the environment or the rate used by plants
GPP	The total quantity of carbohydrates produced by photosynthesis (often omitting the C respired by leaves during photosynthetically active periods)
Net ecosystem production	The net change in ecosystem carbon content over a defined time period; also called net ecosystem exchange (NEE)
Net photosynthesis	The total quantity of carbon fixed by photosynthesis, minus the C respired by leaves during photosynthetically active periods). Often equivalent to GPP
Net primary production (NPP)	Dry matter production, or GPP minus plant respiration (for both synthesis of new tissues, and maintenance of tissues)
Photosynthetically active radiation (PAR)	Light with wavelengths between 400 and 700 nm, commonly with units of photons (μmol of photons $\text{m}^{-2} \text{s}^{-1}$), 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 in transpiration), 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 or time; may be expressed as a proportion of the supply of the resource, or in units of quantity or rate (=resource use, resource interception)
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 or 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
R_{\min} (Pastor and Bridgham, 1999)	The level of a resource required for production to match respiration (or other costs of production); similar to compensation point

Measures of production are commonly given in units of dry mass (or biomass), or in the mass of carbon (C) alone.

unit of light intercepted declined as light interception increased in mid-summer, in both a temperate deciduous forest and a boreal coniferous forest. The decline in light-use efficiency was ascribed to light saturation; light interception by the upper canopy in mid-summer exceeded the capacity of photosynthetic enzymes to fix CO_2 .

Patterns that apply at the scale of seconds or seasons within stands may not apply at scales of years and landscape. Trees and stands may adjust long-term patterns of biomass partitioning and structures in response to resource supplies, and this adaptation may shift the shape of the efficiency pattern (Fig. 2). Increasing water use by a forest may lead to an

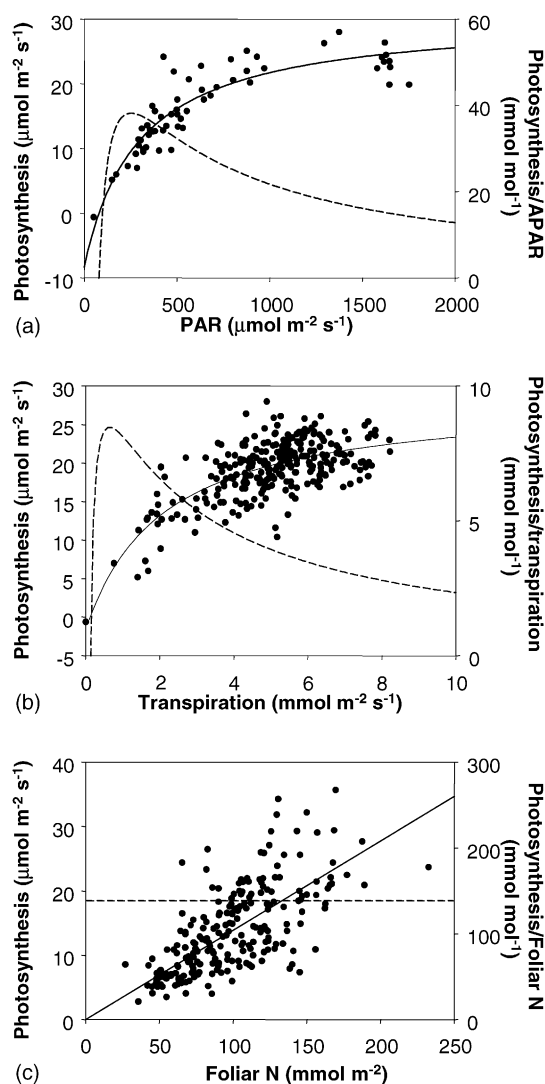


Fig. 1. At the scale of leaves and seconds, *E. saligna* in Hawaii shows declining efficiency (broken lines) in using light (a) and water (b) with increasing rates of use of these resources (PAR, transpiration), but efficiency of using nitrogen (c) was constant. Solid lines represent average photosynthesis. Measurements were made on 5-year-old trees. In (b) photosynthesis was measured under a variety of conditions of photosynthetically active radiation ($>800 \mu\text{mol m}^{-2} \text{s}^{-1}$) and vapor pressure deficit ($<1 \text{ kPa}$). Light-saturated photosynthesis (c) related linearly with the concentration of N in leaves (unpublished data from M.G. Ryan).

increase in growth simply as a result of increased photosynthesis by existing leaves (and constant light interception) or by also increasing the number of leaves (and increasing light interception). A simple

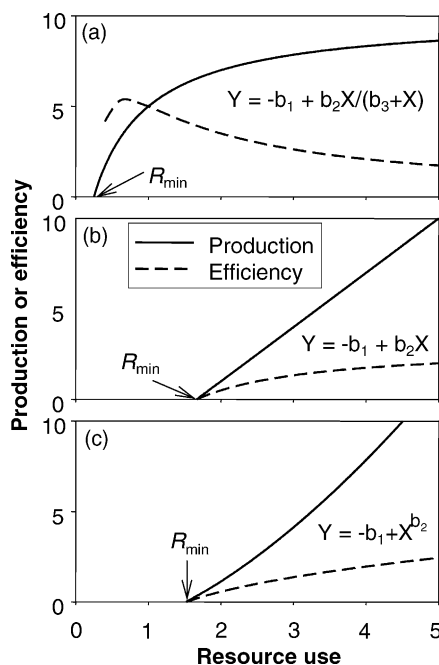


Fig. 2. Three potential patterns in production (—) and efficiency (---) in relation to increasing resource use illustrate that efficiency must increase for at least some domain of low resource use, as a result of the negative Y -intercept (=positive X -intercept, R_{\min}). (a) shows the classic Michaelis–Menten trend, where production increases with increasing resource use, but limitations of other resources or in the concentrations of enzymes slow the rate of increase; (b) would apply in situations where the concentrations of enzymes did not restrict the increase in production with increasing resource use, for example where canopies increase leaf area (and light capture) as water supply increases; and (c) shows production increasing faster than resource use, and might result when the integrated response of trees (biomass partitioning, use of multiple resources) results in improved whole-system efficiency.

increase in photosynthesis per leaf might give a linear increase in the efficiency of water use, whereas an increase in canopy light interception could give an exponential increase in water-use efficiency.

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 per unit 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 root production. For the given amount of available light, trees with more water required less investment in roots to meet the water loss associated with 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.

4. Evidence for increasing resource-use efficiency as forests increase rates of resource use

In the absence of evidence at the scale of stands and years, 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 found for *Eucalyptus* stands indicates that forests often remain in that range of production and resource use where the efficiency of resource use increases with resource use.

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

because of autocorrelation alone (see also Pastor and Bridgman's [1999] theoretical consideration of this point).

This approach works only if litterfall mass is a fixed proportion of ecosystem production, which was not the case across a fourteen-site rainfall gradient examined by Stape et al. (this volume, a). Litterfall mass declined as the proportion of above-ground net primary production (ANPP) increased. As had been found by Vitousek (1982), the pattern of litterfall mass per unit N uptake of these stands showed a decline in N-use efficiency as N use increased. However, ANPP showed the opposite (increasing) trend because of the marked decline of litterfall mass as a proportion of ANPP as ANPP increased (Fig. 3). An assumption that litterfall mass was a constant proportion of ANPP would lead to the wrong conclusion about the pattern of N-use efficiency.

Gonçalves et al. (1997) examined the pattern between annual above-ground increments of biomass and N, and found a linear increase (N uptake in kg ha⁻¹ per year = 1.87 + 3.1 times biomass increment in Mg ha⁻¹ per year, $r^2 = 0.84$). 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 per unit N in wood may have resulted from an actual increase in the overall efficiency of production per unit N use by the trees. These studies indicate that we should not expect the efficiency of N use to decline necessarily as N supply increases.

5. Light-use efficiency in wood production by *Eucalyptus nitens* in Australia

A case study illustrates the increased efficiency (kg MJ⁻¹) of use of absorbed photosynthetically active radiation (APAR, a measure of the amount of incident light intercepted by the canopy) to produce wood as the amount of light interception increased. Smethurst et al. (2003) examined the overall pattern between leaf area index (LAI) and stemwood production across a range of treatments in stands of *Eucalyptus nitens* at four sites (Fig. 4). Wood production increased as LAI increased from 2 to 10, with the

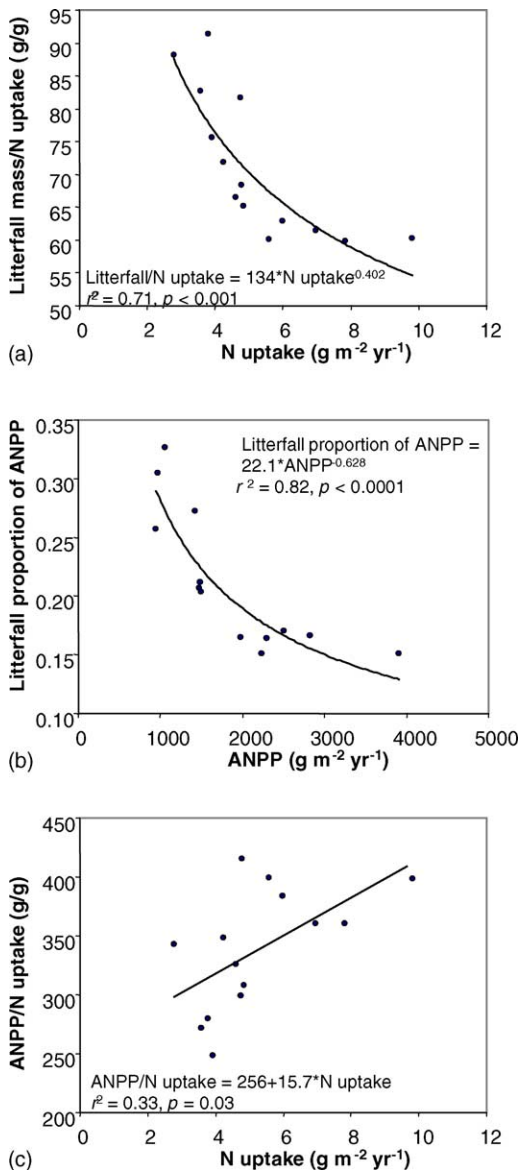


Fig. 3. Litterfall mass per unit nitrogen (n) uptake in clonal *Eucalyptus* plantations declines (a) as N increases across a rainfall gradient in Bahia, Brazil. However, litterfall as a proportion of ANPP declines sharply (b) as ANPP increases, so the actual N-use efficiency (defined as ANPP/N uptake) increased (c) as N uptake increased (based on data in Stape, 2002).

greatest increase in wood growth per unit LAI occurring at an LAI of about 4. This would seem to indicate a declining efficiency of resource use at LAI >4, but light use does not relate linearly with LAI. Light

interception per unit of leaf area declines exponentially as LAI increases (the Lambert–Beer pattern), and conversion of LAI to light interception showed a sustained increase in wood production per unit light intercepted, as well as increasing efficiency of light use.

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 covaried with overall forest growth. An increase in efficiency of light use could also reflect higher rainfall (and water supply) for sites that support higher leaf area. The direct causes of patterns in efficiency cannot be known without more information, but the overall conclusion remains robust: wood production per unit of light intercepted increased with increasing light interception.

6. Resource-use efficiency and GPP for *Eucalyptus grandis* × *urophylla* in Brazil

Stape et al. (this volume, a) found increases in ANPP per unit resource used in clonal stands of *Eucalyptus grandis* × *urophylla* as the rate of resource use increased across a rainfall gradient in Bahia, Brazil. This increase could have resulted from an increased efficiency of GPP per unit resource used 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 vapor pressure deficit (Stape, 2002). We used production data (Table 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 (Fig. 5). Production per unit of light intercepted increased with irrigation, with the greatest increase in efficiency for wood production per unit light intercepted, and the least for GPP per unit light intercepted. The disproportionate increase in efficiency for wood production resulted from an increased allocation of GPP to wood production (and lower proportional

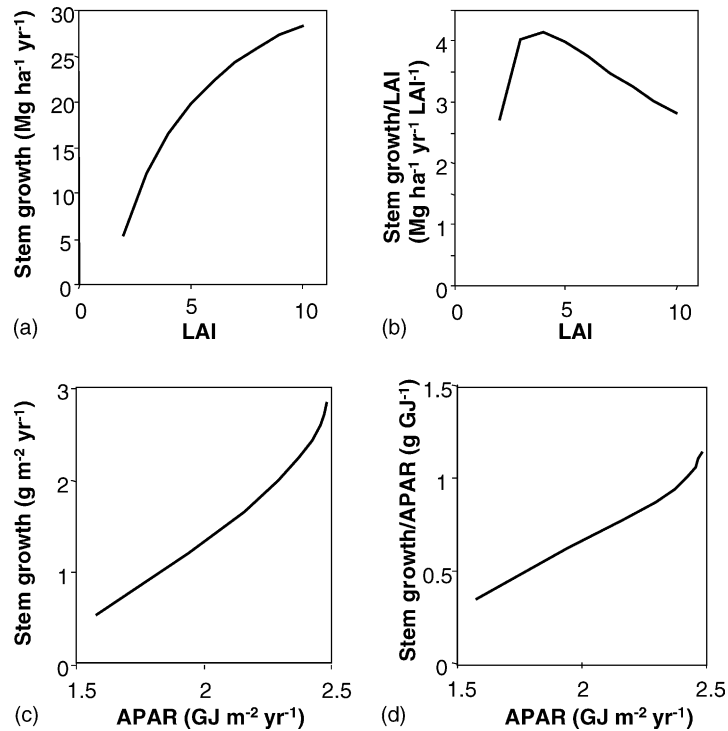


Fig. 4. Stem growth of *E. nitens* (a) related strongly with stand leaf area index, LAI ($r^2 = 0.84$, Smethurst et al., 2003) across 93 plots with varying fertilizer treatments at four sites. Stem growth per unit of LAI (b) peaked at an LAI of about 4.5. Assuming a light extinction coefficient of 0.5 and annual incident photosynthetically active radiation of 2.5 GJ m^{-2} , stem growth (c) tripled as light interception (APAR) increased by 50%. The greater increase in stem growth than light capture means that the efficiency of converting light into wood (d) increased with increasing light capture. The slope and Y-intercept of the increase in efficiency depend on the values of the light extinction coefficient and the annual incident PAR, but all reasonable estimates for these parameters yield a positive slope.

allocation below-ground) 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 the efficiency of water use was smaller (30% increase in GPP per unit water use, 70% increase in wood per unit water use) than the effect on light- or N-use efficiency (58% in GPP per unit light use, 110% for wood per unit N content). 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 are needed for a full accounting of such responses.

7. Patterns in light- and water-use efficiency in the 3-PG model

These ideas about patterns in resource use and efficiency can be explored in models, as well as measured in forests. Stape et al. (this volume, b) parameterized the 3-PG model (Landsberg and Waring, 1997) for plantations of *E. 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. (this volume, b) for the non-irrigated treatment, and the

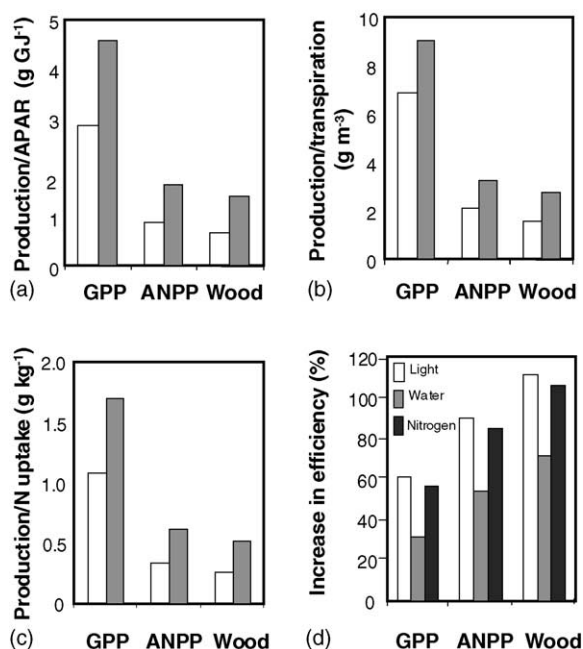


Fig. 5. Irrigation increased GPP, above-ground net primary production (ANPP) and wood growth per unit light intercepted (a), per unit water use (b), and per unit canopy nitrogen content (c) of a 4.5-year-old plantation of *E. urophylla* \times *grandis* in Bahia, Brazil (based on data in Stape, 2002). The increase in efficiency of production per unit of resource used (d) ranged from 32% (for GPP per unit water used) to more than 100% (for wood growth per unit of light intercepted or nitrogen content).

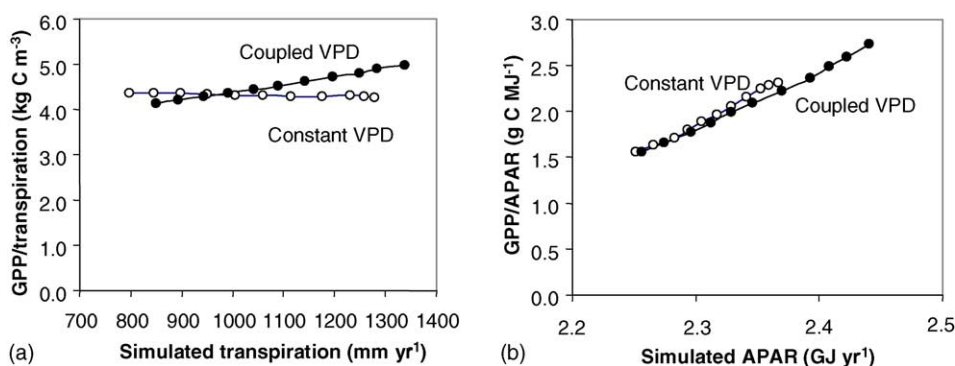


Fig. 6. The 3-PG model and data from Stape et al. (this volume, b) were used to study the effect of increasing rainfall on (a) water and (b) light-use efficiency (based on gross primary production). Each point represents 100 mm per year increase in rainfall, with open circles where vapor pressure deficit (VPD) was constant at 1.2 kPa and closed circles where VPD declined with monthly precipitation over the range 1.4–0.9 kPa. Increasing simulated rainfall had little effect on leaf area and light interception (10–15%, not shown), increased transpiration (a) with no change in the efficiency of water use if VPD was held constant or an increase when VPD declined, and gave (b) a 60–85% increase in the efficiency of light use.

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 per year, with the additional rainfall spread evenly through the year. A second set of simulations allowed vapor pressure to increase when rainfall was increased, based on an empirical relationship for this site. With increasing rainfall, GPP per unit water use was almost constant within a 3% range across a 1000 mm gradient in rainfall (Fig. 6). Allowing the vapor pressure deficit 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 vapor pressure deficit) or 8% (with vapor pressure deficit decreasing with rainfall increment). These simulations did not include the change in cloudiness that would be associated with increasing precipitation (<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 (Table 1 and Fig. 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. The most useful point may be that this model did not predict marginal declines in the efficiency of resource use as resource use increased.

8. Patterns in light-use efficiency for *Eucalyptus* plantations around the world

Several studies have documented patterns of ANPP of *Eucalyptus* plantations in relation to intercepted light (Fig. 7). All stands showed increasing rates of ANPP with increasing light capture, and negative Y -intercepts (=positive R_{\min} , positive X -intercepts), which dictated that the ANPP per unit light intercepted must increase with increasing light interception. Some of this increased efficiency probably resulted from shifts in allocation of GPP away from below-ground production and into above-ground production. The resource-use efficiency was less responsive to changes in resource supply in the Australian cases, we do not have an explanation for the differences among these case studies, but speculate that more intensive silviculture (including complete weed control) in the Brazil and Hawaii cases may have been important. Two studies estimated the entire GPP budget (Stape, 2002; Ryan et al., 2004), and concluded that efficiency of light use also increased in terms of GPP per unit light intercepted. It is possible that the apparent linear increases in Fig. 7 could turn into curves that demonstrate declining marginal returns from light interception beyond 4 GJ m^{-2} per year, but there are no such data for *Eucalyptus* plantations.

9. Extrapolations to other types of forests

The general framework of thinking about resource use and efficiency of use as drivers of patterns in production applies broadly to all forests, but the experiments described above all dealt with young, fast-growing plantations of *Eucalyptus*. Would our tentative conclusions about increasing efficiency of resource use with increasing resource use be true of other types of forests? A variety of case studies are available. For example, Birk and Vitousek (1986) measured ANPP per unit of N uptake from the soil by a series of stands of loblolly pine (*Pinus taeda* L.) and found that a doubling of N uptake was associated with a small (14%) decline in the efficiency of N use (kg ANPP per kg N uptake).

Runyon et al. (1994) examined productivity and light-use efficiency along a climatic gradient in Oregon, and found a strong correlation between light use and ANPP ($g \text{ ANPP} = -0.56 + 0.99 \times \text{MJ light intercepted}$, $r^2 = 0.85$, $P < 0.0001$). The negative Y -intercept indicated that ANPP would be zero at levels of light interception $< 0.56 \text{ MJ m}^{-2}$ per year, representing the R_{\min} . The pattern across sites showed a strongly increasing efficiency of light use ($g \text{ ANPP per MJ light intercepted} = 0.349 \times \text{MJ light intercepted}$, $r^2 = 0.61$, $P = 0.01$), owing to the substantial R_{\min} and linear slope of production per unit light. As light

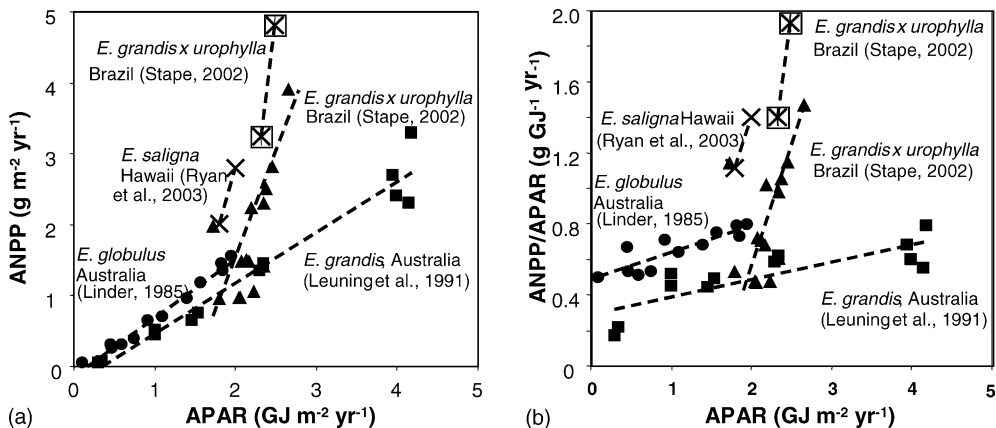


Fig. 7. Estimates of above-ground net primary production (ANPP) and intercepted photosynthetically active radiation (APAR) vary substantially for *Eucalyptus* plantations around the world (a), but ANPP per unit of light intercepted (b) tended to increase with light interception in all cases (Leuning et al., 1991; Linder, 1985).

interception doubled from 1 to 2 MJ m⁻² per year across this transect, ANPP increased by three-fold. Runyon et al. (1994) attributed the decline in efficiency at low light interception to combinations of freezing temperatures, soil water deficits, and high vapor pressure deficits.

The stem growth of Douglas–fir (*Pseudotsuga menziesii*) in a spacing trial in western Washington showed a constant efficiency of light use as light interception increased, whereas light-use efficiency (kg stemwood production per MJ light intercepted) almost doubled in response to fertilizer application (from data in Binkley and Reid, 1984).

An optimal water and nutrition experiment with young loblolly pine (*P. taeda*) in North Carolina found higher stem growth per unit of leaf area (and light interception) as light interception increased in response to increased water and nutrient supplies; the efficiency of N use (kg stem growth per kg N in canopy) varied by <10% among treatments (Albaugh et al., 2004).

Tree age may also affect resource-use efficiencies. Ryan et al. (2004) found that efficiency of use of light, water, and nitrogen declined with age in an *E. saligna* plantation, but heavily fertilized plots remained consistently more efficient in the use of light and water than control plots. Finally, leaf-level water-use efficiency in individual ponderosa pine trees (*Pinus ponderosa*), as assessed using carbon isotopes, did not match the pattern of tree growth: water-use efficiency was greater in taller, older trees (Hubbard et al., 1999), but annual stem growth per unit leaf area and light interception decreased (Ryan et al., 2000).

We hope that future experiments will examine patterns of growth and resource use, providing strong tests of the general patterns we found for *Eucalyptus* plantations. We expect that some broad general trends may apply across a wide diversity of species, ages, and sites, but we also hope that some intriguing deviations from general trends will be found.

10. Implications for managing forest production

This view of the production ecology of forests has three major implications for how foresters and forest

scientists think about forest growth. The first is that the production ecology equation (Eq. (1)) can provide insight to any pattern of forest growth. Why is wood production higher on one soil type than another, or why did fertilizer application lead to a large growth response on one site but not another? Eq. (1) has heuristic value in structuring the possible answers to these (and similar) questions. This simple equation needs to be explored in simulation models to account for interactions among resources, and changes over time. Second, a clear understanding of patterns of resource-use efficiency across resource gradients is fundamental to explaining forest growth. The increase in above-ground net primary production across a rainfall gradient in Brazil resulted more from the effects of water supply and vapor pressure deficit on the efficiency of water use than on the simple increase of water use (Stape et al., this volume, a). 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 cubic metre 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 vapor pressure deficit.

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.

Acknowledgements

D.B. thanks John Aber for opening a door on why the efficiency of resource use is worth thinking about, and John Pastor, John Hof, and Doug Rideout for clarifying thoughts. We thank Sune Linder, Barbara Bond, Chris Beadle, and Peter Sands for helpful comments. This paper was supported in part by McIntire-Stennis appropriations to Colorado State University; J.L. Stape's collaboration was supported

by the CNPq—Conselho Nacional de Desenvolvimento Científico e Tecnológico, of the Ministry for Science and Technology of Brazil (201144/97-2).

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