

Tamm Review: Insights gained from light use and leaf growth efficiency indices



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ABSTRACT

In this Tamm review, we trace the origin and application of two production indices: Light Use Efficiency (*LUE*) and (Leaf) Growth Efficiency (*GE*). Light Use Efficiency usually denoted (ϵ) was originally defined by John Monteith in the 1970s as the rate that dry matter is accumulated by plants in relation to the amount of solar radiation absorbed by leaves; the concept has been a corner-stone of the field of production ecology ever since. Although highly variable at daily intervals, *LUE* becomes linear at longer intervals, providing a major simplification to the construction and application of process-based models. A further simplification in model construction became possible when it was found that the ratio between total dry mass production and gross photosynthesis is approximately constant (≈ 0.5). Simplified process-based models provide a means of estimating the maximum productivity of a species growing inside or outside its native range, and help to identify constraints on production in current and projected environments. Consequently, models that incorporate *LUE* have expanded from research tools to practical ways of assessing silvicultural options in the management of individual forests as well as for measuring and forecasting global trends in forest productivity. The Leaf Growth Efficiency (*GE*) index, defined as annual growth in stemwood per unit of leaf area, has become widely adopted as a means of identifying the spatial variation among trees, which affects stand growth and *LUE*. *GE* was originally used to assess the vulnerability of individual trees to attack by bark beetles but, combined with structural and physiological analyses it has been found useful for interpreting and predicting stand growth responses to tree spacing, aging, and defoliation. Challenges remaining in the field of forest production ecology include prediction of the effects of fast-changing climatic conditions across the globe on the growth and survival of species, and their interactions with continually rising atmospheric concentrations of CO_2 .

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1. Introduction

In 2013 Forest Ecology and Management launched a review series designed to highlight the most important issues that affect the future of forest ecology and management around the world. The series is named in honor of the Swedish forest ecologist, Carl Olof Tamm who, in a career spanning more than 50 active years, made important contributions to forest ecology, forest production ecology and soil science. Most of his research and teaching were done in Sweden, but he made important contributions to international discussions and the development of environmental policies in Europe during the 1980s and 1990s. Tamm's career and contributions to forest science were summarized in an earlier Tamm review by Höglberg and Linder (2014). In the present review we offer a summary and assessment of two concepts that have contributed significantly to the development of a quantitative approach to the field of forest production ecology: light use efficiency (*LUE*) and leaf growth efficiency (*GE*).

Over the last forty years, production ecology has progressed (and matured) from simply quantifying standing biomass (carbon stores) to predicting current and future growth rates in response to changing environmental conditions. The development of the two indices—Light Use Efficiency (ϵ) and Growth Efficiency (*GE*)—has been critical in helping the field to advance. Both indices originate in agriculture but their application to forests, which often grow in more stressful environments than cultivated crops, has provided the scientific underpinnings of most process-based growth models and the basis for sound management practices designed to improve and maintain healthy forests.

In this review, we trace the origins of the two indices and identify the steps in their development and application that have led to quantitative predictions of yields under changing climatic conditions, as well as identifying thresholds that indicate the vulnerability of individual trees to attack from native insects and pathogens. Not surprisingly, there are many cross-linkages between the two, as insights gained from one often offer an explanation for responses observed with the other.

2. Light Use Efficiency (*LUE*)

2.1. Definition

Light Use Efficiency (*LUE*) provides a measure of the productivity of terrestrial vegetation in relation to the photosynthetically active radiation (PAR) absorbed by the leaves (APAR). PAR, representing visible light, constitutes about half the energy in the short-wave solar radiation incident on the earth's surface. *LUE* therefore measures the efficiency with which plant canopies convert the sun's energy into the chemical energy stored in the products of photosynthesis, mainly carbohydrates, measured as dry matter. Efficiency is, technically, dimensionless. Conforming to that convention, we would express *LUE* as the ratio of chemical energy produced per unit of solar energy absorbed (Q_{abs}), but in plant production ecology it is usually expressed in units of dry mass (DM) produced per unit of PAR absorbed.

2.2. Background

The connection between light and photosynthesis has been understood, at least in principle, since the early part of the 20th century, and it was obvious that there must be quantitative relationships between incident light and plant productivity. The first breakthrough in application of the Light Use Efficiency concept was provided by Monteith (1977), who demonstrated that dry matter accumulation by crops is linearly related to the amount of radiation intercepted by the plant canopy. The linear relationship provides a simple, robust model with only one parameter – the slope of the line, generally denoted ϵ . Epsilon is, in effect, a measure of the Light Utilization Efficiency of the plant community.

Monteith estimated the average value of *LUE* in terms of intercepted solar radiation and above-ground production of dry mass as 1.4 g DM MJ⁻¹, i.e. about 2.8 g DM MJ⁻¹ absorbed PAR (APAR). The slopes of the lines for the four crops he considered – sugar beet, potatoes, barley and apples – were similar and linear but not identical. That *LUE* might be nearly constant and linear spurred activity to test the concept. Our aim here is to assess the general usefulness of the concept, the extent of, and reason for, variation in *LUE* and its application to production ecology at small and global scales. More comprehensive reviews of light use efficiency in natural and planted forests are presented by Landsberg et al. (1997), and for crops by Sinclair and Muchow (1999).

Jarvis and Leverenz (1983) were the first to make a thorough analysis and assessment of the application of the ϵ model to forests. They arrived at estimates of *LUE* for above-ground growth (ϵ_a) in relation to total solar radiation ranging from 0.15 g DM MJ⁻¹ for warm area deciduous forests to 0.78 g DM MJ⁻¹ for cool-area evergreens. (Those values would be doubled if the analyses were made in terms of PAR). The first convincing empirical demonstration that there might be a linear relationship between forest growth and intercepted light was provided by Linder (1985), who derived values of *LUE* of about 1.7 g DM MJ⁻¹ (APAR) for above-ground (ϵ_a) production by plantations of *Eucalyptus* and Monterey pine (*Pinus radiata*). Since that time estimates of ϵ for total NPP and above-ground production have been obtained from a number of studies for a range of tree species.

Empirical values of ϵ_a have usually been calculated from biomass data obtained by destructive sampling, or careful measurements of tree growth, or some combination of these techniques. In most cases APAR was, and continues to be, estimated using Beer's Law with time-integrated values of PAR and consideration of seasonal changes in projected Leaf Area Index (*L*). The values for ϵ_a cited by Landsberg and Sands (2011; Table 5.1) ranged from 0.2 g DM MJ⁻¹ to 2.73 g DM MJ⁻¹ APAR. Most of the high values were obtained for wet, tropical eucalypts plantations while the lowest were associated with forests growing in much harsher environments. In the sections below we assess a range of possibilities that might explain the wide variation of ϵ_a .

2.3. Integration of absorbed photosynthetically active radiation

Good estimates of *LUE* depend on accurate estimates of the amount of light (photosynthetically active radiation) absorbed by

canopies. For a uniform, closed canopy in which foliage can be considered as randomly distributed, with spherically symmetrical leaf angle distribution, the absorption of radiation can be described by Beer's Law, first applied to plant stands by [Monsi and Saeki \(1953\)](#):¹

$$Q(z) = Q_0 e^{-kL(z)} \quad (1)$$

where Q_0 and $Q(z)$ are, respectively, the irradiances in horizontal surfaces above the canopy and at some level z within the canopy, $L(z)$ is the accumulated leaf area index of the canopy from the top to that level, and k is called the extinction coefficient. It follows from Eq. (1) that Q_{abs} is given by:

$$Q_{abs} = Q_0(1 - e^{-kL}) \quad (2)$$

Relatively few forest canopies meet the strict requirements for the application of Beer's Law, and considerable effort and resources have been devoted to the development of models that provide accurate descriptions of radiation interception by forest canopies. Such models take into account the extent that foliage is clumped rather than randomly distributed as well as the fraction of diffuse and direct beam radiation that penetrates through layers of leaves. These models have been reviewed and discussed in numerous publications; we note here the pathfinding work of [Norman \(1982\)](#), [Oker-Blom et al. \(1991\)](#) and [McMurtrie et al. \(1990, 1992a\)](#) – see [Landsberg \(1986\)](#) and [Landsberg and Sands \(2011\)](#) for detailed treatments. For a recent summary of models of light interception by heterogeneous forest canopies see the paper by [Duursma and Mäkelä \(2007\)](#).

Some attempts have been made to measure APAR and forest structure directly, with confirmation that as forests grow, the density of foliage as well as the amount decreases, increasing the fraction of light penetrating the canopy (e.g., [Brown and Parker, 1994](#)). More recently, vertical transmittance of light has been compared using towers and balloons to suspect light sensors and scanning Lidar images to assess the 3-dimensional structure of different types of forests ([Parker et al., 2001](#)). These approaches, however, do not provide a time-integrated assessment over days and months. For that, models are required.

2.4. Analysis of why ϵ becomes a linear function of canopy light absorbance

On a given day, at the level of individual foliage elements, the response of photosynthesis to light intensity is highly non-linear. How is it then that the relationship for a canopy might become linear at seasonal or annual time steps? This question was addressed by [Wang et al. \(1992\)](#) and later by [Medlyn \(1998\)](#), using highly detailed models of light interception and canopy photosynthesis. The model of this type most frequently used for studies of forest canopies is MAESTRA (see [Medlyn, 2004](#)), developed from a detailed array model (MAESTRO) produced by [Wang and Jarvis \(1990\)](#), which in turn was derived from the model of [Norman and Welles \(1983\)](#). At that time it was re-named MAESTRA. The model has now been further developed by [Duursma and Medlyn \(2012\)](#) to become MAESPA,² which includes stomatal conductance, water uptake and plant hydraulic routines, as well as all the original features of MAESTRO.

[McMurtrie's \(1990, 1992a\)](#) stand-level model, BIOMASS³ required as inputs information about canopy structure and foliage photosynthetic characteristics. The 1992a version incorporated photosynthetic responses to several variables besides light. Tree crown

shape in BIOMASS was represented by geometrical constructions (ellipsoids, cones, etc.) and the plant community by randomly-spaced arrays of trees. Foliage was divided into three horizontal layers of equal depth; the model calculated the proportions of sunlit and shaded foliage. Photosynthesis in each layer was calculated using the mechanistic model of [Farquhar and von Caemmerer \(1982\)](#).

Daily values of canopy net photosynthesis are in [Fig. 1](#) plotted against daily absorbed PAR, both calculated with the BIOMASS model, parameterized for *Pinus radiata* ([Wang et al., 1992](#)). The simulations, run with recorded daily meteorological data, assessed the growth of a stand of *P. radiata* over a period of eight years, during which L increased linearly from 0.5 to 8.5. It was assumed that there was no soil water limitation, as was the case in the irrigation treatments imposed on the experiment under study. Although there was considerable variability because the simulations encompassed all seasons, with a range of daylengths, leaf areas

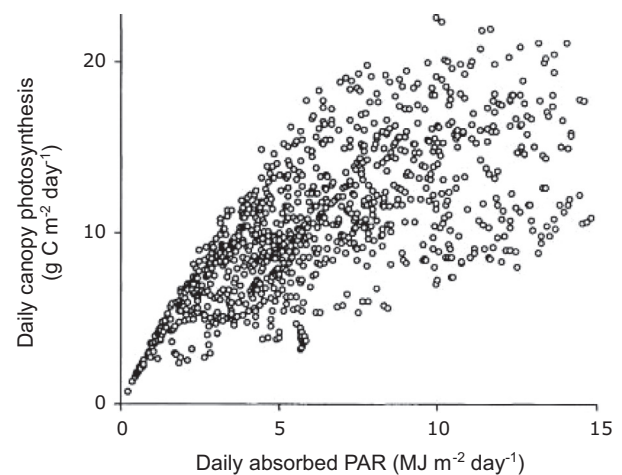


Fig. 1. Simulations of daily absorbed PAR and canopy photosynthesis (g C m^{-2}) for a hypothetical stand of *Pinus radiata* using the BIOMASS model. L increases for 0.5–8.5 over the 8 year period. Reprinted from "Crop Photosynthesis: Topics in Photosynthesis, Vol. 12, Wang, Y.P., McMurtrie, R.E., Landsberg, J.J. Modeling canopy photosynthesis productivity, pp. 43–67 (1992), with permission from Elsevier Pub.

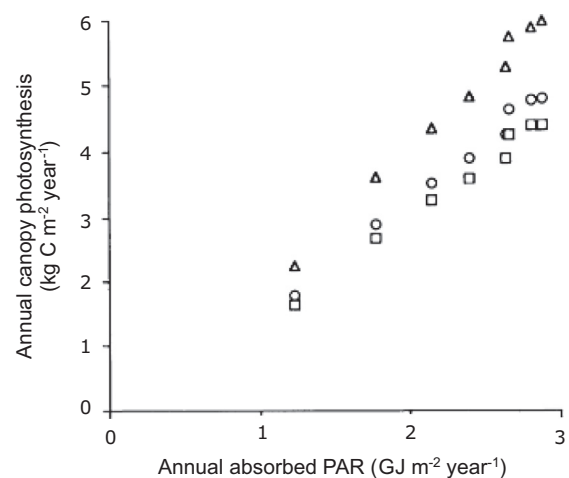


Fig. 2. Annual canopy photosynthesis as a function of absorbed PAR with atmospheric CO_2 concentrations of 350 ppm (open circles); 700 ppm (triangles) and 350 ppm with average temperatures increased by 4°C (squares). Reprinted from "Crop Photosynthesis: Topics in Photosynthesis, Vol. 12, Wang, Y.P., McMurtrie, R.E., Landsberg, J.J. Modeling canopy photosynthesis productivity, pp. 43–67, (1992), with permission from Elsevier Pub.

¹ [Binkley et al. \(2013\)](#) point out that an English translation of the [Monsi and Saeki \(1953\)](#) paper is now available ([Monsi and Saeki, 2005](#))

² See [maespa.github.io](#)

³ Unfortunately the code for the BIOMASS model is no longer available

and environmental conditions, when both photosynthesis and APAR were expressed as annual totals, the relationship between simulated carbon gain (ϵ_g) and absorbed PAR became essentially linear (Fig. 2), with a slope of 1.66 g MJ^{-1} . When the CO_2 concentration was doubled, to $700 \mu\text{mol mol}^{-1}$, the linearity was maintained but increased to 2.07 g MJ^{-1} (McMurtrie et al., 1992b; Wang et al., 1992). The value of 1.66 g MJ^{-1} is very close to the 1.7 obtained by Oker-Blom et al. (1989) for Finnish conditions.

A study by Medlyn (1998) was designed to investigate the physiological basis for the light use efficiency model, and the reasons for the observed and widely-accepted linear relationship between NPP and APAR. Medlyn used MAESTRO, parameterized for the same *Pinus radiata* stand studied by McMurtrie et al. (1992b) and Wang et al. (1992), with the Farquhar-von Caemmerer (1982) leaf photosynthesis model. She showed (Fig. 3) that for a given L and incident radiation there can be a range of values of ϵ_g —in this case from 0.58 to 3.03 g C MJ^{-1} . The highest values at a given value of L occurred when the incident radiation was all diffuse. Leaf angles, whether foliage was clumped, and the distribution of nitrogen through the canopy, also affected mean values of ϵ_g . We note, however, that Oker-Blom et al. (1989) found that the conversion efficiency between intercepted radiation and photosynthesis appeared to be rather insensitive to differences in canopy structure and the properties (direct beam or diffuse) of the radiation. (In her study the photosynthetic properties of the foliage were simulated by a relatively simple model).

For canopies with $L = 1$ and 7 Medlyn (1998) showed that monthly values of light use efficiency (calculated in terms of net canopy photosynthesis, not NPP of the stand) also varied considerably, although over a smaller range than daily values — from 0.66 g C MJ^{-1} in summer to 1.25 g C MJ^{-1} in the winter months — reflecting the fact that monthly growing conditions were highly variable at the Australian Canberra site. Annual values were approximately constant for a given L . This also applied to data from seven other sites, ranging from New Zealand through Thailand and Florida to Sweden. Medlyn concluded that the explanation for

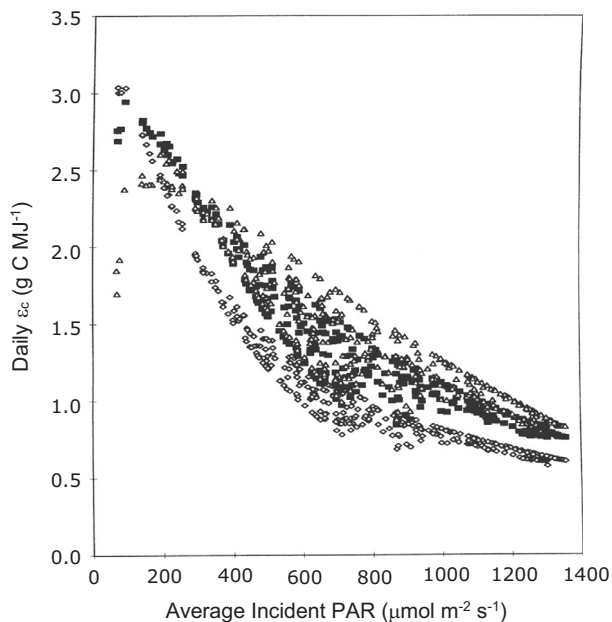


Fig. 3. Daily light use efficiency, calculated by MAESTRO, as a function of average incident PAR recorded daily at a research site near Canberra, Australia, for the period July 1986 – June 1987. L varied from 1 (lower symbols) through 3 (dark symbols) to 7 (upper symbols). From B.L. Medlyn, Physiological Basis of the light use efficiency model. (1998) Tree Physiology 18(3), 167–176, by permission of Oxford University Press.

near-constant values of ϵ is partly a result of integrating over time, but speculated that adjustments in canopy nitrogen concentrations might be required to maintain the linearity of the relationship between net photosynthesis and APAR, as indicated in Fig. 2. The importance of seasonal and within canopy adjustments in foliar nitrogen was demonstrated by Haxeltine and Prentice (1996). By applying the MAXX optimization hypothesis (McMurtrie and Dewar, 2011), which maximizes net canopy carbon export, to a mature stand of Norway spruce (*Picea abies*) trees (Dewar et al., 2012), all canopy traits predicted (leaf N gradient, leaf N concentration, leaf photosynthetic capacity, canopy N content, leaf-area index) were in close agreement with the values observed (Tarvainen et al., 2013).

Besides the modeling studies cited above, numerous empirical observations suggest that, for time intervals of a month or a growing season, we may assume a linear relation between APAR and photosynthesis. The irregular character of forest canopies (clumping, foliage distribution with height, leaf angles), as well as short-term variations in the intensity and nature of incoming radiation (sun angles, proportions of direct beam and diffuse) preclude the use of Beers law over short time intervals, but it generally gives satisfactory results over the longer periods.

2.5. Variation in ϵ associated with partitioning of growth and respiration

Although above-ground NPP is the variable of most practical importance in forestry, and the one that can be most easily measured, it is useful to start with gross primary production (GPP) and attempt to partition the assimilate to respiration and growth, above – and below ground. In the 1990s there was a major effort to assess root growth and turnover, which provided a basis, along with above-ground sampling, for estimating plant respiration associated with tissue maintenance and construction (e.g. Litton et al., 2007; Ryan, 1991; Ryan et al., 1994, 1997). GPP was estimated by developing temperature functions for respiration, along with knowledge of the carbon cost of synthesizing tissue with varying nitrogen content (e.g. Ryan, 1991; Ryan et al., 1996). The proportion of GPP lost by respiration can be calculated on the basis of the empirical data on respiration of various plant tissues.

From comparisons of such carbon balances, made for a wide range of forested sites, Waring et al. (1998) concluded that the ratio of NPP/GPP might be constant. This conclusion has been disputed, but in general the assumption of a constant ratio of ≈ 0.5 NPP to GPP holds remarkably well for most tree species and sites (see reviews by DeLucia et al., 2007; Gifford, 2003). (See also the discussion on p.145 of Landsberg and Sands, 2011).

It follows, from the assumption that the ratio of NPP/GPP is constant, that:

$$\text{NPP}_A = c \cdot \text{GPP}(1 - \eta_{\text{root}}) \quad (3)$$

where η_r denotes the fraction of carbohydrate allocated to roots.

The calculation of respiration as a function temperature and tissue biomass is a potential source of error, which also applies to estimates of GPP assessed with eddy-covariance measurements (cf. Wehr et al., 2016).

2.6. Influence of nutrition on ϵ

Some of the differences in LUE reported by Landsberg and Sands (2011) can be attributed to variation in foliage photosynthetic efficiency (or quantum yield) which is related to the nutritional status of foliage. At the leaf level, the light response curve for net photosynthesis is (approximately) linear at low intensities, becoming asymptotic to the light intensity axis and reaching a maximum value (A_{max}) at saturating irradiance. A_{max} is often linearly related

to the nitrogen concentration [N] of the foliage. Reich et al. (1995) measured A_{\max} , specific leaf area (SLA) and N in 22 broadleaved deciduous and 9 evergreen tree species. They found that A_{\max} was highly correlated with leaf [N] in both the deciduous and evergreen species when expressed on a mass basis, but the slope was lower for the conifers (1.9 vs. 6.4 $\mu\text{mol CO}_2 \text{ g}^{-1} \text{ N s}^{-1}$). On an area basis, there was a strong A_{\max} -N relationship among deciduous species, but no correlation in the evergreen conifers.

Reported values of the maximum quantum yield (or maximum quantum efficiency), Φ , vary almost 4-fold among tree species ranging from ≈ 0.02 to near the theoretical maximum of 0.08 $\text{mol CO}_2 \text{ mol}^{-1} \text{ photon}$ (equivalent to $\approx 10\text{--}50 \text{ g C MJ}^{-1}$ APAR). The reported range is generally smaller for conifers than for deciduous hardwoods, but that is not always the case (Bond et al., 1999). Singsaas et al. (2001) compiled and compared data from 30 published studies with data from two comprehensive quantum yield studies (Björkman and Demmig, 1987; Long et al., 1993). They concluded that the large variation in Φ probably was an effect of methodological problems and supported the conclusion by Björkman and Demmig (1987) and Long et al. (1993) that intrinsic quantum yield varies little from the mean values of 0.092 for ΦCO_2 and 0.108 ΦO_2 unstressed plants.

As well as its effects on photosynthetic efficiency, increasing nitrogen availability significantly affects the partitioning of carbohydrates to above- and below-ground growth (Eq. (3)). After 6 years of combined irrigation and fertilization in young stands of Scots pine (*Pinus sylvestris*) there was a drastic shift in partitioning of carbon between above- and belowground growth (Linder and Axelsson, 1982). The annual net photosynthesis in the untreated stand was 11.6 Mg ha^{-1} of which 59% was allocated belowground. In the irrigated and fertilized stand the annual photosynthesis was almost twice as high (22.2 Mg ha^{-1}) but only 31% was allocated belowground. Similar results were reported by Beets and Whitehead (1996) from an experiment where first rotation *Pinus radiata* trees were grown on a nitrogen-deficient sand dune or with biannual application of balanced fertilizer. In the fertilized treatment, the annual fraction of NPP allocated belowground decreased from 54% to 26%, while the fraction allocated to stem wood and leaf area increased proportionally. Therefore increased nitrogen availability leads to increased leaf area and hence more light interception (Eq. (2)). Limiting availability of nitrogen, and to a lesser extent phosphorus and sulfur, favor growth of small diameter roots over that of shoots, whereas limitations in availability of potassium, magnesium, and manganese have the opposite effect (cf. Ericsson et al., 1996; Wikström and Ericsson, 1995). Ultimately, the extent to which changes in tissue nutrient status affect GPP and ϵ depends on the stomata remaining open for the uptake of CO_2 .

2.7. Climatic limitations on stomatal conductance

Water shortage causes stomatal closure and so reduces the amount of CO_2 that can be absorbed by the plants, which reduces light utilization efficiency. There are various experimental determinations that illustrate the effects of water (as well as nutrition) on ϵ_a in forest stands. Raison and Myers (1992) used data from the experiment on *Pinus radiata* near Canberra, Australia in which water and nutrition were manipulated to cause large differences in tree growth under the different treatments. They found that, over four years ϵ_a (for above-ground growth) in high nutrition, well-watered plots was 1.14 g DM MJ^{-1} APAR; in irrigated plots with low nutrition $\epsilon_a = 0.84$ and in unirrigated plots $\epsilon_a = 0.72$. The effects of water stress on ϵ_a will vary depending on the severity and duration of the water shortage.

In addition to soil water deficits, excess radiation combined with high leaf-air vapor pressure deficits can cause partial to

complete stomatal closure (Running, 1976). Exposure to subfreezing conditions at night also forces stomatal closure, sometimes for days (Tranquillini, 1979). If functional relationships can be defined between stomatal conductance, soil water deficits, temperature, vapor pressure deficits, frost, and CO_2 (Eq. (4)), it is possible to estimate the fraction of APAR that can actually be utilized (APAR_u) in photosynthesis.

McMurtrie et al. (1994) used the BIOMASS model to calculate GPP and plot it against (simulated) utilizable APAR for pine species in Australia, Wisconsin, Sweden and New Zealand. Utilizable APAR was determined by applying a series of environmental modifiers (varying between 0 to 1, optimum) to the initial values of APAR (Eq. (4)), adjusting them for the effects on photosynthesis of soil water deficits ($f_{\text{H}_2\text{O}}$), vapor pressure deficit (f_{vpd} (non-optimal) temperature (f_{Temp}), frost (f_{frost}) and atmospheric carbon dioxide (f_{CO_2}). The result was a very tight fit of multiple points about a straight line with a slope (ϵ_g) of 1.86 g C MJ^{-1} .

$$\text{GPP} = \text{APAR}_u = \text{APAR} \times \Phi(f_{\text{H}_2\text{O}} \cdot f_{\text{vpd}} \cdot f_{\text{frost}} \cdot f_{\text{CO}_2}) \quad (4)$$

Runyon et al. (1994) followed the same approach and reported a similar linear relationship between APAR_u and NPP_A with an ϵ_a of 0.96 and ϵ of 1.25 for nine different coniferous forests in western Oregon representing a 10-fold range in productivity. The only exception was an old-growth forest of Douglas-fir and western hemlock, which, as Koch et al. (2014) have shown, exhibit reduced photosynthesis compared to younger, denser forests in response to added hydraulic constraints imposed on water transport between roots and the foliage (reviewed by Waring and Landsberg, 2011).

2.8. Development of Process-based forest growth models

A large number of process-based ecosystem and forest growth models have been produced using the Light-Use Efficiency concept. The most detailed predict water vapor and CO_2 exchange at hourly or 30-min intervals (e.g., Baldocchi and Harley, 1995; Williams et al., 2001). Others operate at daily time steps and predict the growth of plantations quite well if adequately parameterized (e.g., Battaglia et al., 2004; Kirschbaum and Watt, 2011). There is a trade-off between precision and accuracy. Models with longer time-steps require less detail than more refined models and often prove more accurate in predicting growth at annual intervals (see model comparisons reviewed by Miehle et al., 2009; Siqueira et al., 2006). For this reason, and perhaps because the code is freely available,⁴ the 3-PG (Physiological Principles Predicting Growth) model (Landsberg and Waring, 1997) has become one of the most widely applied forest growth models (Mäkelä et al., 2000).

Besides the advantage of requiring only monthly averaged climatic data, and simplifying the forest canopy so that it might be characterized by L , the 3-PG model gained favor by not requiring detailed information on respiration, assuming that NPP is proportional to GPP. It is a conservation of mass model, with a robust carbohydrate partitioning routine that yields above-ground (stems, branches and foliage) and below-ground growth, consistent with allometry. The below-ground components are sensitive to the availability of N and temperature-related turnover rates (Mäkelä et al., 2016). The model outputs are structural variables that foresters measure: tree numbers, diameters, stand basal area and volume. The model provides the option of investigating the implications of thinning, and additions of fertilizers and water, for forest productivity under a range of climates. Further refinements have been developed by Sands and Landsberg (2002) and are described in detail by Landsberg and Sands (2011).

⁴ <http://3pg.forestry.ubc.ca/publications/>

2.9. Predicting GPP and NPP from satellites

Prince and Goward (1995) developed the first light use efficiency model driven entirely by satellite-derived data. Their model predicted GPP and NPP at monthly intervals at a spatial resolution of 8×8 km across the global land surface. Today, with improvements in spectral resolution and data processing, daily satellite-derived estimates of GPP are integrated over 8-day intervals at a spatial of 1 km. The MODIS model estimates annual productivity for major vegetation types along with estimates of transpiration (Running et al., 2004). It is the most widely used and most widely tested LUE-based global model of GPP and NPP (Turner et al., 2006). For an inter-comparison of different global-scale process-based models, see Cramer et al. (1999).

Repeat global satellite coverage offers a means of identifying warming trends and evidence of disturbance for a range of vegetation but is unable to account for spatial variation in soil properties. Attempts have been made to remedy this situation by adjusting soil properties to match maximum L values acquired from satellites (Coops et al., 2012a). However, the availability of water and nutrients varies with site fertility, soil type, management, and the rooting depth of vegetation.

It is clear from the research and modeling cited above that ϵ is rarely at its maximum value for most forests. This is even true for the wet tropics where, on clear days, the intensity of solar radiation may be higher than can be utilized by light-absorbing pigments. Gamon et al. (1992) took account of this by recognizing that when leaves are exposed to excess light there is a shift in the reflectance spectrum of xanthophyll pigments, with the result that unutilized light is converted to heat, which results in protecting the photosynthetic machinery. They defined a Photosynthetic Reflectance Index (PRI):

$$\text{PRI} = \rho_{570} - \rho_{531} / \rho_{570} + \rho_{531} \quad (5)$$

where ρ_{531} is the wavelength (531 nm) at which leaves increase their reflectance when stressed and ρ_{570} is the wavelength at which xanthophyll pigments remain insensitive. PRI serves as a reference index to assess the extent that photosynthesis is reduced (down-regulated); in effect the value of the quantum efficiency, Φ , is reduced by an amount determined by the index.

Although this remotely sensed index has been applied to boreal temperate, Mediterranean, and tropical vegetation (Drolet et al., 2005; Garbulsky et al., 2008; Hilker et al., 2011; Rahman, 2004; Sousa et al., submitted for publication) there are, as yet, no satellite-borne instruments specifically designed with optimum sensitivity at the 531 and 570 nm wavelengths. Nevertheless, impressive results have been obtained using NASA's two Moderate Resolution Imaging Spectro-radiometer to compare differences in PRI observed on shaded and exposed portions of the same canopies at 1 km resolution, averaged over monthly intervals (Sousa et al., submitted for publication). The slope of the relationship between PRI derived from the shadowed portion of the canopy and the exposed portion is proportional to the light-use efficiency (Hall et al., 2011; Hilker et al., 2011).

3. Growth efficiency

3.1. Origin

The concepts underlying the idea of leaf growth efficiency came from agriculture, where they arose from research, mainly in England, in the general area of growth analysis, developed from the 1940s through the 1960s. Scientists recognized that the time course of dry weight (ΔW) gain by crops was strongly dependent on the development of the crop canopy, which could be specified

in terms of leaf area per plant, or per unit area of land, the leaf area index (L). This led to descriptions of leaf efficiency in terms of 'net assimilation rate' ($(1/L)(dW/dt)$) and the 'leaf area ratio' (L/W). These concepts, and the techniques of growth analysis, were applied to questions such as competition for resources, driven by within-crop plant populations, and the existence (or not) of optimum leaf area indices. It became clear that optimum values of L for production of the harvested crop were, almost invariably, lower than the maximum values that might be attainable (Gastal and Lemaire, 2002). The question of assimilate partitioning was a natural corollary to questions about overall dry matter production.

The ideas arising from growth analysis of agricultural crops were not applied in forestry until the 1970s, mainly because there were no accurate, non-destructive methods available to estimate leaf area for large trees or forest stands. A number of allometric equations, relating foliage mass to tree diameter, were developed as part of the International Biological Program (IBP) (e.g., Gholz et al., 1979). Waring proposed a Leaf Growth Efficiency index ($GE = (\Delta W / \Delta t / L)$), as a simple means of evaluating the efficiency of wood production (Waring et al., 1980; Waring, 1983). GE is exactly analogous to the net assimilation rate, with the difference that W denotes wood, not total above-ground biomass, production. However, the allometric equations for leaf area were inaccurate when applied to large trees (Marshall and Waring, 1986). They also did not work for trees growing in a wide range of stocking densities and age classes (see recent work by Gonzalez-Benecke et al., 2014).

A study designed to measure transpiration in a young plantation of Douglas-fir (*Pseudotsuga menziesii*) using radioisotope tracers suggested a method that could provide more accurate estimates of leaf mass and leaf area (Kline et al., 1976). The problem, in that study, was that the isotope (tritium) had to be injected exclusively into the water conducting sapwood, which varied 10-fold in cross-sectional area among trees in the stand where the experiment was conducted. Based on observations that a unit of sapwood area in the live crown of small trees and herbaceous plants supports a predictable amount of leaf mass, Shinozaki et al. (1964a, 1964b), had proposed a functional correspondence – the pipe-model theory – that led to a linear relationship between sapwood cross-sectional area, immediately below the lowest living whorl, and total foliage mass carried by a tree. Shinozaki et al. assumed that below the live crown not all of the sapwood remained functional, but Waring et al. (1982) considered that an adjustment for taper to the base of the live crown would allow leaf area to be predicted from measurements of sapwood cross-sectional area at breast height. Whitehead et al. (1984) confirmed that the product of sapwood conductivity (permeability) and sapwood area remains stable between the ground and base of the live crown of lodgepole pine (*Pinus contorta*) and Sitka spruce (*Picea sitchensis*). Taking account of stem taper to mid-crown, Long and Smith (1989) demonstrated that general equations could be developed to estimate leaf area accurately for lodgepole pine and subalpine fir (*Abies lasiocarpa*) over a range of site conditions and stocking densities. There have now been numerous studies, on a range of species, of the relationships between sapwood cross-sectional area and projected leaf area. Some of these are listed by Waring and Schlesinger (1985) who pointed out that trees adapted to harsh environments, where freezing and drought commonly occur, support less leaf area per unit of sapwood area than species or varieties adapted to less stressful conditions. Given these relationships and the number and size of stems in a stand, it is possible to estimate the leaf area index of stands, recognizing that the relationships between sapwood area and leaf area may vary with environment and locally with tree height (McDowell et al., 2002). By combining information about tree leaf areas, and leaf area indices, with tree growth measurements, it is possible to calculate GE for a stand, along with error estimates.

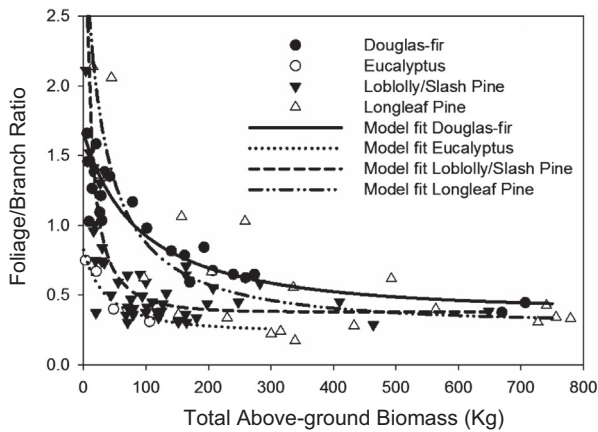


Fig. 4. As tree above-ground biomass increases, the ratio of needle to branch biomass in Douglas-fir decreases exponentially (Bartelin, 1996). Similar plots are presented for three species of southern pines: loblolly (*Pinus taeda*), longleaf (*P. palustris*), and slash (*P. elliottii*). *Eucalyptus grandis* data were obtained from Almeida (2012). Graph drafted by Carlos Gonzalez-Benecke using some original data (Gonzalez-Benecke et al., 2014, 2015).

3.2. Insights into stand dynamics

Detailed models of light interception in plantations (see the section on *LUE*) have shown good agreement between values of *LUE* and *GE* for individual trees (Binkley et al., 2010; Gspatl et al., 2013). Binkley et al. (2010) note that considerable spatial variation in *GE* can be expected in heterogeneous stands. When trees of similar height are clustered they tend to have narrower crowns and are less efficient in absorbing light than those distributed more uniformly in stands with equivalent *L*. In general, dominant trees are more efficient in producing stemwood per unit of leaf area than those of intermediate or suppressed categories (Binkley et al., 2013; O'Hara and Nagel, 2006). On drought-prone sites, larger trees have better access to water because their root systems are deeper and more symmetrical than those of smaller trees (Eis, 1974; McMinn, 1963). However, smaller trees can also reduce the efficiency of larger trees in heterogeneous stands by 10–15%, independent of APAR (Ryan et al., 2010). Thinning or planting to create uniform, evenly spaced trees reduces competition for resources among trees to less than 5% (Trung et al., 2013), even in stands where trees are of similar size and *L*, nutrient availability may cause as much as a 3-fold difference in *GE* (Martin and Jokela, 2004).

In the early stages of stand development, *L* values are low and light absorption is incomplete; a large proportion of the foliage may be strongly illuminated and *GE* is likely to be high. As canopy closure is approached and increasing proportions of the foliage receive only low-intensity illumination, *GE* generally decreases exponentially (Martin and Jokela, 2004; Waring, 1985), but stand growth peaks (Smith and Long, 2001). Detailed studies indicate that the abrupt reduction in stand growth, after the peak, cannot be attributed directly to stand age or to height growth (Ryan et al., 2004; Smith and Long, 2001). In slow-growing forests where *L* remains stable for decades, peak growth still occurs during the decade of canopy closure (Tadaki et al., 1977).

Two main factors appear to cause *GE* and stand growth to be reduced following canopy closure: one structural and one physiological. The structural component relates to shifts in the distribution of biomass with tree size. Structurally, as trees grow in diameter, there is an exponential decline in the ratio of foliage biomass to that of supporting branches (Fig. 5). Although a reduction in the ratio of leaf to branch mass eventually results in less leaf area, the reduction in *L*, as it affects light absorption, is insufficient

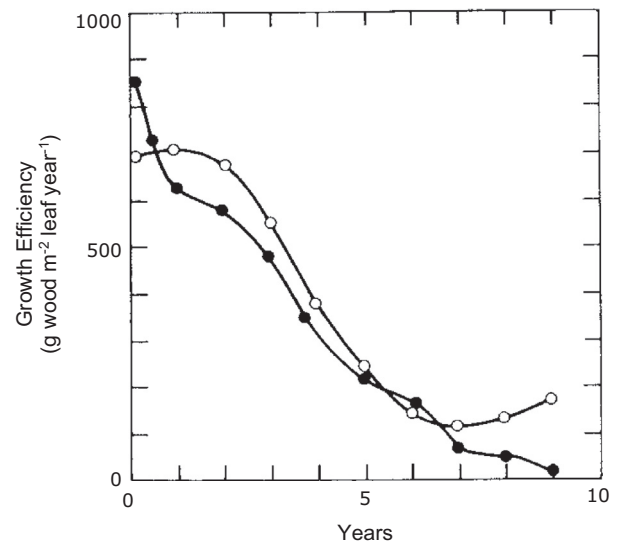


Fig. 5. Reconstructed trends in *GE* values for two similar sized, young Scots pine indicate a crossover between the 6th and 7th year that distinguishes which tree will survive (open circle) and which will die (filled circle). Reprinted from Fig. 2.20, page 36, Waring, R.H., Schlesinger, W.H. (1985) with permission from Academic Press (Elsevier Pub.).

to account for the observed decrease in stand growth. It has been shown that hydraulic conductance decreases as branches grow longer, imposing restrictions on stomatal conductance and photosynthesis (Warren and Adams, 2000). Waring and Silvester (1994) showed that when branch length was artificially reduced by pruning, stomata remained open proportionately longer during the day. If genetic variation among tree populations is expressed in terms of branch growth, stand growth may be influenced by these differences if thinning creates conditions where branch length may vary (Walcroft et al., 1996).

In some studies analysis of *GE* has provided insights into the reasons why stand growth has followed an unexpected path. For example, a detailed analysis of the stems of more than 150 trees in a stand infected by a root pathogen showed that stand growth (but not biomass) remained similar in infected and uninfected stands because, as the canopy of infected trees slowly died, the uninfected trees increased their growth efficiency by nearly 30% (Oren et al., 1985). Similarly, in a 24-year reconstruction of *GE* and *L*, Oren et al. (1987) demonstrated that the presence of a shrub understory in an arid-zone ponderosa pine plantation caused trees to experience water stress that delayed canopy closure.

3.2.1. Predicting tree mortality

Because the age that sapwood converts to heartwood is frequently predictable (Coyea et al., 1990; Gjerdrum, 2003; Sellin, 1994), a historical reconstruction of *GE* is often possible. Where young trees are competing with one another for light, a comparison of *GE* over time provides a good predictor of mortality (Fig. 5). A slow decrease in *GE* may also be indicative of impending mortality brought on by root pathogens (Waring, 1987). The *GE* index has been widely applied to rate the vulnerability of individual trees, and the risk of attack by bark beetles, and to evaluate silvicultural practices designed to reduce the vulnerability of forests to insect-induced mortality.

Studies on lodgepole pine (*Pinus contorta*), ponderosa pine (*Pinus ponderosa*) and Norway spruce (*Picea abies*) identified a critical threshold of ~ 80 g (DM) of stemwood m^{-2} leaf yr^{-1} (Fig. 6a), below which trees become highly vulnerable to attack, and above which their resistance to attack increased markedly

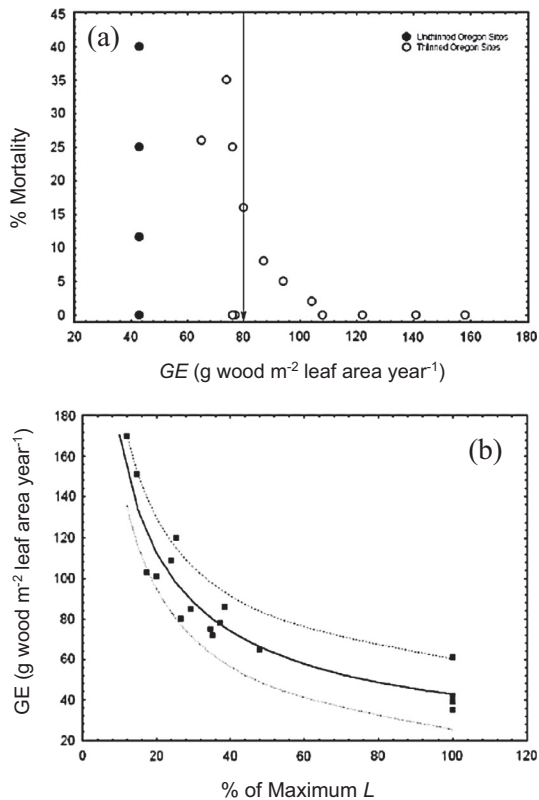


Fig. 6. a: For lodgepole pine, and several other species of conifers, 80 g (dry mass of stemwood production) m⁻² of leaf area yr⁻¹ defines a threshold below which trees are vulnerable to bark beetle attack and above which they are increasingly resistant, b: Thinning with reference to maximum L indicates that more than half the foliage (and sapwood basal area) must be removed to improve GE to a relatively safe level (i.e., $\leq 10\%$ mortality) in previously unthinned stands >80 -year-old. Reprinted from Coops, N.C., Waring, R.H., Wulder, M.A., White, J.C., (2009). Prediction and assessment of bark beetle-induced mortality of lodgepole pine using estimates of stand vigor derived from remotely sensed data. *Remote Sensing of Environment* 113 (5): 1058–1066, with permission from Elsevier Pub.

owing to the ability of these coniferous species to shift production in the vicinity of attack from wood to resin (Christiansen et al., 1987). It is important to recognize that epidemic populations of bark beetles can attack and kill even small diameter trees, although larvae are unlikely to survive. Most conventional risk-rating schemes assume that tree age, basal area, tree density, annual ring growth and other structural indices are able to identify stands at risk from bark beetles (Shore et al., 2000; Stuart, 1984). In addition, thinning experiments that result in no trees with $GE > 50$ g (DM) of stemwood m⁻² leaf yr⁻¹ remain highly susceptible (Amman et al., 1988). From a physiological standpoint, most susceptible tree species are prone to bark beetle attack if the measured GE is <100 g (DM) of stemwood m⁻² leaf yr⁻¹ (Waring and Pitman, 1985).

Although it has long been recognized that thinning can improve the resistance of residual trees to bark beetle attack (Sartwell and Stevens, 1975), there was no consistency in the recommended residual tree basal area per hectare. For example, the recommended 'safe' basal area for ponderosa pine in relation to mountain pine beetle attack varies by twofold between Oregon (Larsson et al., 1983) and Colorado (Negrón and Popp, 2004). Coops et al. (2009) reanalyzed data acquired by Mitchell et al. (1983) and showed that the residual basal area in thinned stands required to create general resistance to bark beetle attack was proportional to maximum L , which varied in stands >80 years old from 2.6 to 7.5 m² m⁻² (Fig. 6b).

The exponential decrease in GE observed in lodgepole pine forests with increasing L (Fig. 6b) is similar to that observed in other infrequently thinned stands of *Pinus sylvestris* (Waring, 1985) and *Pseudotsuga menziesii* (Binkley and Reid, 1984). In more frequently thinned forests of Douglas-fir (Waring et al., 1981), *Pinus ponderosa* (Larsson et al., 1983), and *Eucalyptus* spp. (Medhurst and Beadle, 2005), the lower portions of tree crowns remain alive and can contribute substantially to net carbon uptake (Linder and Lohammar, 1981; Medhurst and Beadle, 2005; Peterson et al., 1997). In such cases, growth per unit of leaf area decreases nearly linearly with increasing L while the safe threshold against insect attack remains essentially unchanged. Under extreme drought, GE is unresponsive to thinning (Fettig et al., 2007; Skov et al., 2004).

3.2.2. Tree mortality associated with defoliation

Although trees are adapted to a certain amount of defoliation through compensating mechanisms (Eyles et al., 2009), sustained defoliation can cause mortality (Luther et al., 1997; Townsend et al., 2012). Some estimate of stand vulnerability can be made from historical analysis (Coyea and Margolis, 1994), but it is necessary to recognize that the sapwood cross-sectional area does not adjust quickly to defoliation (Margolis et al., 1988). Root diseases, on the other hand, develop slowly and cause a concomitant reduction in functional sapwood and leaf area (Tainter and Baker, 1996).

4. Discussion

The two widely applied production indices — LUE and GE — that we have discussed are useful at different scales and for different purposes. LUE -based models lend themselves to the evaluation of stand-level productivity at a range of scales from small plots to regions. At regional scales models of this type can be implemented and analyzed with a variety of remote sensing techniques. In contrast, GE models are designed to evaluate within-stand variation to distinguish differences in performance among species, age and dominance classes. Whereas LUE models generally require one value for the amount of soil water available to the plants of a stand, GE models must take into account the fact that rooting depth and access to light and nutrients often vary among individuals.

Within the last 40 years there have been major advances in the field of production ecology, towards understanding the efficiency with which forests use light, and the factors that cause variation in that efficiency. The simplification recognized by Monteith (1977) — that light use efficiency of net primary production (ϵ_n) is a linear function of intercepted solar radiation, integrated over the growing season — galvanized the field of production ecology. Subsequent research explained why LUE , which is non-linear at daily time steps, becomes linear at monthly or longer intervals, and how other environmental constraints besides PAR interact to affect LUE (Eq. (4)). Another simplification, derived from many growth studies, is that plant respiration and NPP are approximately equal proportions of gross photosynthesis (Litton et al., 2007; Waring et al., 1998). This has led to simplifications in process-based growth models that apply when the analyses are extended from daily to monthly intervals.

As a result of the development of relatively simple process-based growth models, commercial forestry operations in the southern pine area of southeastern USA, Brazil, and Chile are beginning to monitor leaf area index (L) and to rely on model projections to schedule harvests and make economic decisions (Almeida et al., 2003).

Observations and experiments where the size and spatial distributions of trees varied, show that increased variation in GE results in a reduction in LUE . The ability to assess GE on individual trees allows estimates of tree vulnerability to insects and pathogens. It

has also provided a means of quantifying the extent to which management might improve stand growth and reduce crop loss. A useful threshold occurs with regard to reducing insect-related mortality, and the extent to which it might be modified by management actions: *GE* can be kept at safe levels if stand basal areas are maintained at values equivalent to about half or less the basal area observed at maximum *L* (in previously unthinned stands) as suggested by Coops et al. (2009) (see review on the subject by Osem and O'Hara, 2016).

A general explanation as to why growth rates increase rapidly as canopy leaf area index (*L*) increases, and peak shortly thereafter, is based on the observation that there is an exponential decrease in the ratio of foliage to branch mass as trees grow in size, reflecting underlying physiological limitations on water transport and photosynthesis. Faster growing species appear to exhibit a more rapid shift in foliage to branch mass than slower growing ones (Fig. 4). Most species, as they approach maximum height, also experience hydraulic constrictions that cause a reduction in *GE* in comparison to younger trees with fewer leaves (Ryan et al., 2006).

Scientists concerned with biodiversity and ecological forecasting are using process-based models to predict where outbreaks of fire and insects are likely (Coops et al., 2012b; Waring and Coops, 2016), and where and how fast shifts in native and introduced species distributions might occur in response to changing climatic conditions (Coops et al., 2016; Lu et al., 2015; Mummery and Battaglia, 2001; Zhao et al., 2009). Remote sensing has played an increasing role in both parameterizing and testing model predictions. This trend is destined to continue as the spectral and spatial resolution of sensors improve and coverage expands.

There remain major challenges to the field of production ecology. Among them is the need to develop models and techniques that are able to predict the consequences of rapidly changing climatic conditions on *LUE* and *GE* associated with continuously rising concentrations of atmospheric CO₂ concentration and other greenhouse gases.

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