Tamm Review: Light use efficiency and carbon storage in nutrient and water experiments on major forest plantation species

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ABSTRACT

We used published data from nine sites where nutrient and water optimization studies had been installed in a 2×2 factorial design to determine maximum biomass production in response to a simple set of treatments. We tested for site and treatment effects on the relationships between stem, above-ground (stem, branches, foliage) and total (aboveground + roots) biomass production versus intercepted light (light use efficiency, LUE). We also estimated the additional carbon stored as a result of treatment. The sites were located in Australia (*Pinus radiata*), Brazil (*Eucalyptus grandis × urophylla*), France (*Pinus pinaster*), the United States in Georgia and North Carolina (*Pinus taeda*) and Hawaii (*Eucalyptus saligna*), Portugal (*Eucalyptus globulus*), South Africa (*E. grandis*), and Sweden (*Picea abies*). We hypothesized that site, treatment and their interaction would significantly affect LUE; however, we rejected our hypothesis because stem, aboveground and total LUE were not affected by site or treatment. The stem, aboveground and total LUE values were 1.21, 1.51, and 0.85 g MJ^{-1}, respectively. The total LUE value was lower than that for stem and aboveground LUE because a different population was used for the analysis (only five of the nine sites had total production data), and the total LUE relationship had a zero intercept whereas the stem and aboveground LUE relationships had a negative intercept. The average amount of additional carbon that would be stored by the irrigation, fertilization, and fertilization plus irrigation treatments was 3.9, 6.8 and 13.4 Mg CO$_2$ equivalents ha^{-1} yr^{-1}, respectively. These additional carbon storage estimates, based on these research studies with annual nutrient and water applications, were similar to results obtained in operational settings with less intensive nutrient applications.

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1. Introduction

Beginning in the 1970s, studies examining the interaction between nutrient and water applications in forest plantations were installed in different regions (e.g. Persson, 1980; Linder, 1987). These studies built on previous work demonstrating the importance of nutrients and water and their interactive effects (e.g. Tamm, 1964; Ingestad, 1974). The nutrient proportions needed for optimum growth are similar across species (Ingestad, 1987; Knecht and Göransson, 2004), and these studies utilized this concept to design an experiment that could be installed across site and species to optimize nutrient and water availability and ultimately, determine maximum productivity. At the time, and still relevant today, there was concern that nutrients applied to forests might move offsite (Ingestad, 1977; Tamm, 1991); however, these studies utilized a method to provide the nutrients needed for optimum growth without offsite loss (Linder, 1995). A network of experiments was established, and the results from these studies laid the groundwork for a substantial portion of our current understanding of forest plantation ecophysiology (Ryan, 2013). At this point in time, only a few of these sites remain active, with the notable exception of the Flakaliden study, which continues to operate 30 years after the treatments were first applied; however, additional insight may still be gained from the work as a whole.

Resource availability in forest plantations influences foliage production, which in turn affects light interception and ultimately, stand growth (Linder, 1987; Vose and Allen, 1988; Cannell, 1989a; Landsberg and Sands, 2011). After a site has been selected and a stand established, forest managers are somewhat limited in their ability to manipulate available resources. The primary tools for influencing resource availability after stand establishment are managing nutrient and water availability. Nutrients may be added directly through fertilization (e.g. Albaugh et al., 1998; Bergh et al., 1999), and crop tree nutrient availability may be improved through vegetation control (e.g. Hanna et al., 1999). Vegetation control may improve water availability for the crop species (e.g. Byrne et al., 1987), and water can also be added directly (e.g. Coyle et al., 2016). The nutrient and water application studies examined the direct application of nutrients and water and quantified the response to treatment. As a result, annual production estimates, including stem, aboveground (stem, leaves, branches), and total (stems, leaves, branches, roots) production, and leaf area index or canopy light interception data were published from several sites. These data permit an examination of growth efficiency (GE: growth per unit foliage) and/or light use efficiency (LUE: growth per unit intercepted light) across site and species (Monteith, 1977; Waring et al., 1981; Linder, 1985; Waring et al., 2016). At individual sites, changes in GE were observed, especially when examining total production, which likely occurred due to a shift in allocation where treatments with high resource availability resulted in less carbon allocation to the roots (e.g. Albaugh et al., 1998). In the literature, LUE analyses have been completed for aboveground production (Linder, 1985; Cannell, 1989a; Dallatea and Jokela, 1991; McMurtrie et al., 1994; Ahl et al., 2004; Landsberg and Sands, 2011) and for total production estimates (Cannell, 1989a; Runyon et al., 1994; Landsberg and Sands, 2011). However, an examination of LUE where site, and nutrient and water availability effects can be tested across a wide range of species has not been found for forest plantations.

Pioneering work quantifying light use efficiency in crop plants began in the 1970s (Monteith, 1977; Waring et al., 2016). Prior to the development of this concept, researchers were able to observe how plants responded to various treatments but had limited ability to predict how the plants might respond. Light use efficiency focuses on the basic relationship of plant growth, where plants use the sun's energy (light) to fix carbon and then partition that carbon into various plant components (Cannell, 1989b). By quantifying light use efficiency, researchers had a tool they could use to observe how treatments would influence plant growth and from which they could develop mathematical models (e.g. MAESTRO Wang and Jarvis, 1990) to help them predict how a plant might respond to a given treatment, a change in climate or a change in location (planted as an exotic). This work continues with efforts to calibrate and use remotely sensed estimates of LUE to estimate net primary productivity at a global scale (Waring et al., 1993; Running et al., 2000, 2004; Ahl et al., 2004; Wang et al., 2004).

The nutrient and water application studies were useful in refining the predictive abilities associated with the light use efficiency concept. To help make predictions as to how plants may respond to perturbations, the productive potential must be known. The nutrient and water application studies were designed to determine maximum productivity by eliminating nutrient and water limitations while permitting the determination of which of the two resources (nutrients or water) was the most limiting. For example, studies conducted in Australia, Sweden and North Carolina resulted in productivity rates that exceeded expectations or were not considered possible prior to study establishment (Raison and Myers, 1992; Bergh et al., 2005; Albaugh et al., 2009a). Similarly, nutrients were determined as the primary growth limitation in areas that were initially considered to be limited by other factors (e.g. cold temperatures in Sweden, drought in North Carolina). For a given species and site combination, an increase in LUE (more aboveground production for the same amount of absorbed light) would typically indicate an increase in canopy-scale photosynthesis or a change in allocation where more carbon is allocated to aboveground components.

In water-limited systems, irrigation permits photosynthesis to continue under dry conditions, whereas in the absence of additional water, plants reduce or stop photosynthesis (e.g. Campion et al., 2006; Stape et al., 2008). Irrigation allows plants to take advantage of more of the light they absorb to produce additional biomass. Similarly, improved nutrient availability resulting from fertilization may change allocation patterns such that more fixed carbon is allocated to aboveground components so that for the same amount of intercepted light, more aboveground biomass is produced (e.g. Albaugh et al., 1998). However, when observing total biomass production, allocation changes would likely be eliminated as a potential explanation for changes in LUE. In this case, additional hypotheses to explain changes in LUE include age-related decline, a phenomenon observed in many systems where older trees do not produce the same amount of biomass per unit of intercepted light as younger trees (Ryan et al., 1997, 2004) and changes in the hydraulic morphology of fertilized trees, which would permit photosynthesis closer to the wilting point, without cavitation, resulting in greater biomass per unit of intercepted light (Ewers et al., 2000).

When examining species and sites under different resource availability conditions, changes in LUE may be influenced by differences relative to the specific environment in which the trees are growing. For example, *Picea abies* L. Karst. commonly grows in colder climates where low temperatures damage the photosynthetic machinery and soil may remain frozen such that in early spring when conditions are otherwise favorable, photosynthesis does not occur at the same rate as later in the year under similar conditions because the plant is repairing this damage or there is no available soil moisture for photosynthesis to occur (Bergh et al., 1998). Improved nutrient status reduces this effect and thereby, an increase in LUE would be observed with fertilization (Bergh et al., 1998). Similar phenomena have been observed in

the coniferous forests of western North America where climatic and other environmental constraints have a large impact on light use efficiency across a range of species and sites; when adjusting for climatic constraints, however, a common LUE value was identified (Runyon et al., 1994). Water limitations are known to reduce photosynthesis across the spectrum of species and sites examined here; for example, in species that grow in environments where water limitations are severe (*Eucalyptus* in South Africa, Brazil and Australia), the response to increased water availability will be much greater compared to environments not limited by water. Both of these conditions (i.e. variations in water and nutrient availability) could result in a situation where the LUE across site and species would differ with the resources available to the species at a given site. With these studies in mind, we might hypothesize that analysis of LUE from the nutrient and water studies would indicate differences in LUE, where LUE would be higher with the addition of nutrients and water because these treatments have the potential to increase the amount of photosynthesis that would occur in response to a given amount of intercepted light.

Given the emphasis placed on sequestering carbon to mitigate climate change effects (IPCC, 2006), increasing the forest production area and the silvicultural intensity on forested land have been suggested as ways to increase carbon sequestration (Johnsen et al., 2001; Woodbury et al., 2007). Carbon emissions from forest fertilization (the carbon released as a result of the production, delivery and application of nutrients) were considerably lower than the amounts of additional carbon stored in *Pinus taeda* L. stands in the southeastern United States as a result of the fertilization (Albaugh et al., 2012), thus indicating the likelihood of an increase in carbon sequestration in fertilized stands of this species. The addition of water to forest land for irrigation purposes may be problematic given that climate change could result in some water-limited areas receiving even less water in the future; however, it would be interesting to know the potential trade-off between the additional carbon stored in irrigated stands and the additional water needed to produce that carbon (Albaugh et al., 2013).

Our interest was in examining data from the nutrient and water optimization studies to quantify LUE relative to aboveground (LUE-A), stem (LUE-S) and total (LUE-T) biomass production. Specifically, we tested the hypothesis that site (in this case a combination of species and location), fertilization and irrigation treatments and their interactions would influence LUE-A, LUE-S and LUE-T. Additionally, we wanted to determine the amount of additional carbon that would be stored in aboveground biomass if the nutrient and water optimization treatments were applied at a landscape scale.

2. Methods

We examined data from nine experiments where nutrients and water were applied to optimize resource availability in a 2×2 factorial design (Table 1). The experiments were located in Australia (AU) at the Biology of Forest Growth Site (Raison and Myers, 1992), Brazil (BR) near Entre-Rios (Stape et al., 2008), France (FR) near Bordeaux (Trichet et al., 2008), the United States in Georgia (GA) near Bainbridge (Samuelson et al., 2004), in Hawaii (HI) near Hilo (Ryan et al., 2004) and in North Carolina (NC) at the Southeast Tree Research and Education Site (Albaugh et al., 1998), Portugal (PT) at the Furaduro Site (Pereira et al., 1994), South Africa (ZA) in KwaZulu-Natal (Campion et al., 2006), and Sweden (SE) at Flakaliden (Bergh et al., 1999). The species planted at each site were *Pinus radiata* D. Don (AU), *Eucalyptus grandis × urophylla* (BR), *Pinus pinaster* Ait. (FR), *Pinus taeda* (GA, NC), *Eucalyptus saligna* (HI), *Eucalyptus globulus* Labill. (PT), *E. grandis* (ZA), and *Picea abies* (SE). The treatments were a control (C, no additions), irrigation applied to eliminate water stress (I), fertilizer applied to eliminate nutrient limitations (F) and the combination of fertilization and irrigation (FI). The specific irrigation and fertilizer application amounts and timing differed for each study and can be found in the summary papers referenced earlier. However, the primary goal when applying the treatments at each site was the same: to eliminate water and nutrient limitations. When applied alone, fertilizer was broadcast as a solid fertilizer within the treatment plot; when applied with the irrigation treatment, it was applied either as a liquid in the irrigation stream or as a solid broadcast treatment. The broadcast fertilizer treatments were applied annually whereas the liquid fertilization was applied in smaller doses throughout the growing season. The AU site had FI treatments where solid fertilizer was broadcast annually and where it was added in the irrigation stream; the GA site did not have an F treatment; the BR site had F and FI treatments but did not report them separately because there was no fertilizer effect on growth at that site; and the HI site had treatments we considered I and FI even though there was no irrigation because average annual rainfall was approximately 3460 mm yr^{-1} during the study. Other studies have examined nutrient and water applications in forest stands (e.g. Coyle et al., 2016); however, the data necessary to complete LUE calculations were not published.

We examined LUE as biomass production per unit of intercepted light for stem, aboveground (stem, leaves and branches), and total (aboveground plus roots) biomass. Biomass production was the additional biomass produced in one year, and the measurement of intercepted light was from the same year. Biomass production (growth over one year) is distinct from biomass accumulation (growth over the lifetime of the trees, many years), which is the total amount of biomass produced from the time of planting. When perennial tissue (stems, branches and roots) production data were not specifically provided but biomass accumulation (biomass pool size) data for consecutive years were found, we estimated production by calculating the difference between the pool sizes from year to year. When production data were reported as carbon, the data were converted to biomass by multiplying the carbon data by 2 (IPCC, 2006). Aboveground production data were available for all sites, stem production data were available for seven sites (BR, FR, GA, NC, PT, SE, ZA) and total production data were available

Table 1
Location, species, age, years measured and citation details of each experiment examined in this analysis. Negative latitude and longitude indicate south and west, respectively.

Site	Site code	Latitude	Longitude	Species	Age (years)	Years examined	Primary citation
Australia	AU	−35.34	148.94	*Pinus radiata*	10–14	1983–1987	Raison and Myers (1992)
Brazil	BR	−11.97	−38.12	*Eucalyptus grandis × urophylla*	4–5	2000	Stape et al. (2008)
France	FR	44.70	−0.77	*Pinus pinaster*	7–9	1999–2001	Trichet et al. (2008)
Georgia	GA	30.80	−84.65	*Pinus taeda*	4	1998	Samuelson et al. (2004)
Hawaii	HI	19.84	−155.12	*Eucalyptus saligna*	1–6	1995–2000	Ryan et al. (2004)
North Carolina	NC	35.90	−79.48	*Pinus taeda*	8–16	1992–2000	Albaugh et al. (1998)
Portugal	PT	39.03	−9.25	*Eucalyptus globulus*	1–3	1987–1989	Pereira et al. (1994)
South Africa	ZA	−27.23	30.55	*Eucalyptus grandis*	2–4	2000–2002	Campion et al. (2006)
Sweden	FL	64.12	19.45	*Picea abies*	32–33	1995–1996	Bergh et al. (1999)

Table 2
Data sources for estimating aboveground and total biomass production, and intercepted light or the components needed to estimate intercepted light (above-canopy irradiance, the extinction coefficient and leaf area index) for the nine sites examined. NR indicates that the variable was not reported.

Site	Aboveground production	Total production	Intercepted light (I_{abs})	Above-canopy irradiance (I_O)	Extinction coefficient (k)	Leaf area index
Australia	Raison and Myers (1992)	NR	Raison and Myers (1992)	–	–	–
Brazil	Stape et al. (2008)	NR	Stape et al. (2008)	–	–	–
France	Trichet et al. (2008)	Trichet et al. (2008)	–	Agri4cast (2015)	0.47, (Berbigier and Bonnefond, 1995)	Trichet et al. (2008)
Georgia	Samuelson et al. (2001)	Samuelson et al. (2001)	–	CRONOS (2015), SolarCalc (Spokas and Forcella, 2006)	0.5, (Sampson and Allen, 1995)	Samuelson et al. (2004)
Hawaii	Ryan et al. (2004)	NR	–	NOAA National Climatic Data Center, SolarCalc. (Spokas and Forcella, 2006; Menne et al., 2012)	0.36, (Stape et al., 2004)	
North Carolina	Albaugh et al. (1998) and Albaugh et al. (2004)	Albaugh et al. (1998) and Albaugh et al. (2004)	–	On site weather station	0.5, (Sampson and Allen, 1995)	Albaugh et al. (1998) and Albaugh et al. (2004)
Portugal	Madeira and Pereira (1990) and Pereira et al. (1994)	NR	–	Agri4cast (2015)	0.48, (Gazarini et al., 1991)	Pereira et al. (1994)
South Africa	Campion et al. (2006)	Campion et al. (2006)	–	Campion (2005)	Treatment specific 0.42–0.55 (du Toit, 2008)	Campion et al. (2005)
Sweden	Albaugh et al. (2009b)	Unpublished	–	On site weather station	Treatment specific 0.45–0.60	Unpublished

for five sites (FR, GA, NC, SE, and ZA) (Table 2). Intercepted light was defined as photosynthetically active radiation (PAR) absorbed by the canopy. Some studies reported absorbed PAR; where absorbed PAR (I_{ABS}) was not reported, we estimated it as

$$I_{ABS} = I_O[1 - \exp^{(-kL)}] \tag{1}$$

where I_O is above-canopy irradiance, k is the extinction coefficient, and L is leaf area index (Landsberg, 1986). When above-canopy irradiance was not found in the literature for a site, we acquired these data from publicly available data stores (Agri4cast 2015), or we acquired temperature and rainfall data from other sources (CRONOS (2015) and NOAA NCDC (Menne et al., 2012)) and used SolarCalc (Spokas and Forcella, 2006) to estimate the above-canopy irradiance. When absorbed PAR was presented in moles of absorbed PAR, we converted to MJ by dividing by 4.6 (Boelee et al., 2012). Extinction coefficients and leaf area indices were obtained from the literature or were measured for this analysis (Table 2).

We estimated the additional carbon that would be stored in aboveground biomass in response to treatment by subtracting the aboveground biomass production of the control from that of the treatments at each site. The result was divided by 2 to calculate the carbon in the biomass (IPCC, 2006) and then multiplied by 3.667 to convert the biomass carbon into CO_2 equivalents (USEPA, 2005). If multiple years of data were available for a given site, the CO_2 equivalents were averaged across years. This calculation was only completed for sites (AU, FR, NC, PT, SE, ZA) that had all four (C, I, F, FI) treatments.

PROC MIXED (SAS-Institute, 2002) was used to examine our hypothesis regarding site and treatment effects on the relationships between intercepted light and aboveground, stem and total biomass production. We tested site, site by fertilization, site by irrigation and site by fertilization by irrigation as random effects on the relationship between intercepted light and aboveground, stem and total biomass production (Littell et al., 2006). Intercepted light was a fixed effect. Eight of the nine studies (all except GA) had production and absorbed PAR estimates from multiple years. Consequently, stand age was used as a repeated measure in the mixed model. As noted previously, not all treatments were installed at

all sites, which resulted in missing data points for these sites and an unbalanced design. Heteroscedasticity was observed in the aboveground and stem biomass production data, and a log transformation was used to normalize these data. If terms in the full model were not significant, they were removed from the model until all model terms were significant. When all terms in the model were significant, parameter estimates were generated to produce a regression line to fit the data. The slopes of the production versus intercepted light regression lines were scaled from Mg ha^{-1} yr^{-1} per MJ m^{-2} yr^{-1}, to g MJ^{-1} by converting the units to a common area and scaling to grams. All statistical tests were evaluated with alpha = 0.05.

3. Results

Site, site by fertilization, site by irrigation and site by fertilization by irrigation were not significant factors for any of the biomass versus intercepted light relationships examined. When converted to g MJ^{-1}, the slopes for the aboveground, stem and total biomass versus intercepted light relationships were 1.51, 1.21, and 0.85 g MJ^{-1}, respectively (Figs. 1–3, respectively).

The average amount of additional carbon that could be stored in aboveground biomass by the I, F, and FI treatments was 3.9, 6.8 and 13.4 Mg CO_2 equivalents ha^{-1} yr^{-1}, respectively (Fig. 4).
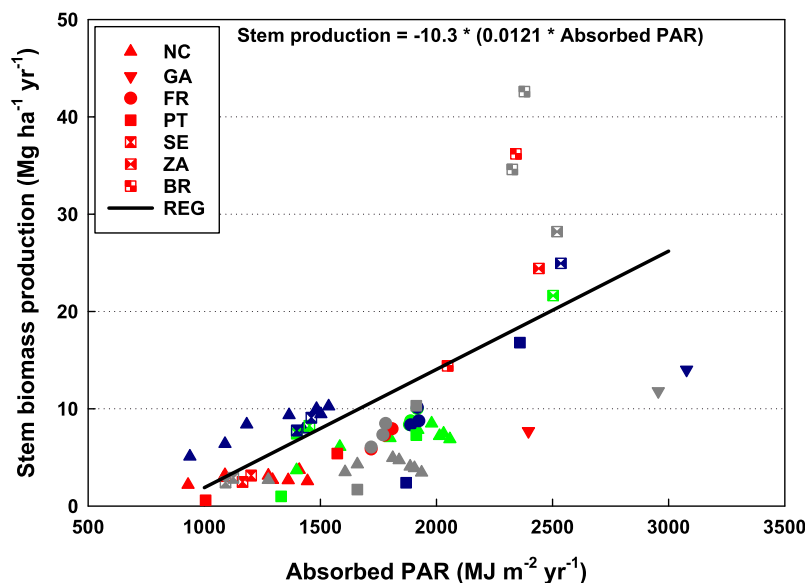
4. Discussion

The FI treatment was applied using two distinct methods, one where fertilizer was broadcast annually as dry material to the soil surface and one where fertilizer was added in the irrigation stream throughout the growing season. Only the AU site included both treatments; however, the study design did not permit a statistical analysis of treatment differences (Snowdon and Benson, 1992). The potential differences arising from the fertilizer application method are that the dry material applications could be susceptible to urea volatilization such that less nitrogen would be available to the trees than what was applied (Cabrera et al., 2010), although the use of urease inhibitors can effectively eliminate this as an issue (Zerpa and Fox, 2011). Additionally, applying fertilizers in the
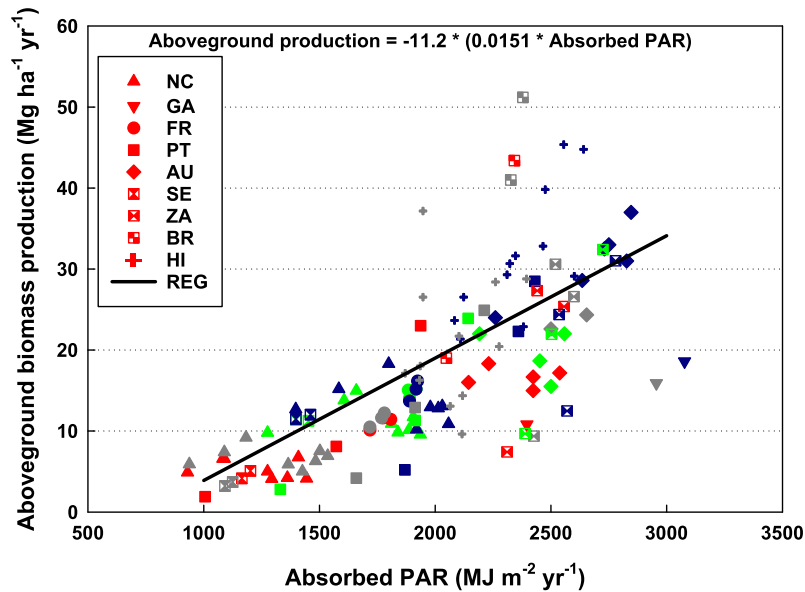
Fig. 1. Aboveground biomass production versus absorbed photosynthetically active radiation (PAR) for nine sites (AU – *Pinus radiata* in Australia; BR – *Eucalyptus grandis* × *urophylla* in Brazil; FR – *P. pinaster* in France; GA – *P. taeda* in Georgia, United States; HI – *E. saligna* in Hawaii, United States; NC – *P. taeda* in North Carolina, United States; PT – *E. globulus* in Portugal; SE – *Picea abies* in Sweden; and ZA – *E. grandis* in South Africa) where nutrient optimization and irrigation studies were installed with four treatments (C – control with no additions (red symbols), I – optimum irrigation (gray symbols), F – optimum fertilization (green symbols), FI – optimum fertilization and irrigation (blue symbols)). Multiple points for a site-treatment combination indicate different years where the measurements were completed. The regression line (REG) is for all data; there were no significant site, treatment or interactive effects on the relationship. The regression equation is shown.


Fig. 2. Stem biomass production versus absorbed photosynthetically active radiation (PAR) for seven sites (BR – *Eucalyptus grandis* × *urophylla* in Brazil; FR – *Pinus pinaster* in France; GA – *P. taeda* in Georgia, United States; NC – *P. taeda* in North Carolina, United States; PT – *E. globulus* in Portugal; SE – *Picea abies* in Sweden; and ZA – *E. grandis* in South Africa) where nutrient optimization and irrigation studies were installed with four treatments (C – control with no additions (red symbols), I – optimum irrigation (gray symbols), F – optimum fertilization (green symbols), FI – optimum fertilization and irrigation (blue symbols)). Multiple points for a site-treatment combination indicate different years where the measurements were completed. The regression line (REG) is for all data; there were no significant site, treatment or interactive effects on the relationship. The regression equation is shown.

irrigation stream may supply the nutrients at the time of demand and in a manner that makes uptake relatively efficient. In the studies where solid fertilizer was applied with irrigation, the annual applications were completed at the start of the growing season; however, the level of nitrogen in the soil was increased for several months (Mudano, 1986). At the same time, at the sites where fertilizer was added as a dry material, care was taken to apply the fertilizer in a manner to reduce or eliminate the possibility of volatilization and consequently, we believe there was no reason to consider these as different treatments.

For the individual sites, treatment did influence growth, with positive fertilizer responses observed at AU, FR, HI, NC, and SE and positive irrigation responses at AU, BR, NC, PT and ZA (Raison and Myers, 1992; Pereira et al., 1994; Albaugh et al., 1998; Bergh et al., 1999; Ryan et al., 2004; Samuelson et al., 2004; Campion et al., 2006; Stape et al., 2008; Trichet et al., 2008). In addition, several sites, including AU and GA, had strong positive responses to the combination of fertilizer and irrigation. The typical aboveground biomass response to either treatment (water or nutrients) was an increase in foliage and stem
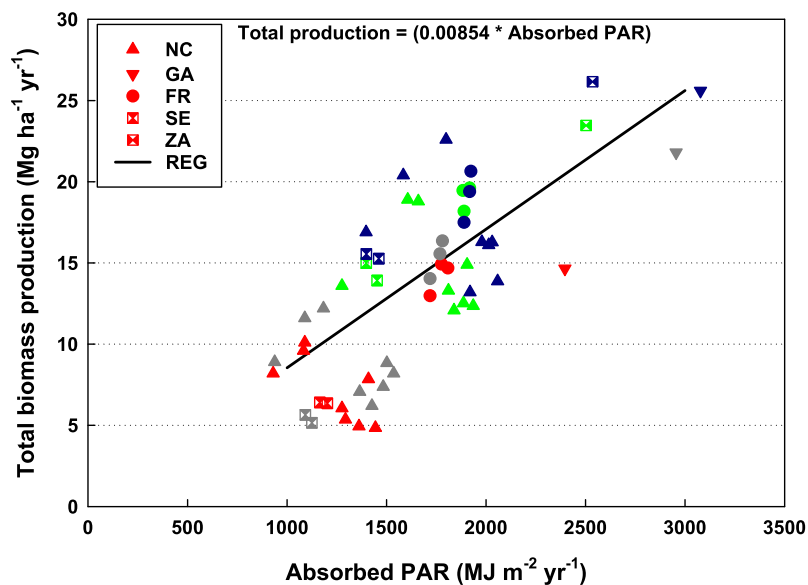
Fig. 3. Total biomass production versus absorbed photosynthetically active radiation (PAR) for five sites (FR – *Pinus pinaster* in France; GA – *P. taeda* in Georgia; United States, NC – *P. taeda* in North Carolina, United States; SE – *Picea abies* in Sweden; and ZA – *E. grandis* in South Africa) where nutrient optimization and irrigation studies were installed with four treatments (C – control with no additions (red symbols), I – optimum irrigation (gray symbols), F – optimum fertilization (green symbols), FI – optimum fertilization and irrigation (blue symbols)). Multiple points for a site-treatment combination indicate different years where the measurements were completed. The regression line (REG) is for all data; there were no significant site, treatment or interactive effects on the relationship. The regression equation is shown; the intercept was not significantly different from zero and therefore a no-intercept model was used.
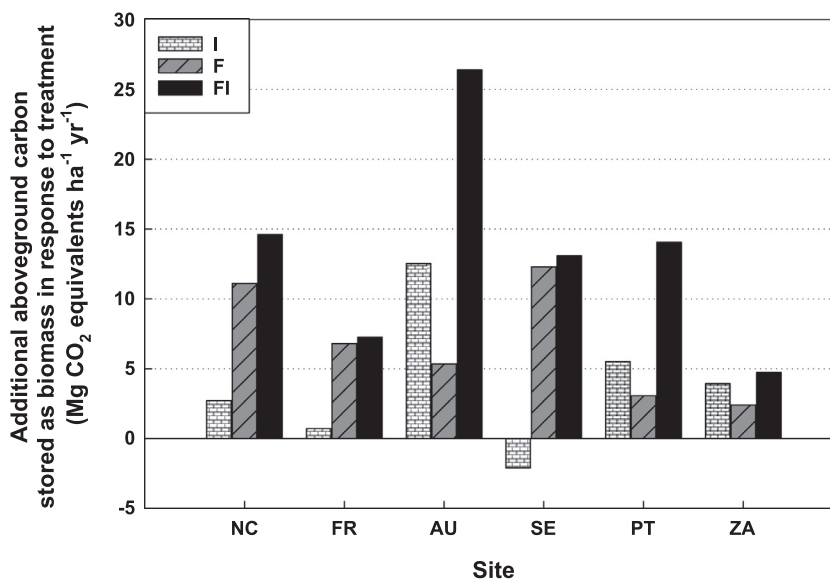
Fig. 4. Additional aboveground carbon stored in response to treatment for six sites (AU – *Pinus radiata* in Australia; FR – *P. pinaster* in France; NC – *P. taeda* in North Carolina, United States; PT – *E. globulus* in Portugal; SE – *Picea abies* in Sweden; and ZA – *E. grandis* in South Africa) where nutrient optimization and irrigation studies were installed with four treatments (C – control with no additions, I – optimum irrigation, F – optimum fertilization, FI – optimum fertilization and irrigation). Data are the treated minus control values showing the average response over all years where measurements were completed. Negative values indicate that the control grew better than the treated plots at that site.

production. When examining total production, the typical response was an increase in foliage and stem production and a decrease in belowground production with improved nutrition (e.g. Samuelson et al., 2004). This effect was repeated in some cases, although to a lesser degree, with irrigation (Albaugh et al., 1998).

However, in our study, site and site by treatment interactions did not affect LUE calculated using aboveground, stem or total biomass production. Consequently, we rejected our hypothesis. This was surprising given the wide range in species and sites included in the analysis. Species from three genera (*Eucalyptus*, *Pinus* and

Picea) and sites ranging from 12 to 64 degrees of latitude were examined (Table 1). The imposed treatments induced large gradients in nutrient and water availability at each site, and the responses observed differed by site, where some sites responded well to irrigation (Raison and Myers, 1992; Campion et al., 2006; Stape et al., 2008) while others responded primarily to fertilization (Albaugh et al., 1998; Bergh et al., 1999; Ryan et al., 2004). Across all studies, absorbed PAR ranged from 1000 to 3000 MJ m^{-2} yr^{-1}, and aboveground, stem and total biomass production ranged from 3 to 30, 2 to 28, and 5 to 32 Mg ha^{-1} h^{-1}, respectively. Even with

these large differences in site and imposed treatments, we did not detect differences in LUE due to site and site by treatment interactions. Multiple species-site combinations have exhibited similar LUE for crops (Monteith, 1977) and tree species (Linder, 1985; Cannell, 1989a). In addition, Runyon et al. (1994) reported similar LUE values across species after adjusting for climatic and environmental constraints. In our analysis, no adjustments were made for these constraints. Other studies have identified differences in aboveground LUE. For example, Dallatea and Jokela (1991) reported different aboveground LUE values for *P. taeda* and *Pinus elliottii* Engelm., which these authors attributed to variation in crown structure between the two species. In addition, Ahl et al. (2004) examined aboveground LUE for five forest cover types (aspen, northern hardwoods, red pine, forested wetlands and upland conifers) and found differences due to cover type and year.

The slope of the aboveground biomass production versus intercepted light regression line was 0.0151 Mg ha^{-1} yr^{-1} per MJ m^{-2} yr^{-1}, which, after converting the units to a common area and scaling to grams, results in 1.51 g MJ^{-1} of biomass production on an annual basis. This is similar to Monteith's (1977) estimate of 1.4 g MJ^{-1} for annual dry matter production for crops, Linder's (1985) estimate of 1.7 g MJ^{-1} for aboveground production in *Eucalyptus*, *Pinus* and *Picea* stands in Australia, New Zealand, Sweden and the United Kingdom, and the range of aboveground production for plantation species around the world (0.2–2.4 g MJ^{-1}) listed by Landsberg and Sands (2011). The range in aboveground LUE for forests and forest plantations clusters around 1.0–1.5 g MJ^{-1}, which is in agreement with our estimate (Waring et al., 1998). Waring and Running (1998) suggested that Monteith's estimate would not be achieved in forests due to typical suboptimal conditions that limit stomatal opening and cause trees to allocate excess carbon belowground. Temperature differences, vapor pressure deficit and water stress have been identified as causing variation in LUE (McMurtrie et al., 1994). In addition, it has been hypothesized that the canopy nitrogen content may influence light use efficiency to maintain it at a constant level (Medlyn, 1998). Given that the nutrient and water treatments imposed in these studies would have a large effect on water stress (i.e. reduce it in irrigated treatments) and the canopy nitrogen content (increase it and reduce within-canopy variation), and that these effects would occur across site and species may help explain the lack of a significant site effect. Using a biochemical approach, Amthor (2010) estimated the theoretical maximum light use efficiency for C$_3$ crop plants as 0.092 J J^{-1}. Converting our aboveground biomass LUE estimate to the same units using 20 MJ kg^{-1} as the approximate phytomass heat of combustion (Gower et al., 1984), our LUE estimate is 0.03 J J^{-1}, approximately one-third of the theoretical maximum. Reduction from the maximum LUE would be a result of non-optimal temperature and nutrient and water limitations (Landsberg, 1986).

Stem biomass LUE was similar in both slope and intercept to the aboveground biomass LUE (Figs. 1 and 2). This is not surprising because stem production represents a large proportion of aboveground and total production. In the studies examined here, stem production was, on average, approximately 65% and 51% of aboveground and total production, respectively. Stem production was relatively sensitive to nutrient and water availability in the studies examined here, where changes in resource availability resulted in large effects on stem production, often due to a change in carbon allocation from belowground to aboveground components (Ryan et al., 2004).

Similarly, the slope of the total production versus intercepted light was 0.00854 Mg ha^{-1} yr^{-1} per MJ m^{-2} yr^{-1}, which results in 0.85 g MJ^{-1} of biomass production. This result is in the range of estimates from the literature for total production (1.4–1.6 g MJ^{-1} (du Toit, 2008), 1.25 (Runyon et al., 1994), 0.30–0.45 (Ahl et al.,

2004) and 0.3–3.3 g MJ^{-1} (Landsberg and Sands, 2011)). The intercept for the aboveground biomass production versus intercepted light relationship was −11.2 and significantly less than zero. Linder's (1985) intercept estimate for the same relationship was also less than zero, and he indicated this was to be expected because only aboveground production was included. Consequently, we concluded that by including belowground biomass production, the intercept should be zero. The intercept for our total biomass versus intercepted light relationship was not significantly different from zero (Fig. 3), as predicted by Linder (1985). Given the difficulty in quantifying belowground production (Stone and Kalisz, 1991), this result gives confidence that the root production estimates from these studies well estimated belowground production. It is counterintuitive that the total biomass production slope (0.85 g MJ^{-1}) was less than both the stem (1.21 g MJ^{-1}) and aboveground (1.51 g MJ^{-1}) slopes. This is a result of using a different population for each estimate, where all nine sites were used for aboveground biomass, whereas only seven and five sites, respectively, were used for the stem and total production estimates. Additionally, the total production regression equation has an intercept of zero while the aboveground and stem relationships have negative intercepts.

Intercepted light was the independent variable in this analysis. It is important to note that even though light is being intercepted, additional carbon may not be fixed and growth may not continue. In extreme northern climates, for example, the photosynthetic machinery is damaged by extended cold periods and in spring, light may be intercepted by the foliage, but photosynthesis remains well below what would be expected (Bergh et al., 1998). However, improved nutrition can reduce this effect, allowing the photosynthetic machinery to recover more rapidly when conditions improve (Bergh et al., 2003). Similarly, when water limitations occur, stomates close to conserve water so that photosynthesis is reduced or stopped even though the foliage continues to intercept light (Campion et al., 2006; Stape et al., 2008). On the other end of the spectrum, growth may be limited even though the photosynthetic machinery is operating at a maximum for a particular species. While growth may continue through the utilization of stored carbohydrates, once these are depleted, the additional growth that would be expected based on the total amount of intercepted light does not occur (Sampson et al., 2001). Additionally, increasing stand age during the experiments would have influenced the observed LUE, where older stands would likely have less aboveground biomass production for a given level of intercepted light than a younger stand (Ryan et al., 2004). Sites in this study had quite varied environmental constraints that may have resulted in a situation where light was intercepted but additional carbon was not fixed. Low temperature certainly influenced growth at SE and would have also had an effect at NC, GA and FR, whereas high vapor pressure deficit likely influenced growth at AU, ZA and BR. Linder (1985) reported a common LUE for sites from Australia, New Zealand, the United Kingdom and Sweden and after adjusting for environmental constraints, Runyon et al. (1994) reported a common LUE along a transect in Oregon, which included a wide range of vegetation zones. Medlyn (1998) suggested that there may be a compensatory mechanism among PAR, leaf area index and leaf nitrogen content that resulted in similar LUE values across the different sites in the Runyon et al. (1994) study. Nutrient applications in the studies examined here would have increased the foliar nitrogen content, and the nutrient and water treatments affected leaf area index. It is possible that part of the explanation for our common LUE values is related to these factors as well.

The amount of carbon that might be stored as biomass if these treatments were applied on a broader scale would be influenced by the amount of fertilizer applied and the response achieved. The

studies examined here were designed as nutrient optimization studies to ameliorate all nutrient deficiencies. The trees were monitored on a regular basis to ensure they received not only nitrogen and phosphorus but all elements that were or might become limiting. While this level of monitoring may be problematic at an operational scale, responses similar to those observed in the optimum nutrition studies have been obtained from less frequent applications of nitrogen and phosphorus applied to *P. taeda* in the southeastern United States (Fox et al., 2007). For example, a typical mid-rotation fertilizer application in a *P. taeda* stand sequestered 19.2 Mg CO_2 equivalents ha^{-1} as additional stem growth per unit of CO_2 equivalent emissions associated with the fertilizer application (Albaugh et al., 2012). Similarly, in a series of experiments with *P. abies* in Sweden, biannual application of fertilizers did not reduce the growth response nor increase nitrogen leaching to soil water compared to annual applications (Bergh et al., 2008).

Additional carbon is likely stored in increased branch, root mass, and soil organic matter associated with the response to fertilization. Generally, less carbon is proportionally allocated belowground as root mass in response to additional nutrients (e.g. Albaugh et al., 1998; Campion et al., 2006); however, fertilized trees are typically larger than non-fertilized trees, and the absolute root mass will be higher. This additional carbon storage is only focused on what occurs in the forest, whereas other benefits exist after stands have been harvested. In one modeling analysis, after five successive rotations where fertilizers were applied once in mid-rotation stands, 38% of the CO_2 equivalents resulting from fertilization remained in use or in a landfill compared with 36% that was used as an energy source (Albaugh et al., 2012).

In the southeastern United States, up to 600,000 ha have been fertilized annually, resulting in increased annual carbon sequestration of more than 8 Tg yr^{-1} CO_2 equivalents on an area basis. Other parts of the world have fertilized large amounts of forest areas, for example, 190,000 ha yr^{-1} were fertilized in Sweden in the 1970s (Nohrstedt, 2001) and as much as 110,000 ha yr^{-1} were fertilized in Finland up to the 1990s (Saarsalmi and Mälkönen, 2001). These amounts have dropped considerably due to concern over negative environmental impacts associated with nutrient movement offsite, including eutrophication of water systems (e.g. Bennett et al., 2001; Driscoll et al., 2003). However, the nutrient optimization studies have demonstrated that nutrients can be added to the forest without nutrient movement offsite (Linder, 1995). Irrigating forest stands may not be logistically practical on a large scale; however, our data indicate a substantial increase in stored carbon that could be gained with irrigation alone on some sites. One possibility for irrigating forest stands, which may alleviate wastewater disposal problems, is to use wastewater treated to remove heavy metals, toxins, microbes and other components that might be problematic as the source for the irrigation water, similar to the AU experiment (Raison and Myers, 1992) and other studies (Cromer et al., 1983). Regardless of the water source, irrigation might become an important consideration in areas such as Brazil, Australia and South Africa, where water may be severely limiting at times. In Brazil, there was no response from fertilization, but there was a large response to irrigation (Stape et al., 2008), while in Australia, fertilization alone provided a modest response but there was a synergistic response when fertilization and irrigation were combined (Raison and Myers, 1992). In South Africa, *Eucalyptus* species require nutrient additions to develop high levels of leaf area needed for high productivity but then require water additions to sustain that leaf area (Campion, 2005). These benefits need to be considered in light of potential water limitations for other needs in the future (King et al., 2013). In addition to the potential for mitigating climate change by increasing carbon stored in forest stands, bioenergy from forest products has interesting potential. It already provides one third of Sweden's energy, and in the southeastern United States, demand for bioenergy exceeds 90 million Mg yr^{-1} (Dougherty and Wright, 2012), and there is renewed interest in intercropping in forest stands for the simultaneous production of bioenergy crops (King et al., 2013; Albaugh et al., 2014).

In this analysis, we did not detect site or treatment effects on the biomass production versus intercepted light relationship. Consequently, effects on biomass production per unit intercepted light were represented with one relationship at a scale covering a wide range in species, environments and resource availability. Treatment effects on growth efficiency (described as stem growth per unit leaf area) were evident in the studies included in this analysis (e.g. Raison and Myers, 1992; Trichet et al., 2008) and have been reported in other studies (Waring et al., 1981; Linder, 1987; Will et al., 2002). Examining intercepted light, rather than leaf area index directly, likely incorporated the treatment effect in the independent variable, thus eliminating treatment as a significant regressor. Additionally, the nutrient applications may have increased foliar nitrogen content, and the nutrient and water treatments may have increased leaf area index such that there was a compensatory mechanism among PAR, leaf area index and leaf nitrogen that resulted in similar LUE values across site (Medlyn, 1998). The information presented here will be useful for predicting responses to silvicultural treatment and in modeling efforts involved in quantifying global productivity from remotely sensed data.

Acknowledgements

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