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, aboveground (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