BOSQUE 20(1): 3-8, 1999 DOI: 10.4206/bosque.1999.v20n1-01

OPINIONES

Ecophysiological basis for plantation production: A loblolly pine case study*

Bases ecofisiológicas para la producción de plantaciones: un caso de estudio en pino taeda

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RESUMEN

Históricamente, la práctica de la silvicultura ha estado orientada a controlar la composición, cantidad y estructura de la vegetación forestal y mantención de la calidad del sitio. En la medida en que las plantaciones forestales se han transformado en una fuente importante de fibra, combustible y material estructural, esta aproximación tradicional ha dado paso a una intervención activa para mejorar tanto los recursos genéticos como los del suelo. Una manipulación efectiva de los recursos genéticos y del suelo requiere un conocimiento básico de cómo la disponibilidad de recursos limita la producción forestal, y cómo los árboles de una plantación pueden diferir en su habilidad para adquirir y utilizar dichos recursos. En la actualidad, es ampliamente aceptado que la mayor parte de la variación en la producción de madera puede ser explicada por variaciones en intercepción de la luz. En las plantaciones de pino en el Sureste de Estados Unidos la baja disponibilidad de nutrientes es el principal factor que causa niveles subóptimos de área foliar y de este modo en la producción. Pocos estudios han examinado el efecto de la disponibilidad de nutrientes y agua sobre la producción. Aquí se presentan los resultados de uno de esos estudios, el estudio SETRES, que se está desarrollando actualmente en el Sureste de los Estados Unidos con *Pinus taeda.*

Palabras claves: productividad, área foliar, nutrientes, agua, silvicultura.

ABSTRACT

Historically, the practice of silviculture has focussed on controlling the composition, quantity, and structure of forest vegetation and the maintenance of site quality. As forest plantations have become important sources of fiber, fuel, and structural material, this custodial approach has given way to active intervention to improve both genetic and soil resources. Effective manipulation of the genetic and soil resources requires a basic understanding of how resource availability limits forest production and how crop trees may differ in their ability to acquire and utilize these resources. It is now generally accepted that much of the variation in wood production can be accounted for by variation in light interception. In pine plantations in the southeastern U.S., low nutrient availability is the principal factor causing suboptimal levels of leaf area and therefore production. Few studies have examined the effects of both nutrient and water availability on production. We highlight the results from one such study, the SETRES study that is now underway in the southeastern USA with loblolly pine.

Key words: productivity, leaf area, nutrients, water, silviculture.

* Trabajo presentado en X Silvotecna. IUFRO Conference. Site Productivity Improvement.

INTRODUCTION

Historically, the practice of silviculture has focussed on controlling the composition, quantity, and structure of forest vegetation and the maintenance of site quality. As forest plantations have become important sources of fiber, fuel, and structural material, this more custodial role has given way to active intervention to improve both plant and soil resources. In this regard, plantation silviculture is much more like agronomy where both the plant and the soil have been actively managed for centuries. Clearly, effective manipulation of both genetic and soil resources are essential for cost-effective and environmentally sustainable forest production. Effective manipulation of the genetic and soil resources requires a basic understanding of resource availability, particularly water and nutrient availability limits forest production, and how crop trees may differ in their ability to acquire and utilize these resources.

At the stand level, water and nutrient availability influence stemwood production through effects on light interception, photosynthesis, and carbon partitioning. It is now generally accepted that much of the variation in wood production can be accounted for by variation in light interception (Cannell 1989, Linder 1987, Gower *et al.* 1994). Light interception is principally a function of the amount of leaf area and the duration of leaf area display. Differences in individual tree crown architecture and stand canopy structure can also affect light interception. Empirical data from optimum nutrition x water field studies with Scots pine, Norway spruce (Axelsson and Axelsson 1986, Linder 1987), Monterey pine (Linder *et al.* 1987, Benson *et al.* 1992, Snowdon and Benson 1992), loblolly pine (Albaugh *et al.* 1998), and *Eucalyptus globulus* (Pereira *et al.* 1989) have shown that leaf area and production are far below optimum levels in many areas of the world. In pine plantations in the southeastern U.S., low nutrient availability has been shown to be the principal factor causing suboptimal levels of leaf area (Colbert *et al.* 1990, Vose and Allen, 1988, Albaugh *et al.* 1998). Water availability, high temperatures, and elevated ozone levels have also been implicated (Hennessey *et al.* 1995, Stow *et al.* 1991, Teskey *et al.* 1987, Albaugh *et al.* 1998).

Improved nutrient availability has been shown to increase photosynthetic efficiency (Linder 1987, Murthy *et al.* 1996) and above-ground productivity proportionally more than below-ground productivity in stand-level studies (Axelsson and Axelsson 1986, Gower *et al.* 1992, Haynes and Gower 1995, Vogt *et al.* 1986). These effects do contribute to changes in productivity, but none contribute as much as changes in leaf area.

While many studies have quantified the impacts that individual environmental factors may have on leaf area and growth efficiency, few studies have examined the effects of both nutrient and water availability applied in factorial combination. We will highlight the results from one such study, the SETRES (Southeast Tree Research and Education Site) study that is now underway in the southeastern USA with loblolly pine. This study is a partnership with participating scientists from the U.S. Forest Service, North Carolina State University, and Duke University.

SETRES

A detailed description of the study site and treatment design for SETRES is provided in Albaugh *et al.* (1998). Briefly, the study was established in North Carolina (35°N latitude, 79°W longitude) on an infertile, well-drained, sandy site. Annual precipitation and temperature average 1210 mm and 17°C respectively. The site was hand planted on a 2 x 3 m spacing with loblolly pine in 1985 after felling of the previous natural longleaf pine stand and application of Velpar™ grid balls.

Sixteen 50 x 50 m (0.25 ha) treatment plots with 30 x 30 m measurement plots centered in the treatment plot were established in January, 1992 in the eight-year-old stand. Site index for loblolly pine was estimated to be about 14 m (base age 25). Height, diameter, basal area, volume, LAI, and density (1260 stems ha^{-1}) were standardized in all plots prior to treatment imposition. Complete control of non-pine vegetation in the treatment plots has been maintained since 1992 through a combination of mechanical and chemical (glyphosate) methods.

The experimental design includes a 2 x 2 factorial of nutrient and water treatments replicated four times. The nutrition treatments, begun in March, 1992, are (1) optimum nutrition or (2) no addition. Optimum nutrition is defined as maintaining N concentrations of 1.3% in foliage in the upper third of the crown. Other nutrients additions are balanced with N levels so that target nutrient/N ratios of 0.10 for P, 0.35 for K, 0.12 for Ca, and 0.06 for Mg are maintained. Foliar B levels are maintained above 12 mg/kg. Solid fertilizer is applied as needed in March of each year to maintain target foliar nutrient concentrations. Water treatments, which began in April, 1993, are (1) natural precipitation and (2) natural precipitation plus irrigation applied to maintain soil water content at greater than 3.0 cm soil water content in the surface 50 cm of soil (40% available water). The irrigation system consists of Rainbird irrigation nozzles on 35 cm risers spaced 10 m x 10 m apart. During each irrigation event, 2.5 cm of water is added to the plot. The system is operated on an as needed basis to maintain the target soil water level during the growing season.

A variety of parameters have been assessed over the six years since treatment imposition, including carbon pools and fluxes, water balance and tree water relations, microclimatic parameters, nutrient pools and fluxes, and phenology of above- and below-ground tree growth. These measurements have been synthesized in a number of manuscripts (Murthy *et al.* 1996, King *et al.* 1997, Murthy and Dougherty 1997, Murthy *et al.* 1997, Albaugh *et al.* 1998, Dougherty *et al.* 1998, Maier *et al.* 1998, Warren *et al.* 1998, Sampson and Allen in review) and are being integrated through our parameterization of the physiologically based production model BIOMASS (Sampson and Allen in review) and NUTREM, our Loblolly Pine Nutrient Use Model (Ducey and Allen 1997).

The optimum nutrition treatment has dramatically increased leaf area and stem volume growth each year since treatment imposition (Figures 1 and 2). By 1997, leaf area was increased by 100% (3.1 versus 1.5) and current annual volume growth by 150% (25 versus 10 m^3/ha/year) on fertilized as compared to non-fertilized plots. Surprisingly, irrigation has not had a significant effect on leaf area and has had only a very modest positive effect on volume increment. During two dry years (1993 and 1995), irrigation significantly increased annual stem wood volume growth (up to 30%), although these increases were much less than the gains observed due to fertilization alone. Interactions between fertilization and irrigation have not been significant in any year. Clearly, the native levels of nutrient availability on this site strongly limit production. What nutrients are actually limiting is uncertain; however, pretreatment foliar N, K, and B concentrations were below critical values for loblolly pine (Albaugh *et al.* 1998). Two of these elements, N and K, are commonly linked to leaf area production.

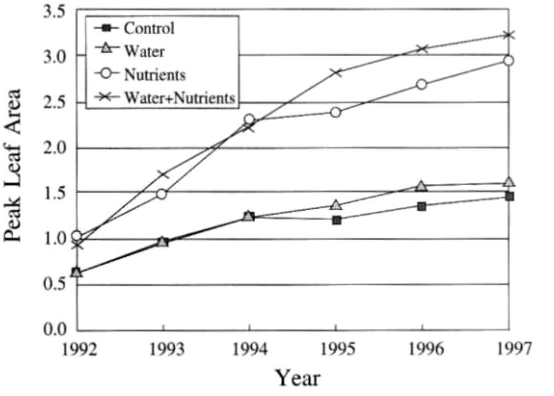

Figure 1. Effects of water and nutrient availability on peak leaf area at SETRES.

Efecto de la disponibilidad de agua y nutrientes sobre el área foliar máxima según SETRES.

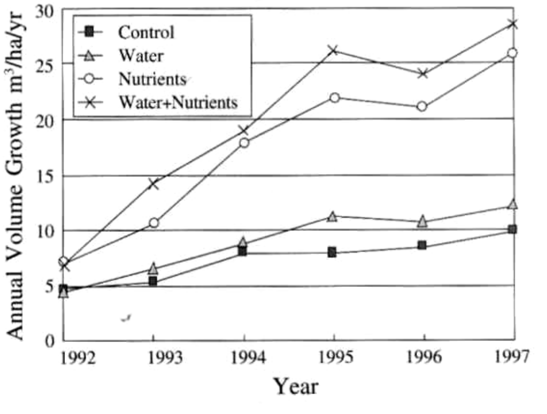

Figure 2. Effects of water and nutrient availability on current annual volume growth at SETRES.

Efecto de la disponibilidad de agua y nutrientes sobre el incremento anual corriente en volumen según SETRES.

The lack of a strong growth response to irrigation contrasts with results from the Biology of Forest Growth (BFG) study in Australia, where substantial increases in leaf area production and growth were observed with irrigation during dry years (Linder *et al.* 1987, Benson *et al.* 1992). On our site, the period of foliage production typically does not overlap with periods of low soil water. Complete recharge of soil water always occurs during the winter months prior to the initiation of foliage growth. At the BFG site, low soil water content did occur during the period of foliage production. Although our site has low water holding capacity, it usually has frequent growing season rains and relatively low evaporative demand such that the deep sandy profile apparently provides enough water to meet transpiration losses. We have also hypothesized that as higher leaf area levels were attained on fertilized plots, a positive interaction between irrigation and fertilization might develop (Albaugh *et al.* 1998). Such an effect was observed for *Eucalyptus* plantations on sandy sites in Portugal (Pereira *et al.* 1989). This interaction has yet to develop at our site, although leaf area levels on fertilized plots have now exceeded 3.0.

Even with the dramatic responses to resource additions, leaf area and volume growth remain strongly coupled throughout the six-years of study with leaf area accounting for ~90% of the variation in growth (Figure 3). In addition, stem volume growth efficiency was increased 20% and 8%, by fertilization and irrigation, respectively and their effects were additive. Growth efficiency increased from ~7 m^3 ha^{-1} yr^{-1} per unit of LAI in control plots to ~9 m^3 ha^{-1} yr^{-1} per unit of LAI in fertilized and irrigated plots (Albaugh *et al.* 1998). Similar gains were also found for annual biomass growth efficiency. The positive effect of treatment on growth efficiency results in part from the significant reduction in fine root production with fertilization and a concomitant increase in stem wood production. The allocation of total biomass production to fine roots was 10%, 8%, and 6% in fertilized plots and 25%, 22%, and 16% in nonfertilized plots in 1993, 1994, and 1995, respectively (Albaugh *et al.* 1998).

The change in partitioning among biomass components does not explain the observed increase in total biomass production efficiency. Murthy *et al.* (1996) found 26% higher photosynthesis rates in fertilized plots than in nonfertilized plots over the life of the 1993 foliage cohort. On the other hand, Maier *et al.* (1998) found increased stem (130%) and branch (40%) maintenance respiration rates with fertilization. Fine root respiration did not increase with fertilization or irrigation, but fine root respiration rates were up to 15 times greater than stem or branch respiration rates. Based on the observed changes in partitioning, photosynthesis rates, and respiration rates, we hypothesize that increased total production efficiency resulted when more biomass was allocated to foliage (photosynthesizing tissue) and less to fine roots (a high respiration rate tissue).

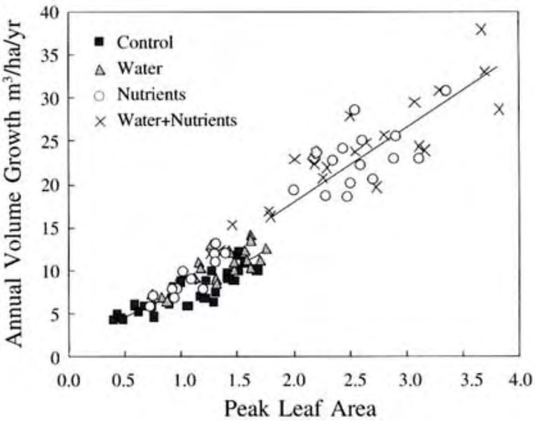

Figure 3. Relationship between current annual volume increment and leaf area at SETRES.
Relación entre incremento anual corriente en volumen y área foliar según SETRES.

Biomass and nutrient content determinations of above- and belowground components have been made every two years. These data, coupled with detailed annual inventory assessments, provide the basis for estimating nutrient content in the standing biomass as well as the annual nutrient use for current biomass production. By subtracting the amount of nutrients that are remobilized from previous year foliage, the amount of nutrients taken up from the soil on an annual basis can be estimated. These estimates of annual nutrient uptake provide the basis for defining the level of soil nutrient supply that will be required to maintain desired levels of production (Figure 4). Clearly, if high levels of production (>25 m^3/ha/year) are to be sustained, over 100 kg/ha/year of available N will be needed. Most soils are not able to provide this level of available N without N additions except during the first few years following site preparation (Allen *et al.* 1990). The actual fertilizer additions needed to maintain high rates of soil nutrient supply are now being addressed as part of a new Forest Nutrition Cooperative dose-frequency study.

Given the stage of stand development and existing site conditions, growth appears to be limited primarily by nutrients and secondarily by water. This finding contradicts conventional wisdom that would rank similar sites as poor candidates for N+P fertilization. The imposition of an optimum nutrition treatment, rather than N+P fertilization, is probably responsible for the strong response to

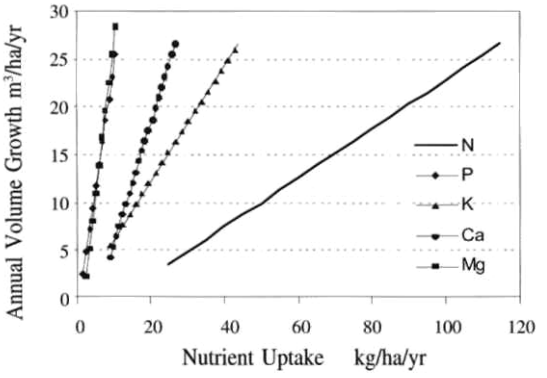

Figure 4. Relationships between current annual volume growth and nutrient uptake from soil.
Relación entre incremento anual del volumen y la absorción de nutrientes desde el suelo.

nutrient additions. The potential for applying a "complete" nutrition treatment to enhance growth on droughty sites is intriguing. The strategic importance of enhancing growth on sites that can be harvested under almost any condition without soil degradation cannot be overlooked.

FUTURE RESEARCH NEEDS

The growth potential for plantations in the southeastern United States is much higher than commonly thought just a few years ago. Our challenge now is to develop and implement the appropriate silvicultural systems to realize this potential in a cost effective and environmental sustainable way. To be successful will require a basic understanding of how resource availability limits forest production and how crop trees may differ in their ability to acquire and utilize these resources. Key challenges remaining include: understanding the relative contributions of water and nutrient limitations to stand productivity across a range of site and stand developmental conditions, developing the treatment regimes to ameliorate these limitations, and understanding the impacts of intensively managed plantations within a landscape context.

ACKNOWLEDGMENTS

This work contributes to the Global Change and Terrestrial Ecosystem (GCTE) core project of the International Geosphere-Biosphere Program (IGBP). We gratefully acknowledge the support provided by the USDA Forest Service Southern Forest Experiment Station, the Southern Global Change Program, the Department of Forestry, North Carolina State University, and members of the North Carolina State Forest Nutrition Cooperative. We greatly appreciate the dedicated efforts of the many staff and graduate students who have assisted in the field sampling and laboratory analyses aspects of this study.

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Recibido: 05.10.98.