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Biomass production physiology and soil carbon dynamics in short-rotation-grown *Populus deltoides* and *P. deltoides* × *P. nigra* hybrids

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ABSTRACT

Fast-growing woody species grown in dense, short-rotation plantations on land previously in agriculture offer potential economic benefits in products such as engineered construction material, boiler fuel, non-food-based biofuel feed stocks and other carbon (C)-based products and credits. However, information on the effects on major C pools of short-rotation culture is relatively sparse. In this study, *Populus deltoides* and *P. deltoides* × *P. nigra* hybrid clones were grown for 5 years at 1 m × 1 m spacing in plantations on a former pasture of high native fertility in the Missouri River floodplain in the lower Midwest U.S.A. Above- and below-ground biomass production, leaf area-based production efficiency, photosynthetic attributes and soil C dynamics were studied.

Populus clones yielded up to 70 Mg ha^{-1} over 5 years, results that compare favorably to poplar culture in other regions. *P. deltoides* clones yielded almost twice as much as hybrids (66.3 vs. 36.9 Mg ha^{-1}) despite more rapid early growth by the latter. Superior yields of *P. deltoides* clones were associated with greater (32–120%) production efficiency (total biomass yield per unit of time-integrated leaf area) and greater (17–42%) photosynthetic capacity, but not with differential allocation patterns of C above and below ground. Soil C losses were observed over 5 years, mostly from the top 12.5 cm of soil. Soil C loss in this study was associated with conversion from organic matter input-rich pasture culture, and subsequent rotations might not be accompanied by losses of the magnitude observed in the first. Net C sequestration in measured carbon stocks ranged from 11.4 to 33.5 Mg ha^{-1} in the two plantations.

1. Introduction

Rates of growth in *Populus* species are among the fastest of deciduous hardwood tree species and unequaled by most north-temperate woody plants (Dickmann et al., 1992). Members of the *Populus* genus are capable of quickly producing large amounts of valuable wood products (Zsuffa et al., 1977; Heilman, 1999; Zhang et al., 2003). There also is increasing interest in poplar wood for use in long-term storage products such as lumber and oriented strand board and as a carbon-neutral, non-food-based replacement for fossils fuels in energy production (Vitousek, 1991). Poplar species are particularly attractive for short-rotation intensive plantation culture (Ceulemans et al., 1992). Short-rotation production systems employ densely planted, rapidly growing woody plants to produce a simple dry matter product as opposed to traditional forest management where the emphasis is often on more widely spaced, naturally regenerated trees tended over many decades to produce dimension lumber and plywood.

From a production physiology perspective, a plant's capacity to intercept solar radiation and convert it into usable energy is critical to biomass accumulation (Landsberg, 1986). Biomass production has been linearly related to the radiant energy intercepted by the foliage in agricultural crops and forest stands (Monteith, 1981; Cannell et al., 1988). The fraction of light intercepted by the canopy is largely controlled by the amount of foliage and canopy architecture (Cannell, 1989). The ratio with which an organism converts radiant energy into biomass is defined as light-use efficiency (LUE) or conversion efficiency (Heilman et al., 1996). Canopy components that influence LUE include leaf area index (LAI), leaf area duration (LAD), leaf and branch morphology and their orientation, and photosynthetic attributes of the foliage (Isebrands et al., 1983). These attributes, as well as plantation spacing, determine how quickly short-rotation plantations achieve canopy closure and how full and photosynthetically capable those canopies are, key requisites for successful plantation establishment and growth (Cannell et al., 1988; Heilman and Xie, 1994; Harrington et al., 1997). An indirectly related but important factor

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contributing to biomass productivity is the pattern of photosynthate partitioning between the roots and shoot (Tschaplinski and Blake, 1989). Assimilate partitioning is a complex process that involves morphological, environmental, managerial, and physiological events (Gifford and Evans, 1981; Keyes and Grier, 1981). In order for optimum growth of harvestable material, a balance must exist between plant growth supporting absorption (roots) and production (leaves and supporting tissues) (Ledig and Perry, 1965; Ledig et al., 1970), along with adequate resource availability (light, nutrients and water, which are influenced by plant density) and competition control (Albaugh et al., 1998).

Genetic variation in leaf area formation and display, allocation and photosynthetic traits has been linked with differential productivity in *Populus* (Tschaplinski and Blake, 1989; Milne et al., 1992; Green et al., 2001). Hence it is desirable and necessary, in any research program aimed at deployment of superior genotypes, to screen a variety of clones for performance. Identification of physiological mechanisms contributing to clonal differences in productivity strengthens confidence in clone selection decisions and can inform tree improvement efforts.

Given the documented capacity of poplar plantings to fix substantial amounts of CO_2, there are potential roles for *Populus* and other short-rotation intensive culture crops in sequestering atmospheric C by storing it in terrestrial pools, such as plant biomass and soil (Markewich and Buell, 2005). A combination of land clearing through traditional agriculture, deforestation, and most recently, increased development, have resulted in large increases of atmospheric C over the past century (Vitousek, 1991). Soils are the largest land pool of C, accounting for approximately 80% of all terrestrial carbon (Sartori et al., 2006), Short-rotation plantations of *Populus* can rapidly accrete C in stable components such as stems, branches and coarse roots, while at the same time cycling C and nutrients to the soil through more labile litter pools consisting of leaves twigs and fine roots (Grigal and Berguson, 1998; Berthelot et al., 2000; Sartori et al., 2006; Meiresonne et al., 2007). Various patterns of change in soil C have been associated with short-rotation tree plantations, including transient losses (Hansen, 1993), subsequent gains (Hansen, 1993; Makeschin, 1994) and no change (Ulzen-Appiah et al., 2000). One important variable in tree plantation culture as it relates to soil C sequestration is rotation length. As rotation length shortens, soil C may decrease, resulting in a long-term decline if frequent harvests result in extensive soil disturbance (Harrison et al., 1995; Grigal and Berguson, 1998; Turner and Lambert, 2000; Paul et al., 2002; Russell et al., 2004; Sartori et al., 2006). Thus, changes in soil C in short-rotation culture must be weighed against biomass production capability in any C sequestration accounting scheme.

The objectives of this research were to: (1) evaluate biomass production in dense, short-rotation plantations of *Populus* spp. in the lower Midwest U.S.A., (2) relate allocational, physiological and canopy attributes to any observed clonal variation in production capacity, and (3) examine soil C changes associated with plantation culture and integrate these data into an assessment of the impact of plantation culture on major C stocks. These results expand an earlier report of 2-year growth patterns in one of the plantations described here (Pallardy et al., 2003).

2. Methods and materials

2.1. Site description and plantation design

The study site was a former tall fescue (*Festuca arundinacea* Schreb.) pasture on the Missouri River floodplain at the University of Missouri's Horticulture and Agroforestry Research Center at New Franklin, MO, U.S.A. (Lat. 39°01′N, Long. 92°46′W). Soil at the site is a Nodaway silt loam (fine-silty, mesic, Mollic Udifluvent) (Grogger et al., 1978). This soil is fertile, moderately well drained and permeable with 0–5% slope, low surface runoff and occasionally flooded. Depth to water table is 90–150 cm. Pre-planting soil analysis (Nathan et al., 2006) indicated that high soil fertility levels were present ($NO_3^{-} + NH_4^{+} = 12.2 \pm 2.3$ ppm (SE, $n = 6$); Bray 1-P = 29.4 ± 4.0 ppm; K = 203 ± 40 ppm) and no fertilizer was applied during the study.

Two plantings were established about a year apart (early May 1999 and mid-April 2000) and about 100 m distant to provide replication and some idea of variation across sites. Hardwood cuttings (20 cm long) of three eastern cottonwood (*Populus deltoides* Bartr.) and two *P. deltoides* Bartr. × *Populus nigra* L. hybrid clones (Table 1) were selected for planting. Hybrid clone I45/51 is recommended for and widely planted in the upper Midwest and eugeneii is a commonly studied clone in North America; the three *P. deltoides* clones were collected by the Missouri Department of Conservation and distributed through the state tree nursery. A randomized complete block design similar to that of Scarascia-Mugnozza et al. (1997) was laid out, with six (1999) and five (2000) blocks, each consisting of four (1999) or five (2000) single-clone plots (7 rows × 10 columns). As noted below, loss of some plots to mortality resulted in an unbalanced incomplete block design. Spacing was 1 m × 1 m (10,000 trees ha^{-1}).

Before planting, sites were treated with a non-selective herbicide to eliminate grass competition to establishing cuttings. Post-planting irrigation from a nearby slough was applied to support rooting and establishment in both plantations, but some mortality of plants did occur, particularly in 1999. As it was important to obtain complete plots for a homogeneous growth environment, dead plants were replaced with potted cuttings or cuttings transplanted from other blocks to obtain a complete 10 × 7 matrix for each retained plot. This reduced the number of plots available to between 2 and 6 per clone in the 1999 plantation (2 for clone 26C6R51, 3 for 2019, 5 for 1112 and 6 for I45/51). Only one plot (of clone 26C26R51) in the 2000 plantation had insufficient survival to prevent inclusion in the analysis. Periodic irrigation was continued through the first season of the 1999 plantation because of seasonal drought (Table 2); the growing season of 2000 was wetter and irrigation was discontinued after establishment. There was no irrigation applied during the second through fifth years in either plantation. In the year of establish-

Table 1
Origin and source information for five *Populus* clones grown in a short-rotation plantation

Clone	Parentage	Source	Origin	Latitude	Longitude
145/51	*P. deltoides* × *P. nigra*	Iowa State Tree Nursery	–	–	–
Eugeneii	*P. deltoides* × *P. nigra*	Iowa State Tree Nursery	–	–	–
26C6R51	*P. deltoides*	MDC[a] Nursery	Pope County, IL	37°35′N	88°34′W
2059	*P. deltoides*	MDC Nursery	Osage County, MO	38°27′N	91°52′W
1112	*P. deltoides*	MDC Nursery	New Madrid County, MO	36°35′N	89°37′W

[a] MDC: Missouri Department of Conservation.