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Contrasting effects of flooding on tree growth and stand density determine aboveground production, in baldcypress forests

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ABSTRACT

Stand production, a common indicator of site productivity, is often low in flooded wetland forests. However, it remains unclear whether the low production reflects flood stress limiting tree growth, flood disturbance limiting tree density, or both. Here, we investigate how tree growth and stand density vary in baldcypress forests, across gradients of flooding by both fresh and saline waters. We used three investigations to conduct this analysis: (a) a meta-analysis of previously reported tree- and stand-production measurements; (b) an analysis of tree cores from 204 baldcypress trees in 16 sites; and (c) intensive stand surveys and growth measurements across two freshwater flooding gradients in southern Louisiana. The meta-analysis (a) showed that stand production generally varies linearly with stand density, and that detrimental effects of flooding on tree-level growth are only consistently evident in saline systems. The tree-core investigation (b) showed that tree basal area growth was largely a function of tree sapwood area, but basal area growth per sapwood area (i.e. sapwood efficiency, a measure of how efficiently trees grow per growing space occupied) was higher in the more flooded sites of freshwater gradients and lower in the more saline sites of salinity gradients. The intensively studied sites (c) showed that deeper flooding was associated with sparse stands with lower production; however, trees in those sparser sites had higher sapwood efficiency, implying that the benefits of reduced competition were greater than any potential physiological limitations caused by that deeper flooding. Our findings generally show that sparser stands with saline flooding contained poorly growing trees, but sparser stands with freshwater flooding generally did not. These dichotomous effects of freshwater flooding on tree growth versus stand density demonstrate the need to conceptualize production as a dual function of disturbance effects on stand structure and environmental limitations on individual trees, each with potentially different limiting factors.

1. Introduction

The effects of climatic conditions and other exogenous factors on forest ecosystems are often measured in terms of stand production. Differences in stand production are often interpreted as differences in the production potential of the site, i.e., productivity. Whereas productivity is a property of the site, production is a dual function of the density of individuals and the growth of individuals (Fig. 1), which are controlled by different, but often interrelated factors. Changes in stand density occur by self-thinning, where competition-induced mortality removes individuals from crowded stands of growing trees (Long et al., 2004), or by exogenous disturbance factors that kill trees. While some disturbances, such as drought, affect stand density and also limit tree growth (Anderegg et al., 2013), others, such as fire or grazing, decrease stand density without limiting tree growth (Peterson and Reich, 2001; Riginos, 2009). When disturbances release individual trees from competition, the redistribution of resources among fewer individuals can increase individual tree growth, even where stand production is reduced by disturbance (Connell et al., 1984); equivalent rates of production may arise from multiple alternative stand conditions (Fig. 1). The relative roles of environmental factors as either stand disturbances or tree-growth limitations are often neglected when production is quantified and reported as a stand-integrated measure. Reconciling the potentially contrasting effects of environmental factors on tree growth versus stand density is necessary for interpreting the state and trajectory of forests.

The dichotomy between stand production and individual tree growth is a basic principle in silviculture (Assman, 1970; Long et al., 2004). Thinning decreases competition so more resources are available to individual trees. Forestry studies clearly show that stand production

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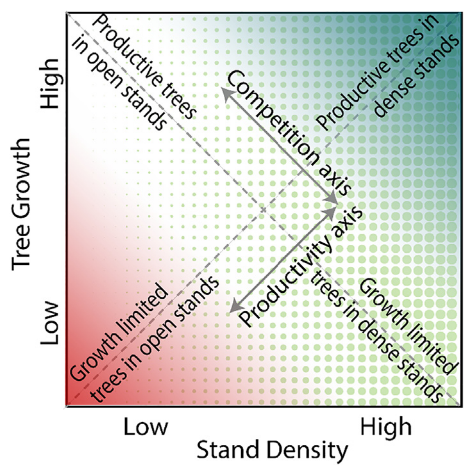

Fig. 1. Variability in stand production among sites is a product of both stand density and individual tree growth, which are often orthogonal to each other but inherently related. The red-blue gradient marks variations attributable to differences in site productivity, rather than those related to stand structure. For a given productivity, a site could be sparsely stocked with trees that grow quickly because competition is low or densely stocked with trees that grow slowly because competition is intense. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

increases with increased utilization of growing space (expressed in terms of stand density), with a concomitant decrease in average tree growth (Long, 1985), or growth per unit area (i.e., efficiency; Brix, 1983; Waring et al., 1981). Density reduction by natural disturbance agents logically has the same effect on stand production and individual tree growth as artificial stand thinning, unless the disturbance agent also creates a physiological stress that depresses tree growth.

How stand density, tree growth, and stand production relate to each other in forested wetlands is an open question. A defining feature of wetlands is that flooding alters the quality of growing conditions and causes disturbances. Saline flooding, especially in freshwater forests, generally inhibits growth (Allen et al., 1996). Freshwater flooding can act as a subsidy to trees, for example by alleviating water deficits (Allen et al., 2016), or as a stressor, by causing hypoxia (Parolin and Wittmann, 2010; Rodríguez-González et al., 2010). Flooding also affects soil chemistry and nutrient availability, which can have diverse effects on production (Burke et al., 1999). The potential for flooding to augment or suppress ecosystem production has been described in the subsidy-stress hypothesis (Odum et al., 1979), but within its context or that of other ecosystem-level concepts, many studies in forested wetlands have used *stand* production measurements to infer both *stand* and *tree* conditions (Clawson et al., 2001; Megonigal et al., 1997; Middleton and McKee, 2004). However, stand production measurements are insufficient for understanding flooding effects on trees if density variations are neglected (Fig. 1). Freshwater and saline flooding suppress stand density by limiting regeneration and causing mortality (Broadfoot and Williston, 1973; Conner et al., 1986; Middleton, 2008; Krauss et al., 2009), constituting a disturbance. Therefore, the link between stand production and stress status of individual trees is only circumstantial until tree-level growth is also examined simultaneously.

Analyzing the separate influences of flooding on stands and trees may be especially important in understanding forests with tree species that have evolved to be morphologically and physiologically adapted to flooding. For example, baldcypress (*Taxodium distichum* (L.) Rich var. *distichum*) is one of the most flood-tolerant, freshwater tree species so it can persist and grow vigorously in severely flooded conditions where other species have died (i.e., a disturbed stand). Baldcypress will also tolerate mesohaline flooding, albeit not necessarily with vigorous growth (Krauss et al., 2009), that kills most other tree species. Identifying which flooding conditions are stressful to baldcypress trees is important because stands generally transition to marsh or open water beyond its physiological limits (Shaffer et al., 2009); elsewhere, sparse baldcypress stands may appear to be degrading, but growing conditions for the surviving trees may improve, in accordance with the trade-off between stand density and individual tree growth. For example, at one site where Megonigal et al. (1997) inferred tree stress from low stand production, flood-tolerant baldcypress trees grew especially well (Conner et al., 1993). At the same site, a later study found that per-tree growth of baldcypress increased over the subsequent two decades, despite decreases in stand density due to mortality of other species with increased flooding (Conner et al., 2014). This example illustrates how compensating growth effects in response to disturbances can complicate inferring tree-level stress effects from stand production.

In this work, we seek to understand the potentially dichotomous effects of flooding (freshwater and saline) on stand versus tree growth in forested wetlands. We focus on baldcypress-dominated forests in the cypress-tupelo (i.e., water tupelo; *Nyssa aquatica* L.) community, which extensively occurs in low-lying flooded regions of the southeastern United States. First, we deduced patterns of stand production expected to result from alternative hypothetical effects of flooding on how growing space is occupied and how vigorously trees grow within the space they occupy (Section 2). Then, we examined density, production, and growth patterns in three investigations: a meta-analysis of tree growth and stand production (*Investigation A*), a tree-ring study comparing growth per unit sapwood area (*Investigation B*), and an intensive study of both tree and stand growth across two flooding gradients (*Investigation C*). The three investigations were used to address these questions about flooded cypress-tupelo forests: Are variations in stand production driven by disturbance-related density differences, or by differences in how vigorously trees grow (*Investigation A*), and how does intense flooding affect individual-tree growing conditions (*Investigation B*), especially in sites where flooding disturbs stand density (*Investigation C*)? Investigations A and B focus on both freshwater and saline flooding gradients, which we hypothesize differently affect tree growing conditions and thus also the relationship between density and stand production.

2. A Framework for comparing tree growing conditions and stand production across sites

In addition to many environmental factors, tree size and stand density (and competition intensity) are also important drivers of tree growth. To compare the effects of environmental factors on tree growth, analyses should control for the growing space occupied by a tree. However, common size metrics such as diameter at breast height are not ideal because they reflect developmental history and age; for example, leaf area is a better measure of growing space occupied by a tree because it represents potential light acquisition. To infer the effects of environmental factors on individual tree growth, the effects of density and competition on resource availability must also be considered (Long et al., 2004). The relationships among tree growth, stand structure, and stand production have been explored elsewhere (e.g., Binkley et al., 2013; Roberts et al., 1993); here, our objective is to develop an applicable framework for assessing how environmental factors affect individual tree growing conditions, using growth metrics and analytical approaches that account for tree-size and stand-density effects.

A well-suited diagnostic metric is tree annual basal area increment (BAI_{tree}) per sapwood area (Waring et al., 1980), here referred to as sapwood efficiency (E_{SA}). E_{SA} approximates growth per canopy growing space occupied (O'Hara, 1988), because it is functionally related to tree leaf area (Waring et al., 1982; Whitehead et al., 1984), although that relationship is partially site dependent (Dean et al., 1988; McDowell et al., 2007). Vigorously growing trees produce highly permeable sapwood (Coyea and Margolis, 1992; Dean, 1991; Reid et al., 2003; Shelburne et al., 1993) that is more effective at supplying water to