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Wetland-tree growth responses to hydrologic variability derived from development and optimization of a non-linear radial growth model

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A R T I C L E I N F O

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A B S T R A C T

Growth responses of wetland trees to flooding and climate variations are a critical link in hydrological control of wetland carbon budgets, but they are difficult to model because they depend on multiple interacting and nonlinear factors. To more generally understand hydrological influence on tree growth, we modeled non-linear responses of tree ring growth to flooding and climate at sub-annual time steps using a new model employing Vaganov-Shashkin response functions. The model was developed and calibrated to explain six baldcypress tree-ring chronologies from two hydrologically distinct sites in southern Louisiana. The model outperformed traditional multiple linear regression. More importantly, optimized response parameters were similar among sites with different hydrologic conditions and consistent across time periods, suggesting generality to the response functions. Model forms that included hysteretic growth responses to flooding performed better than those without, indicating that wetland tree responses to present hydrologic conditions vary with previous hydrologic conditions. Optimal parameter values suggested that growth inhibition by flooding was rare and lower water levels were more often limiting.

1. Introduction

The interaction between vegetation and hydrological variability underlies wetland ecosystem structure and function (e.g., Junk et al., 1989; van der Valk, 1981). However, inferring vegetation responses to this hydrologic variability is a challenge (Rodriguez-Iturbe et al., 2007) because of the multiple dimensions of potential responses to hydrologic variability that itself is difficult to characterize qualitatively or quantitatively (Nuttle, 1997). These hurdles impede inter-site and inter-study comparisons that are needed to formulate a generalized understanding of wetland vegetation responses, which is important for predicting ecosystem responses to changing hydrological and climatic regimes.

In forested wetlands, a particularly important and recurrent question is when flooding becomes stressful to vegetation. At the ecosystem scale, several studies (Mitsch et al., 1991; Odum et al., 1979; Rodríguez-González et al., 2010) have concluded that pulsed, shallow flooding enhances production, and stagnant or deep flooding limits production, but this relationship does not universally apply (Megonigal et al., 1997). At the plant scale, both flood-stress and drought-stress effects reduce stomatal conductance, growth, and leaf area (Nash and Graves, 1993; Pezeshki and Chambers, 1986), with effects exacerbated by high temperatures (McLeod et al., 1986). Detrimental effects from flooding may be reduced by acclimation to stressors (Anderson and Pezeshki, 2001), and thus relationships between flooding and plant responses may vary in time because of plant morphological adjustments to environmental variations. However, most ecophysiological responses have been measured in seedlings or saplings, and studies of mature trees (including the same species) have not always shown flooding to be detrimental (Allen et al., 2016; Duberstein et al., 2013). Tree rings are another source of information on tree responses to flooding, and have generally shown that growth correlates positively with high water over timescales less than a few years (Day et al., 2012; Ford and Brooks, 2002; Keim et al., 2012), but longer periods of high water lead to lower growth (Keim et al., 2012; Keim and Amos, 2012; Young et al., 1995). Further investigation is required to resolve apparent inconsistencies across these study results, and to better understand which aspects of flooding influence tree growth the most.

Tree ring records contain a wealth of ecological information, but conventional dendrochronological methods may not be ideal for interpreting environmental effects on tree growth, especially flooding in wetlands. A conventional approach is to fit linear regression

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models of ring chronologies from potentially dozens of monthly, seasonal, and annual climate metrics (Speer 2010). Many such analyses are based on expectations of water limited growth in upland forests (Fritts, 2001), which cannot be assumed for wetlands. There are important reasons to investigate alternative model structures, especially in wetlands. First, climate-growth relationships are often non-monotonic, especially for flooding in wetlands (Mitsch and Gosselink, 2007). Second, linear modeling approaches are often based on a single static response to the full suite of conditions during a year, which impedes representation of non-stationary and interacting responses to dynamically varying conditions (Vaganov et al., 2006a). These assumptions are potentially particularly problematic for wetland trees because of non-stationarity in responses to stressors such as occur upon morphological adjustment to flooding (Anderson and Pezeshki, 2001; Kozlowski, 1997).

The so-called Vaganov-Shashkin type models (Vaganov et al., 2006a, 2006b) are an alternative method for analyzing tree rings that allows more complex behavior to be easily incorporated (e.g., non-linear responses, interactions among drivers, and sub-annual variations), thereby avoiding some of the shortcomings associated with linear models (Hughes, 2002). The full VS model (Vaganov et al., 2006a, 2006b) aggregates growth as the sum of periodic responses to meteorological inputs that modify the production rate and physical attributes of xylem elements. For a simpler alternative to VS, Vaganov et al. (2006a) developed a dendrochronologically oriented model by replacing cambium-cell-process representation with growth response functions to temperature and soil water availability; Tolwinski-Ward et al. (2011) referred to this model as VS-Lite. Both VS and VS-Lite employ the principle of Leibig's Law of the Minimum, which holds that growth is limited by the single most-limiting factor. In contrast, growth models based on multivariate explanatory variables, such as multiple linear regressions or principal-component response functions (Briffa and Cook, 1990), model growth as a function of multiple controlling factors simultaneously. It is not necessary for VS-based models to assume a single limiting factor, so it is worthwhile to investigate whether that assumption improves models of tree growth or whether modeling interactions of factors is more efficacious.

In this study, the VS-Lite framework is used to develop a model of radial growth responses to monthly environmental conditions specific to wetlands (VSL-Wet). Our overarching objectives are to better understand the nature of wetland tree responses to water level variations and to further develop the conceptual basis of the VS-Lite framework. Our approach was to develop a simple, deterministic model that can predict growth and be optimized to clarify underlying tree-growth behavior. The model was developed by validating against six baldcypress (*Taxodium distichum* (L.) Rich. var. *distichum*) chronologies, a species that often occupies frequently flooded sites. Chronologies were across two wetlands—one connected to and one disconnected from the Atchafalaya River, USA—with distinctly different water level variability. Model form varied by including and omitting parameters representing concepts that we hypothesize may be important to explaining growth in wetlands: (1) non-linear versus linear growth responses, (2) water level and temperature independently controlling growth, or with interaction effects, and (3) static growth responses to water level versus hysteretic growth responses that depend on both present and past hydrologic conditions. Analyses tested VSL-Wet performance, compared fit with linear-regression models, and determined parameter set generalizability across sites and years. To drive the model we used monthly temperature, water level, and potential solar radiation, recognizing these as commonly important factors with readily available data. The goal of the model is to evaluate the model form and attempt to isolate hydrological effects rather than comprehensively modeling tree growth, which would require accounting for other factors that have been shown to limit baldcypress growth (e.g., nutrients and pests; Effler et al., 2007).

2. VSL-Wet model

2.1. Theory and development

VSL-Wet was designed similarly to the upland-oriented VS-Lite, being based on monthly radial growth responses to two non-linear growth response functions, but modified to wetland considerations:

$$G(y) = \sum_{m=1}^{12} g_E(m) \times f[g_W(m, y),\ g_T(m, y)], \tag{1}$$

where G is radial growth increment (ring width) of year y, g_E is a solar energy function that varies by month m (Vaganov et al., 2006a) and represents the maximum potential growth, g_W is a growth response function to water depth, and g_T is a growth response function to temperature. Values of g_E, g_W, and g_T range from zero to one. The primary differences between Eq. (1) (VSL-Wet) and the VSL model are that, in VSL-Wet, the interaction of g_W and g_T is not set (Section 2.2), and there is a growth response function for water level instead of soil moisture (Fig. 1).

Both high and low water depths (W) and temperatures (T) may limit growth. Thus, the growth response function to water level, g_W, was defined with lower ($w2$) and upper ($w3$) inflection points beyond which growth is reduced and lower ($w1$) and upper ($w4$) inflection points beyond which growth is zero (Fig. 1), consistent with previous similar models (Vaganov et al., 2006b), as

$$g_W(m, y) = \begin{cases} 0, & \text{if } W(m, y) \le w1 \\ 0, & \text{if } W(m, y) \ge w4 \\ 1, & \text{if } w2 \le W(m, y) \le w3 \\ \dfrac{W(m, y) - w1}{w2 - w1}, & \text{if } w1 < W(m, y) < w2 \\ \dfrac{W(m, y) - w4}{w3 - w4}, & \text{if } w3 < W(m, y) < w4 \end{cases}, \tag{2}$$

where W is water level of month m and year y. In parallel, the growth response function to temperature, g_T, was defined as

$$g_T(m, y) = \begin{cases} 0, & \text{if } T(m, y) \le t1 \\ 0, & \text{if } T(m, y) \ge t4 \\ 1, & \text{if } t2 \le T(m, y) \le t3 \\ \dfrac{T(m, y) - t1}{t2 - t1}, & \text{if } t1 < T(m, y) < t2 \\ \dfrac{T(m, y) - t4}{t3 - t4}, & \text{if } t3 < T(m, y) < t4 \end{cases}. \tag{3}$$

Terms $w1$, $w2$, $w3$, $w4$, $t1$, $t2$, $t3$, and $t4$ are free parameters (Fig. 1, Table 1) with values between each site's minimum and maximum monthly T or W. Benefits of the piece-wise trapezoidal function include the flexibility to take on many shapes, including the full range of triangular and monotonic functions, so that this modeling approach is applicable in a range of systems with varying environmental controls. While the model presented here has important distinctions from previously proposed VS and VSL models, many details regarding the general versatility of this framework have been previously discussed in detail (Vaganov et al., 2006a).

2.2. Candidate models and associated hypothesis tests

Multiple candidate models were tested to find the best representation of the measured data. Candidate models omitted or included several model options (terms in parentheses are how candidate models are referenced thoughout): g_W and g_T interactions