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

Scott T. Allen*

Richard F. Keim

School of Renewable Natural Resources, Louisiana State University, Baton Rouge, LA, USA.

*Corresponding Author

Abstract: 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 varying hydrological 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 vary with recent hydrologic conditions. Optimal parameter values suggested that growth inhibition by flooding was rare and lower water levels were more often limiting.

Keywords: wetland ecology; baldcypress; dendroecology; law of the minimum

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 (Nuttall, 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

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 (VS; 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:

$$G_{y=m} = 1/2 g_E m \times f g_W m, y, g_T m, y, \quad (1)$$

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 (Figure 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 (Figure 1), consistent with previous similar models (Vaganov et al., 2006b), as

$$g_W(m,y) = \begin{cases} 0, & \text{if } W_{m,y} \leq w1 \\ 0, & \text{if } W_{m,y} \geq w4 \\ 1, & \text{if } w2 \leq W_{m,y} \leq w3 \\ W_{m,y} - w1, & \text{if } w1 < W_{m,y} < w2 \\ w3 - W_{m,y}, & \text{if } w3 < W_{m,y} < w4 \end{cases} \quad (2)$$

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

$$g_T(m,y) = \begin{cases} 0, & \text{if } T_{m,y} \leq t1 \\ 0, & \text{if } T_{m,y} \geq t4 \\ 1, & \text{if } t2 \leq T_{m,y} \leq t3 \\ T_{m,y} - t1, & \text{if } t1 < T_{m,y} < t2 \\ t4 - T_{m,y}, & \text{if } t3 < T_{m,y} < t4 \end{cases} \quad (3)$$

Terms $w1$, $w2$, $w3$, $w4$, $t1$, $t2$, $t3$, and $t4$ are free parameters (Figure 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 throughout): g_W and g_T interactions (*multiplicative*, *additive*, *minimum*, *univariate-W*, or *univariate-T*); number of free parameters defining g_W and g_T functions (*two-parameter* or *four-parameter*); and, whether a growing-season shift parameter was included (*seasonal shift*), filtered W levels were used (*filtered-W*), both (*seasonal shift* and *filtered-W*), or neither parameter was used so that W values were fixed and growing season was fixed and not defined by free parameters (*fixed*). Candidate models were tested by optimizing iteratively for all combinations of model options (i.e., full-factorial design) so that all possible models and component interactions were evaluated (Table 2).

The interaction of growth response functions was tested by comparing models using the product of g_T and g_W , addition of g_T and g_W weighted by a free parameter cI , minimum of g_T and g_W , and univariate models of g_T or g_W alone:

$$\text{Multiplicative: } G(y)=m=112 \quad gE(m) \times [gW(m,y) \times gT(m,y)] , \quad (4)$$

$$\text{Additive: } G(y)=m=112 \quad gE(m) \times [cI \times gW(m,y) + (1-cI) \times gT(m,y)] , \quad (5)$$

$$\text{Minimum: } G(y)=m=112 \quad gE(m) \times \min \{ gW(m,y), gT(m,y) \} , \quad (6)$$

$$\text{Univariate-}W: G(y)=m=112 \quad gE(m) \times gW(m,y), \text{ and} \quad (7)$$

$$\text{Univariate-}T: G(y)=m=112 \quad gE(m) \times gT(m,y). \quad (8)$$

The form for response functions (g) was also evaluated by comparing the performance of simpler, two-free-parameter forms to four-parameter versions (Eqs. 2 and 3). To simplify, the lower (wI , tI) and upper inflection points ($w4$, $t4$) respectively equaled the minima and maxima of monthly W and T . Consequently, g_W and g_T were forced to zero for months with maximum and minimum W and T values.

Similar to Tolwinski-Ward et al. (2011), we tested a growing-season shift parameter to account for part of one year's growth to be a product of the previous year's conditions and responses. Because baldcypress is deciduous with a winter leaf-off period of mid-November to mid-March (Eggler, 1955; MacClurkin, 1965), g_E was set to zero for December through February and set to half of solar-geometry defined values for March and November yielding g_E values between 0.25 in November and 1.0 in June. A free parameter, s , defined which fixed-width 12-month growing period window contributed to each ring. Four growing season intervals contributing to a ring were tested when seasonal shift parameter, s , was included: Mar_y to Nov_y ($s = 0$, equal to when s was omitted), Nov_{y-1} to Oct_y ($s = 1$), Oct_{y-1} to Sept_y ($s = 2$), or Sept_{y-1} to Aug_y ($s = 3$).

To examine the importance of hysteretic growth responses to water level, as expected with tree morphologic plasticity, model performance was compared between conditioning growth responses to raw W and to high-pass filtered W . The high-pass filtering created a time series of water level deviations from recent longer-term means, and was executed using a square window with width defined through optimizing the free parameter n (with $n = 1, 2, \dots, 10$ years). This is a computationally simpler but mathematically equivalent procedure to defining wI , $w2$, $w3$, and $w4$ with respect to mean W over the previous n years.

3 METHODS

3.1 Study Sites and Environmental Data

Six study plots were in two hydrologically distinct sites—the Atchafalaya Basin (Atch) at Grand Lake and Verret Basin—that are extensive baldcypress-tupelo swamps in southern Louisiana (Figure 2). While both are within the former Atchafalaya River basin, now levees disconnect Lake Verret plots from Atchafalaya River flows (Figure 2), decreasing water level variability and sediment and nutrient inputs (DeLaune et al., 1987). In contrast, Atch plots are within the Grand Lake area in the active floodplain of the Atchafalaya River, a distributary of the Mississippi River. Trees in the sampled stands were established between 1798 and 1902 CE (Keim and Amos, 2012).

All Lake Verret plots—Attakapas Landing (AT; 29° 51' 14" N, 91° 05' 50" W) Godchaux Canal (GC; 29° 56' 14" N, 91° 7' 41" W), and Elm Hall Wildlife Management Area (EH; 29° 55' 36" N, 91° 8' 18" W)—were within 10 km of each other and all Atchafalaya sites—Six Mile Lake (SM; 29° 47' 27" N, 91° 24' 17" W), Verdunville landing (VU; 29° 46' 4" N, 91° 23' 44" W), and Gray Horse Island (GH; 29° 45' 30" N, 91° 22' 56" W)—were within approximately 5 km of each other. Of the Verret sites, GC was the deepest flooded with mean water level over the study period (1955-2004) of 0.81 m, compared to 0.29 m at AT and 0.19 m at EH. Of the Atch sites, the three were more similar, with mean flooding depths of 0.79, 0.87, and 0.72 m in SM, VU, and GH respectively. Elevation differed among plots, resulting in differences in flood frequency, depth, and duration within sites (Figures 3, 4). We developed plot-specific hydrographs from 1955 to 2004 from long term water level records in nearby lakes; this was possible because standing water extended from plots to the gauges most of the time (Keim and Amos, 2012). Temperature data (Figure 4C) were regional climate data published by the National Climatic Data Center, so temperature data were the same for all sites. Temperatures and water levels were monthly means of daily mean values. More details on sites, water level records, and climate records were described by Keim and Amos (2012).

3.2 Tree Ring Analysis

Baldcypress is ideal for dendroecological study because its growth is highly responsive to climate variations (Stahle et al., 1985). We used the same sample trees, cores, measurements, and cross dating techniques as presented by Keim and Amos (2012). For each of the six plots, 10 or

11 co-dominant baldcypress trees were sampled, with two cores from each tree at 3 m above ground level to be above stem buttressing. Conventional methods were used for preparing and measuring cores, and the statistical software Cofecha was used to verify cross-dating (Speer, 2010).

Ring data were compiled into plot-specific chronologies from 1955-2004 as the mean of detrended, whitened time series of ring widths from individual trees. Ring-width time series were detrended as ratios of ring width to a fitted spline using ARSTAN software, which extracts interannual environmental effects rather than longer-term variations in growth related to competition, disturbance, or inherent tree radial growth patterns (Cook, 1985). A 20-year spline with spline parameter of 0.5 (Figure 5) was selected because of the short hydrologic record and our interest in annual responses rather than long term signals. Autoregressive signals from ring-width time series were also removed with ARSTAN. These procedures differed from that used by Keim and Amos (2012), due to this study's focus on year-to-year variations, rather than long term trends. All ARSTAN chronologies were also normally distributed (Shapiro-Wilk test; $\alpha = 0.05$) and were normalized by subtracting the mean and dividing by the standard deviation (over the 50-year periods) so that both VSL-Wet output and normalized chronologies had the same distribution and domain (mean of zero, standard deviation of one). Here forward, all analyses were only applied to the processed 1955-2004 segments, referred to as site chronologies.

3.3 Model assessment and analysis

Model performance, sensitivity, and parameterizations were analyzed through Monte-Carlo iteration of random parameter sets. The ranges of values for the parameters defining g_w and g_T were the ranges of W and T observed. For each candidate model, 100,000 iterations of random parameter combinations were tested; for both *filtered-W* and *seasonal shift* models, 100,000 runs were performed for each value of n (0-10) and s (0-3).

The Akaike Information Criterion (AIC) for normally distributed data (Burnham and Anderson, 1998) was used to select appropriate model form because it is an assessment of fit that also penalizes for the number of parameters. The Pearson correlation coefficient, R , was used as an objective function, for consistency with conventional dendroclimatological approaches (Speer, 2010). Although R is insensitive to both multiplicative and additive differences between measurements and model outputs (Legates and McCabe, 1999), these limitations are not problematic because results were normalized to the same scales. In describing relative model

performance, we qualified “better performing” models as those with lower AIC, and optimal parameters as those that yielded a better fit with respect to R . Because optimal values often occupy a range and are not single values, we used a “dotty plot” approach (Beven and Freer, 2001) to characterize optimal parameter values. Dotty plots compare values of the objective function, R to candidate parameter values from the Monte-Carlo process, indicating the zone of optimal values and sensitivity to those parameters. This approach was used instead of other analyses of optimization results that yield a single value because there may be a wide range of near-optimal parameter values that contain ecological meaning. Variation in R with parameter value also illustrates model sensitivity to deviations from the single optimal parameter set. Here R values were plotted with respect to two parameters to show effects of parameter interactions on model fit.

To assess its relative utility, performance (AIC) and model fit (R) for VSL-Wet were compared those of regression models: simple correlation with monthly temperatures or water levels (two free parameters each); multiple regression of mean annual temperature and water level (three free parameters); and multiple regression including all monthly water levels (13 free parameters); and an iterative approach to minimize AIC through testing multiple regression models omitting and including all possible combinations of monthly T and W (up to 25 free parameters).

Generalizability was examined in space and time through cross-site and cross-time validation of fitted VSL-Wet models. Cross-site model validation was by applying best-fit parameter sets from each chronology to all other chronologies; this was done within and across Verret or Atch plots. For temporal validation, all models were run after splitting the datasets into 25-year segments (1955-1979 and 1980-2004); models were parameterized for one and then tested applying that parameterization to modeling the other segment. For comparison to VSL-Wet performance, these same validation approaches were applied to test the efficacy of multiple regression models for predicting growth at other sites or times.

4 RESULTS

4.1 Model Assessment

The *multiplicative* and *univariate-W* forms of VSL-Wet generally performed best (Table 2), but relative performance was also conditional on whether models used *two-parameter* versus *four-parameter* response curves and *fixed* versus *filtered-W* representation of water levels.

Without exception, models including *filtered-W* (i.e., deviation from recent water level) performed better than models using *fixed W* (absolute water level) (Table 2). The *seasonal shift* parameter generally yielded higher AIC than those models omitting it; *R* values with *seasonal-shift* were on average only 0.0016 higher than those without (Table 3) and the parameter *s* optimized to zero shift (i.e., March_y to November_y contributed to *G*(y)) for most chronologies for *multiplicative*, *additive*, *minimum*, and *univariate-W* models. The effect of using *two-parameter* versus *four-parameter* growth response curves was scenario dependent, but generally the *four-parameter* models were better. The exception to this was for the *two-parameter, multiplicative* model using *filtered-W*, which was the overall best performing model (followed by *four-parameter* of the same other options). Although the single limiting factor model (*minimum*) performed better for at least one chronology, AIC was substantially higher on average compared to models incorporating interacting environmental factors (*additive* and *multiplicative*; Table 2).

Expectedly, more complex models often had better optimized fits (Table 3), but resulted in worse fits for validation runs (Table 4). The best fits were for most complex model examined—the *multiplicative* model with *filtered-W*, *four-parameter* curves, and a *seasonal shift* term—which yielded a maximum *R* of at 0.80 (for VU), although models with *seasonal-shift* were not further investigated because AIC showed the seasonal shift term was not well justified (Table 2). Of those further tested for validation (Table 4), the *four-parameter, multiplicative* model with *filtered-W* yielded highest *R* on average (Table 3), but the validation runs for the *two-parameter, multiplicative* model with *filtered-W* were all better fits than the respective *four-parameter* models (Table 4). Not only did the *two-parameter, multiplicative* model with *filtered-W* have the lowest mean AIC, it also served best in predicting other sites and other times (i.e., temporal and spatial validation); mean *R* of validation runs (i.e., parameters optimized to other sites or times) was 0.57 spatially, and 0.60 temporally (Table 4). The *two-parameter, univariate-W* model with *filtered-W* performed next best by these metrics. For the *fixed* models, cross-site and cross-time (Table 4) validation fits were poorer, especially for Verret chronologies.

The performance (by AIC) of optimized multiple regression models was similar to that of the better performing VSL-Wet candidate models, but validation runs yielded worse fits (Table 4). Simple linear regressions yielded low AICs, with best performing models describing growth as a function of *W* in April, May, and June; there was also a strong inverse relationship with June *T* at Verret sites. The best AIC was achieved through multiple regression with independent

variables June W , Sept W , Dec W , May T , and Nov T ; this regression model yielded AIC values similar to the *two-parameter, multiplicative* VSL-Wet model with *filtered-W*, but with lower optimized R (Table 3), and substantially lower R for validation runs. Results from the monthly W multiple regression model and the annual mean- T -mean- W multiple regression model similarly showed AIC and R values close to those or better than VSL-Wet, but R for validation runs were much lower. Of the regression models, the simple linear regressions provided the best validation fits (Table 4).

4.2 Optimal parameter sets

Parameterizations of g_W for the *fixed, two-parameter, univariate-W* model were similar across sites and plots, explaining the strong cross-site validation. While the best-fit curves were not identical (Figure 6), they all indicated increased growth with increased flooding. At Verret plots, the optimal growth response curves showed increasing growth with increasing water levels nearly over the full range of W (Figures 6 and 7). The differences in g_W among Verret plots were consistent in magnitude with differences in plot water levels (Figure 7); that is, w_2 was approximately 0.75-1.0 m above plot minimum W , and w_3 covaried inversely with w_2 , ranging from 0.0 to 0.5 m above w_2 . The Atch plots, despite varying elevation and water depths among plots, were more similar to each other with respect to absolute depth (rather than depth relative to site-mean W ; Figure 4), resulting in nearly identical zones of optimal response function parameters (Figure 7), ranging from roughly 1.5 to 2.75 m for w_2 and 2.0 m to the upper limit for w_3 . Despite differences in water level ranges, the optimal inflection points for Atch g_W response functions, if applied in cross-validation to Verret input data, would have similarly resulted in a monotonic increasing growth with increasing water level; there was substantial overlap in optimal zone of the parameter spaces (Figure 7) if considered with respect to the relative distribution of water levels observed (Figure 6). Independence (from g_T) of optimal parameterizations for g_W was shown by the similarity in g_W optimal parameter values between those for the *fixed, two-parameter, multiplicative* model (third and fourth columns in Figure 6) and those for the *fixed, two-parameter, univariate-W* model (first and second columns in Figure 6).

The zone of optimal parameters was similar between the *fixed* and *filtered-W* versions of the *two-parameter, univariate-W* model, although ranges of W differed slightly (Figures 6 and 8) because of differences in optimal n —the filter averaging period for the W trend signal removed for *filtered-W*. As a deviation from mean, the *filtered-W* results showed more overlap in optimal

zones among plots within in each wetland (Figure 8). Optimized n differed among sites but was similar among candidate models; that is, the optimal n for *two-parameter, univariate-W* model with *filtered-W*, n was 10, 3, 7, 7, 5, and 2 years, and, for the parallel *multiplicative* model, was 8, 3, 7, 8, 6 and 2 years, respectively, for AT, GC, EH, SM, VU, GH.

Optimal parameters for g_T were less consistent across sites despite identical T inputs. Growth in the Verret plots was generally more related to T than it was in the Atch plots (Table 3), and optimal t_2 from the *fixed, two-parameter, univariate-T* model was roughly 15-20°C and t_3 (after which growth is reduced) varied from about 20-25°C. For Atch sites, t_2 values were approximately 25°C for SM and GH—higher than in Verret plots; for VU, g_T was only less than one (maximum growth) for very high or low temperatures (Figure 9).

For the *fixed, two-parameter, multiplicative* model, the g_T response curves had similar shapes and parameter values to those for the *fixed, two-parameter, univariate-T* model (Figure 9).

5 DISCUSSION

5.1 Model performance

Several VSL-Wet candidate models explained and predicted ring width variability in baldcypress more effectively than regression approaches. Furthermore, VSL-Wet response functions were applied equivalently to every monthly interval, unlike multiple regressions where months each can have highly different parameters, potentially implying inconsistent and idiosyncratic tree responses among months. The better performance was also consistent with empirical observations that trees respond to conditions (whether temperature or water level) non-monotonically and with plasticity (Mitsch and Gosselink, 2007). The value of representing these aspects of tree growth in the model was most apparent in cross-site and cross-time validation runs, which demonstrate the generalizability of the model and indicated that superior performance was unlikely a consequence of the overfitting that typically pervades regression models.

The VSL-Wet approach provides a means of circumventing a major obstacle in inter-site comparison of tree responses to water level variability: identifying specific aspects of flooding important for controlling tree growth. The multiple dimensions of variability of a hydrologic regime (e.g., depth, duration, frequency, and timing of flooding) are not easily characterized by simple metrics as would be convenient for site intercomparison; for example, flooding depth

alone is insufficient for site characterization because sites VU and AT were nearly permanently flooded with mean depths of 0.82 m and 0.83 m, but mean intra-annual variability was 1.60 m and 0.47 m respectively. VSL-Wet provides a better model of tree response to wetland variability because the optimized g_W response curve is transferrable and defined by parameters with physical meaning. Although the model was developed using mean monthly water levels and temperatures, increased temporal resolution or substitution of more direct drivers of growth may increase physiological interpretability (Vaganov et al., 2006a). The VSL-Wet model form can also be extended beyond our simple treatment of water level and temperature to include growth response functions for other predictors of wetland tree growth, such as number of days of flooding (Anderson and Mitsch, 2008; Mitsch and Rust, 1984) or Palmer drought severity index (Conner et al., 2014; Keim et al., 2012; Keim and Amos, 2012; Stahle et al., 1985).

We hypothesize that VSL may be a broadly more appropriate tree-level model of growth than are regression-based approaches, but the limits of its applicability need further exploration. The VSL-Wet assumptions are not specific to wetlands except for the use of a water-level growth function. General applicability is likely aided by the flexibility of the trapezoidal response functions applied equally at a monthly timestep; even without explicitly modifying the growing season, representation of complex behavior such as drought deciduousness could theoretically be achieved through the calibration process. In a practical sense, the nature of the growth functions that can be applied depends on the data available; temperature and precipitation are generally useful because long measurement series are available. Furthermore, simpler models may better support inter-comparison, as evidenced here. Invertability of the model for climate reconstruction remains problematic (Tolwinski-Ward et al., 2011) because of non-linear and sub-annual responses (Vaganov et al., 2006a), so the primary utility of this model approach is likely as used here—using the optimization process to gain more mechanistic insight into tree behavior—although other applications and forms of this approach could be pursued.

Given the abundance of water (especially in permanently flooded sites), it was unclear whether to expect growth to be sensitive to both water levels and temperatures. The AIC analysis results warranted inclusion of g_W and g_T terms, demonstrating sensitivity to both terms. However, given the relative performance of *univariate-W* models versus *univariate-T* models, using only g_W or g_T (Table 2), we concluded that model performance was more sensitive to g_W parameterization. Simplicity with respect to number of parameters defining growth curves (i.e.,

two-parameter versus *four-parameter* growth curves) proved important in the validation process (Table 4) and suggested that establishing the location of the maximum-growth plateau (w_2 and w_3 or t_2 and t_3 values) was most important. Beyond its importance to refining an appropriate model structure, the superior performance achieved with the *multiplicative* model using *two-parameter* growth functions and high-pass *filtered-W* also provided ecological insights.

5.2 Ecological implications of best-fit models and parameters

The principle of limiting factors—that biological processes cannot occur at a rate beyond that allowed by the most limited resource or factor—underlies many applications in dendrochronology (Fritts, 2001; Speer, 2010), but the poorer performance of *minimum* models compared to *multiplicative* or *additive* models showed benefits of accounting for interactions of limitations by T and W . Interaction of stressors can increase their impact (Mooney et al., 1991; Niinemets, 2010), and single limiting factors are not easily tested in nature. In our application, it is possible that monthly resolution or over-simple environmental metrics masked true physiological responses, yet representing g_W - g_T interactions enabled better performance at the resolution examined here (Table 2). For wetland trees, interacting stress effects have been observed such as flooding effects that are conditional on temperature (McLeod et al., 1986). Reasons for this could be that flooding inhibits trees by rhizosphere hypoxia (Pezeshki, 2001), and dissolved oxygen is inversely related to temperature (Joyce et al., 1985). Alternately, limited water uptake by smaller root systems in flooded individuals (Kozłowski, 1997) may reduce transpiration thereby increasing surface temperature and resulting in foliar temperature stress (Larcher, 1995). Contrasting behavior of interacting vs. single limiting factor models could facilitate parameter interpretation. For example, given greater temperature variability within years than among years, the better performance of *multiplicative* models could have arisen by g_T acting as a secondary (in addition to g_E) seasonal adjustment, reweighting g_W effects. However, the similarity in g_T between derived from *multiplicative* and *univariate* models (Figure 9) did not support the conclusion that the optimal $t1$ -4 parameter values were simply an artifact of the interaction representation.

The consistent and substantial performance improvement by representing hysteretic growth responses to water (*filtered-W* models) suggested the importance of tree acclimation to environmental conditions. While best-fit window lengths of n varied (from two to ten years), all

were short compared to the 50-year record. Plants show phenotypic plasticity at multiple spatial and temporal scales (De Kroon et al., 2005), and plasticity is particularly important in species, such as baldcypress that we modeled, that are adapted to be long-lived and span highly variable conditions (Kramer, 1995; Magnani et al., 2002). Our results are consistent with observations that flood tolerance in baldcypress partially arises by its morphological responsiveness to flooding. Low oxygen in the rhizosphere reduces root growth but also stimulates the development of aerenchyma, which can facilitate greater oxygen transport in wood (Megonigal and Day, 1992; Pezeshki, 1991), and adventitious roots (Megonigal and Day, 1992; Pezeshki and Anderson, 1996) that allow access to shallower water that is generally less anoxic.

The small effect of the seasonal shift term on model performance and the optimized shifts of zero (Mar(y)-Nov(y) growing season for year y) were a departure from known tree behavior. Growth in one year is a function of photosynthesis in the previous year because late-season photosynthate supports early root and shoot growth in the next year (Kozlowski, 1991), and photosynthesis in baldcypress occurs later into the year than does radial growth (Conner et al., 1981; Egler, 1955). This inconsistency between model behavior and known tree behavior may be either idiosyncratic to our dataset (late season water levels were least variable (Figure 4) and thus had little effect on model performance) or integral to the VS-Lite concept (late-season conditions contribute a small fraction to annual growth because of low g_E). Another possible limitation was that interaction between s and W was not accounted for, despite the known relationship that interannual variability in water level creates variability in effective growing season length (Allen et al., 2016; Keeland and Sharitz, 1995). An investigation of longer-term lagged effects were omitted from this study, but such effects are likely (Keim and Amos, 2012) and could be modeled using, for example, growth-response decay rates controlled by free parameters.

The g_W functions optimal values for w_2 and w_3 were similar across sites in that they indicated tree growth was augmented by wetter conditions (Figures 6,7) regardless of hydrologic differences between sites. While the range of optimal parameters values differed between sites because of the different means and ranges of water levels in each location, parameterizations of ~ 1 m above mean W for w_2 and w_3 slightly higher than w_2 yielded good fits for all sites when using *filtered-W* (Figure 8). At these sites, particularly Verret, best fits showed linearly increasing growth response to water levels over most of the range of water levels observed. This

was particularly true in Verret where the zone of optimality (Figure 7) from both *fixed* and *filtered-W two-parameter, univariate-W* models included inflection points that extended to the upper limit of W variability. Performance was better in the high W -variability Atch sites, where optimal g_w had a trapezoidal shape with reduced growth at extremely high water level (Figures 7, 8); that is, with deeper flooding in Atch, optimal models suggested flood stress. However, these limiting depths were rare; at Atch sites, depth was >1.0 m above mean W 8% of the time and >2.0 m above mean W 1% of time (Figure 6). Drier conditions were frequently limiting in all plots, shown by optimal w_2 exceeding the mean $W(m,y)$ (Figures 6, 7). In addition to the model suggesting that flood stress was relatively infrequent, another surprising result was that permanently flooded plots (GC and VU) also apparently benefitted from deeper flooding; in both cases, growth apparently increased up until at least 0.5 m and 1.0 m above the mean (GC and VU respectively; Figure 8). Other studies have shown that baldcypress is positively stimulated by flooding, demonstrated at both coarse resolution (annual resolution; Conner et al., 2014; Keim and Amos, 2012) and fine resolution ($<$ weekly resolution; Duberstein et al., 2013; Keeland and Sharitz, 1997). Of course inferences from model results have limitations, but the conceptually more literal process representation by VSL-Wet (compared to regression) provides more confidence.

Explanations are needed for how flooded trees apparently benefitted from deeper flooding. One potential explanation is that water level was related to precipitation which also affected vapor pressure deficits, but water level was unrelated to monthly precipitation in both Verret ($R^2 = 0.08$) and Atch ($R^2 = 0.01$). Atchafalaya River stage and water quality are mostly controlled by the Mississippi River (Pasco et al., 2015). Given that high discharge is often coupled with other beneficial inputs, like nutrients (Junk et al., 1989; Tockner et al., 1999), a second potential explanation is that water quality differences associated with high water levels stimulated tree growth. Dissolved oxygen in Grand Lake (Atch) responds to river flow (Sabo et al., 1999), but Verret trees also showed benefits of deeper flooding where this same relationship between water quality and level is unlikely (Keim and Amos, 2012). A third hypothesis is that high water levels are not as stressful as previously assumed and may simply result in a transition to water and nutrient uptake via adventitious water roots or potentially unexplored mechanisms. Fourth, carbon exchange through stomata is sensitive to vapor pressure deficits (Bond et al., 2008) and lower water levels resulted in more areas of exposed soils regionally (even if not at the

tree), which could have increased sensible heat fluxes and temperature—especially with dark organic soils (Oke, 1988)—resulting in higher vapor pressure deficits in the canopy. Fifth, variations in radial growth were possibly caused by changes in carbon allocation (to favor or disfavor stem radial growth) rather than changes in production. Regardless, the differences between these results and the commonly held opinion that stagnant flooding results in stress and reduced growth (Megonigal et al., 1997; Mitsch, 1988) require further investigation.

6 CONCLUSIONS

The presented model, VSL-Wet, was developed to explain inter-annual variation in six baldcypress chronologies from plots with different flooding depths in two hydrologically distinct wetlands in south Louisiana, USA. Model performance was better than regression-based approaches performance and model fits exceeded those often reported in dendroecological studies. The particularly high explanatory power—in some cases, VSL-Wet explained > 50% of variance in inter-annual ring widths—was achieved by representing interacting temperature and water response functions and temporally varying water response functions (defined with respect to recent water levels). The better fit achieved by including these two components may reflect the ecophysiological roles of interacting stressors and plasticity in responses to stressors, and contradicts the often assumed applicability of single limiting factors in tree growth models.

The growth response functions to water level obtained by optimizing VSL-Wet improved inter-site comparison and gave insight into controls on wetland tree growth. Optimal parameters defining the growth response functions to water levels were similar among sites, despite difference in hydrologic variability. Transferability of parameters defining growth response curves across sites and across different time periods may demonstrate that these growth functions have ecological meaning instead of being a product of overfitting. Best-fit growth response functions showed that shallower water levels reduce growth, inconsistent with common assumptions about flooding limiting wetland tree growth.

Acknowledgements: Funding was through the Gilbert Foundation graduate research fellowship and USDA NIFA, LAB94181. Any opinions, findings, conclusions, or recommendations expressed in this publication are those of the author and do not necessarily reflect the view of the U.S. Department of Agriculture. We thank Blake Amos for developing the tree ring measurements.

7 REFERENCES

- 524 Allen, J.A., Pezeshki, S.R., Chambers, J.L., 1996. Interaction of flooding and salinity stress on
525 baldcypress (*Taxodium distichum*). *Tree Physiol.* 16, 307–313.
- 526 Allen, S.T., Krauss, K.W., Cochran, J.W., King, S.L., Keim, R.F., 2016. Wetland tree
527 transpiration modified by river-floodplain connectivity. *J. Geophys. Res. Biogeosciences*
528 2015JG003208. doi:10.1002/2015JG003208
- 529 Anderson, C.J., Mitsch, W.J., 2008. Tree basal growth response to flooding in a bottomland
530 hardwood forest in central Ohio. *J. Am. Water Resour. Assoc.* 44, 1512–1520.
531 doi:10.1111/j.1752-1688.2008.00255.x
- 532 Anderson, P.H., Pezeshki, R., 2001. Effects of flood pre-conditioning on responses of three
533 bottomland tree species to soil waterlogging. *J. Plant Physiol.* 158, 227–233.
534 doi:10.1078/0176-1617-00267
- 535 Beven, K., Freer, J., 2001. Equifinality, data assimilation, and uncertainty estimation in
536 mechanistic modelling of complex environmental systems using the GLUE methodology.
537 *J. Hydrol.* 249, 11–29. doi:10.1016/S0022-1694(01)00421-8
- 538 Bond, B.J., Meinzer, F.C., Brooks, J.R., 2008. How trees influence the hydrological cycle in
539 forest ecosystems, in: Lecturer, P.J.W.S., Lecturer, D.M.H.S., Reader, J.P.S. (Eds.),
540 *Hydroecology and Ecohydrology*. John Wiley & Sons, Ltd, pp. 7–35.
- 541 Burnham, K.P. and Anderson, D.R., 1998. Model selection and inference: a practical
542 information-theoretic approach Springer-Verlag. New York.
- 543 Conner, W.H., Duberstein, J.A., Jr, J.W.D., Hutchinson, S., 2014. Impacts of Changing
544 Hydrology and Hurricanes on Forest Structure and Growth Along a Flooding/Elevation
545 Gradient in a South Louisiana Forested Wetland from 1986 to 2009. *Wetlands* 34, 803–
546 814. doi:10.1007/s13157-014-0543-0
- 547 Conner, W.H., Gosselink, J.G., Parrondo, R.T., 1981. Comparison of the vegetation of three
548 Louisiana swamp sites with different flooding regimes. *Am. J. Bot.* 68, 320.
549 doi:10.2307/2442768
- 550 Cook, E.R., 1985. A time series analysis approach to tree ring standardization (Dissertation).
551 University of Arizona, Tucson, AZ, USA.
- 552 Day, J., Hunter, R., Keim, R.F., DeLaune, R., Shaffer, G., Evers, E., Reed, D., Brantley, C.,
553 Kemp, P., Day, J., Hunter, M., 2012. Ecological response of forested wetlands with and
554 without Large-Scale Mississippi River input: Implications for management. *Ecol. Eng.*
555 46, 57–67. doi:10.1016/j.ecoleng.2012.04.037
- 556 De Kroon, H., Huber, H., Stuefer, J.F., Van Groenendael, J.M., 2005. A modular concept of
557 phenotypic plasticity in plants. *New Phytol.* 166, 73–82. doi:10.1111/j.1469-
558 8137.2004.01310.x

- 559 DeLaune, R. d., Patrick, W.H. jun, Pezeshki, S. r., 1987. Foreseeable Flooding and Death of
560 Coastal Wetland Forests. *Environ. Conserv.* 14, 129–133.
561 doi:10.1017/S0376892900011486
- 562 Duberstein, J.A., Krauss, K.W., Conner, W.H., Jr, W.C.B., Shelburne, V.B., 2013. Do
563 hummocks provide a physiological advantage to even the most flood tolerant of tidal
564 freshwater trees? *Wetlands* 33, 399–408. doi:10.1007/s13157-013-0397-x
- 565 Effler, R.S., Shaffer, G.P., Hoeppner, S.S., Goyer, R.A., 2007. Ecology of the Maurepas Swamp:
566 Effects of Salinity, Nutrients, and Insect Defoliation, in: *Ecology of Tidal Freshwater*
567 *Forested Wetlands of the Southeastern United States*. Springer Netherlands, pp. 349–384.
- 568 Egger, W.A., 1955. Radial growth in nine species of trees in southern Louisiana. *Ecology* 36,
569 130–136. doi:10.2307/1931438
- 570 Ford, C.R., Brooks, J.R., 2002. Detecting forest stress and decline in response to increasing river
571 flow in southwest Florida, USA. *For. Ecol. Manag.* 160, 45–64. doi:10.1016/S0378-
572 1127(01)00440-6
- 573 Fritts, H., 2001. *Tree Rings and Climate*, 2nd ed. Blackburn Press, Caldwell, NJ, USA.
- 574 Hughes, M.K., 2002. Dendrochronology in climatology – the state of the art. *Dendrochronologia*
575 20, 95–116. doi:10.1078/1125-7865-00011
- 576 Joyce, K., Todd, R.L., Asmussen, L.E., Leonard, R.A., 1985. Dissolved oxygen, total organic
577 carbon and temperature relationships in southeastern U.S. coastal plain watersheds.
578 *Agric. Water Manag.* 9, 313–324. doi:10.1016/0378-3774(85)90041-1
- 579 Junk, W., Bayley, P.B., Sparks, R.E., 1989. The Flood Pulse Concept in River—Floodplain
580 Systems, in: Dodge, D.P. (Ed.), *Proceedings of the International Large River Symposium*.
581 Presented at the International Large River Symposium, 106, Ontario, CA, pp. 110–127.
- 582 Keeland, B.D., Sharitz, R.R., 1997. The Effects of Water-Level Fluctuations on Weekly Tree
583 Growth in a Southeastern USA Swamp. *Am. J. Bot.* 84, 131–139. doi:10.2307/2445890
- 584 Keeland, B.D., Sharitz, R.R., 1995. Seasonal growth patterns of *Nyssa sylvatica* var *biflora*,
585 *Nyssa aquatica*, and *Taxodium distichum* s affected by hydrologic regime. *Can. J. For.*
586 *Res.* 25, 1084–1096. doi:10.1139/x95-120
- 587 Keim, R.F., Amos, J.B., 2012. Dendrochronological analysis of baldcypress (*Taxodium*
588 *distichum*) responses to climate and contrasting flood regimes. *Can. J. For. Res.* 42, 423–
589 436. doi:10.1139/x2012-001
- 590 Keim, R.F., Izdepski, C.W., Jr, J.W.D., 2012. Growth Responses of Baldcypress to Wastewater
591 Nutrient Additions and Changing Hydrologic Regime. *Wetlands* 32, 95–103.
592 doi:10.1007/s13157-011-0248-6

- 593 Kozlowski, T.T., 1997. Responses of woody plants to flooding and salinity. *Tree Physiol.* 17,
594 490–490. doi:10.1093/treephys/17.7.490
- 595 Kozlowski, T.T., 1991. Environmental stresses to deciduous trees, in: Mooney, H.A., Winner,
596 W.E., Pell, E.J. (Eds.), *Response of Plants to Multiple Stresses*. Academic Press, San
597 Diego, CA, pp. 391–411.
- 598 Kramer, K., 1995. Phenotypic plasticity of the phenology of seven European tree species in
599 relation to climatic warming. *Plant Cell Environ.* 18, 93–104. doi:10.1111/j.1365-
600 3040.1995.tb00356.x
- 601 Larcher, W., 1995. *Physiological plant ecology*. Springer-Verlag.
- 602 Legates, D.R., McCabe, G.J., 1999. Evaluating the use of “goodness-of-fit” Measures in
603 hydrologic and hydroclimatic model validation. *Water Resour. Res.* 35, 233–241.
604 doi:10.1029/1998WR900018
- 605 MacClurkin, D.C., 1965. Diameter growth and phenology of trees on sites with high water
606 tables. Southern Forest Experiment Station, Forest Service, U.S. Dept. of Agriculture.
- 607 Magnani, F., Grace, J., Borghetti, M., 2002. Adjustment of tree structure in response to the
608 environment under hydraulic constraints. *Funct. Ecol.* 16, 385–393. doi:10.1046/j.1365-
609 2435.2002.00630.x
- 610 McLeod, K.W., Donovan, L.A., Stumpff, N.J., Sherrod, K.C., 1986. Biomass, photosynthesis
611 and water use efficiency of woody swamp species subjected to flooding and elevated
612 water temperature. *Tree Physiol.* 2, 341–346. doi:10.1093/treephys/2.1-2-3.341
- 613 Megonigal, J.P., Conner, W.H., Kroeger, S., Sharitz, R.R., 1997. Aboveground production in
614 southeastern floodplain forests: A test of the subsidy–stress hypothesis. *Ecology* 78, 370–
615 384. doi:10.1890/0012-9658(1997)078[0370:APISFF]2.0.CO;2
- 616 Megonigal, J.P., Day, F.P., 1992. Effects of Flooding On Root and Shoot Production of Bald
617 Cypress in Large Experimental Enclosures. *Ecology* 73, 1182–1193.
618 doi:10.2307/1940668
- 619 Meko, D.M., Touchan, R., Anchukaitis, K.J., 2011. Seascorr: A MATLAB program for
620 identifying the seasonal climate signal in an annual tree-ring time series. *Comput. Geosci.*
621 37, 1234–1241. doi:10.1016/j.cageo.2011.01.013
- 622 Mitsch, W.J., 1988. Productivity-Hydrology-Nutrient Models of Forseted Wetlands, in: Mitsch,
623 W.J., Straškraba, M., Jorgensen, S.E. (Eds.), *Wetland Modelling*. Elsevier, Amsterdam,
624 Netherlands.
- 625 Mitsch, W.J., Gosselink, J.G., 2007. *Wetlands*, 4th ed. John Wiley & Sons, Inc., New York, NY,
626 USA.

- 627 Mitsch, W.J., Rust, W.G., 1984. Tree growth responses to flooding in a bottomland forest in
628 northeastern Illinois. *For. Sci.* 30, 499–510.
- 629 Mitsch, W.J., Taylor, J.R., Benson, K.B., 1991. Estimating primary productivity of forested
630 wetland communities in different hydrologic landscapes. *Landsc. Ecol.* 5, 75–92.
631 doi:10.1007/BF00124662
- 632 Mooney, H.A., Winner, W.E., Pell, E.J. (Eds.), 1991. *Response of Plants to Multiple Stresses*.
633 Academic Press, San Diego, CA.
- 634 Nash, L.J., Graves, W.R., 1993. Drought and flood stress effects on plant development and leaf
635 water relations of five taxa of trees native to bottomland habitats. *J. Am. Soc. Hortic. Sci.*
636 118, 845–850.
- 637 Niinemets, Ü., 2010. Responses of forest trees to single and multiple environmental stresses
638 from seedlings to mature plants: Past stress history, stress interactions, tolerance and
639 acclimation. *For. Ecol. Manag.* 260, 1623–1639.
- 640 Nuttle, W.K., 1997. Measurement of wetland hydroperiod using harmonic analysis. *Wetlands* 17,
641 82–89. doi:10.1007/BF03160720
- 642 Odum, E.P., Finn, J.T., Franz, E.H., 1979. Perturbation theory and the subsidy-stress gradient.
643 *BioScience* 29, 349–352. doi:10.2307/1307690
- 644 Oke, T.R., 1988. *Boundary Layer Climates*, 2 edition. ed. Routledge.
- 645 Pasco, T.E., Kaller, M.D., Harlan, R., Kelso, W.E., Rutherford, D.A., Roberts, S., 2015.
646 Predicting Floodplain Hypoxia in the Atchafalaya River, Louisiana, USA, a Large,
647 Regulated Southern Floodplain River System. *River Res. Appl.* n/a-n/a.
648 doi:10.1002/rra.2903
- 649 Pezeshki, S.R., 2001. Wetland plant responses to soil flooding. *Environ. Exp. Bot.* 46, 299–312.
650 doi:10.1016/S0098-8472(01)00107-1
- 651 Pezeshki, S.R., 1991. Root responses of flood-tolerant and flood-sensitive tree species to soil
652 redox conditions. *Trees* 5, 180–186. doi:10.1007/BF00204341
- 653 Pezeshki, S.R., Anderson, P.H., 1996. Responses of three bottomland species with different
654 flood tolerance capabilities to various flooding regimes. *Wetl. Ecol. Manag.* 4, 245–256.
655 doi:10.1007/BF02150538
- 656 Pezeshki, S.R., Chambers, J.L., 1986. Variation in Flood-Induced Stomatal and Photosynthetic
657 Responses of Three Bottomland Tree Species. *For. Sci.* 32, 914–923.
- 658 Rodríguez-González, P.M., Stella, J.C., Campelo, F., Ferreira, M.T., Albuquerque, A., 2010.
659 Subsidy or stress? Tree structure and growth in wetland forests along a hydrological
660 gradient in Southern Europe. *For. Ecol. Manag.* 259, 2015–2025.
661 doi:10.1016/j.foreco.2010.02.012

- Rodriguez-Iturbe, I., D'Odorico, P., Laio, F., Ridolfi, L., Tamea, S., 2007. Challenges in humid land ecohydrology: Interactions of water table and unsaturated zone with climate, soil, and vegetation. *Water Resour. Res.* 43, W09301. doi:10.1029/2007WR006073
- Sabo, M.J., Bryan, C.F., Kelso, W.E., Rutherford, D.A., 1999. Hydrology and aquatic habitat characteristics of a riverine swamp: II. Hydrology and the occurrence of chronic hypoxia. *Regul. Rivers Res. Manag.* 15, 525–544. doi:10.1002/(SICI)1099-1646(199911/12)15:6<525::AID-RRR554>3.0.CO;2-Q
- Speer, J.H., 2010. Fundamentals of tree-ring research. University of Arizona Press, Tucson.
- Stahle, D.W., Cleaveland, M.K., Hehr, J.G., 1985. A 450-year drought reconstruction for Arkansas, United States. *Nature* 316, 530–532. doi:10.1038/316530a0
- Tockner, K., Pennetzdorfer, D., Reiner, N., Schiemer, F., Ward, J.V., 1999. Hydrological connectivity, and the exchange of organic matter and nutrients in a dynamic river–floodplain system (Danube, Austria). *Freshw. Biol.* 41, 521–535. doi:10.1046/j.1365-2427.1999.00399.x
- Tolwinski-Ward, S.E., Evans, M.N., Hughes, M.K., Anchukaitis, K.J., 2011. An efficient forward model of the climate controls on interannual variation in tree-ring width. *Clim. Dyn.* 36, 2419–2439. doi:10.1007/s00382-010-0945-5
- Vaganov, E.A., Hughes, M.K., Shashkin, A.V., 2006a. Modeling External Influence on Xylem Development, in: *Growth Dynamics of Conifer Tree Rings, Ecological Studies*. Springer Berlin Heidelberg, pp. 189–243.
- Vaganov, E.A., Hughes, M.K., Shashkin, A.V., 2006b. Simulation of tree-ring growth dynamics in varying and changing climates, in: *Growth Dynamics of Conifer Tree Rings, Ecological Studies*. Springer Berlin Heidelberg, pp. 244–280.
- van der Valk, A.G., 1981. Succession in Wetlands: A Gleasonian Approach. *Ecology* 62, 688–696. doi:10.2307/1937737
- Young, P.J., Keeland, B.D., Sharitz, R.R., 1995. Growth response of baldcypress [*Taxodium distichum* (L.) Rich.] to an altered hydrologic regime. *Am. Midl. Nat.* 133, 206–212. doi:10.2307/242638

Table 1 Abbreviations and model terms

<u>Response curves and parameters</u>	
g_W	Growth response to water level (eq. 2)
g_T	Growth response to temperature (eq. 3)
g_E	Growth response to solar energy
$T(m,y)$	monthly temperature
$W(m,y)$	monthly water level, unique to each plot
m	month
y	year
$w1, w2, w3, w4$	water levels parameters defining g_W (eq. 2; Table 2)
$t1, t2, t3, t4$	temperatures parameters defining g_T (eq. 3; Table 2)
s	free parameter defining the growing season window shift (eq. 10)
n	free parameter defining the number of years over which mean W is calculated for defining varying inflection points (eq. 9)
G	Relative ring width proxy annual output of VSL-Wet model
<u>Model descriptors</u>	
<i>multiplicative</i>	Model using g_T and g_W multiplied (eq. 4)
<i>additive</i>	Model using g_T and g_W added (eq. 5)
<i>minimum</i>	Model using minimum of g_T and g_W (eq. 6)
<i>univariate-W</i>	Model using univariate g_W (eq. 7) without g_T
<i>univariate-T</i>	Model using univariate g_T (eq. 8) without g_W
<i>fixed</i>	Model with no <i>seasonal shift</i> and fixed inflection points (no <i>filtered-W</i>)
<i>filtered-W</i>	Model with $w1-4$ defined as deviations from mean W over past n years
<i>seasonal shift</i>	Model using shift parameter to optimize effective growing season
<i>two-parameter</i>	Model with g_T or g_W inflection points defined by four free parameters
<i>four-parameter</i>	Model with g_T or g_W inflection points defined by two free parameters
<u>Research Sites</u>	
Verret	Verret Basin site
Atch	Atchafalaya Basin site at Grand Lake
AT	Attakapas Landing, in Verret
GC	Godchaux Canal, in Verret
EH	Elm Hall Wildlife Management Area, in Verret
SM	Six Mile Lake, in Atch
VU	Verdunville Landing, in Atch
GH	Gray Horse Island, in Atch

Table 2 Full set of Akaike Information Criterion (AIC) for model performance (modeled versus measured) for VSL-Wet candidate models and all sets of options [model g_T - g_W factor interaction, two-parameter versus four-parameter curves, and with *seasonal shift*, *filtered-W*, or neither (*fixed*)] as compared to regression models (last four rows): multiple regression of the combinations of monthly W or T that yielded the lowest AIC, multiple regression of annual mean W and T , multiple regression of all monthly W , and simple linear regression with best-fit individual-month temperature (T) or water level (W).

Model	g_T, g_W Params	Base ^A Params	AIC, mean of plots				AIC, minimum of plots			
			<i>Fixed</i>	<i>Seasonal Shift (s)</i>	<i>Filtered -W (n)</i>	<i>Seasonal Shift & Filtered-W</i>	<i>Fixed</i>	<i>Seasonal Shift (s)</i>	<i>Filtered -W (n)</i>	<i>Seasonal Shift & Filtered-W</i>
<i>multiplicative</i>	4	9	4.7	6.6	-4.7	-3.7	-16.1	-15.7	-20.6	-24.1
"	2	5	1.8	4.0	-7.2	-5.3	-16.0	-14.4	-20.9	-19.5
<i>additive</i>	4	10	3.0	4.6	-4.3	-3.2	-16.3	-13.5	-17.3	-17.0
"	2	6	4.2	5.5	-3.1	-2.6	-7.8	-5.9	-13.8	-12.5
<i>minimum</i>	4	9	4.2	6.6	-5.0	-3.8	-16.9	-13.9	-22.2	-22.7
"	2	5	5.2	7.9	-3.1	-0.6	-6.8	-4.6	-12.5	-10.4
<i>univariate-W</i>	4	5	3.3	5.3	-5.9	-4.1	-11.1	-8.7	-17.8	-14.8
"	2	3	7.6	9.9	-2.0	0.0	-6.2	-3.9	-14.8	-12.8
<i>univariate-T</i>	4	5	15.0	15.2	16.7	16.1	10.9	7.7	12.5	8.2
"	2	3	23.3	20.6	25.3	22.6	12.5	5.7	14.5	7.7
multiple regression $T(m), W(m)$	na	5 ^B	-7.5	na	na	na	-25.4	na	na	na
multiple regression T, W	na	3	-4.4	na	na	n	-10.0	na	na	na
multiple regression $W(m)$	na	13	6.4	na	na	na	0.7	na	na	na
simple regression $T(m)$ or $W(m)$	na	2	-4.9	na	na	na	-8.2	na	na	na

^A Parameter count; value was one higher for models with *seasonal shift* or *Filtered -W* options, and was two higher for models with both options

^B In optimizing, parameter count varied from one to 24 among possible combinations

Table 3 Model correlation coefficients, R , for all sites for selected candidate VSL-Wet models as well as regression models: multiple regression of the combinations of monthly W or T that yielded the lowest AIC, multiple regression of annual mean W and T , multiple regression of all monthly W , and simple linear regression with best-fit individual-month temperature (T) and water level (W).

Candidate Model	Site						
	AT	GC	EH	SM	VU	GH	Mean
<i>multiplicative, fixed, four-parameter</i>	0.56	0.57	0.50	0.67	0.74	0.54	0.60
<i>multiplicative, fixed, two-parameter</i>	0.51	0.53	0.45	0.66	0.70	0.47	0.55
<i>univariate-W, fixed, two-parameter</i>	0.31	0.45	0.38	0.60	0.60	0.41	0.46
<i>multiplicative, filtered-W, four-parameter</i>	0.63	0.70	0.59	0.72	0.77	0.67	0.68
<i>multiplicative, filtered-W, two-parameter</i>	0.59	0.67	0.58	0.72	0.74	0.58	0.64
<i>univariate-W, filtered-W, four-parameter</i>	0.45	0.61	0.52	0.68	0.64	0.54	0.57
multiple regression $T(m), W(m)$	0.42	0.54	0.45	0.63	0.68	0.49	0.53
multiple regression T, W	0.36	0.43	0.38	0.54	0.53	0.35	0.43
multiple regression $W(m)$	0.37	0.64	0.55	0.61	0.63	0.57	0.56
simple regression $W(m)$ ^A	0.30	0.43	0.41	0.48	0.46	0.43	0.43
simple regression $T(m)$ ^B	0.39	0.31	0.20	0.29	0.32	0.24	0.29

^Ahighest R were for July, June, April, June, April, June, respectively

^Bhighest R were for June, June, April, October, May, October, with inverse relationships for all but SM and GH

Table 4 Mean correlation coefficients, R , for cross-site validation and cross-time validation model fits. Data were calibrated using training chronologies from time periods or plots not included in performance testing. For example of cross-site validation, Ver|Ver was the mean correlation coefficient of AT and GC predicted by parameters for EH, AT and EH predicted by parameters for GC, and AT and GC predicted by parameters for EH. For example of cross-time validation, Ver₈₀₋₀₄|₅₅₋₇₉ was the mean correlation coefficient of: each Verret site with the chronology from 1980 to 2004 predicted from parameters calibrated using only 1955-1979 data.

Candidate Model	Cross-site Validation				Cross-time Validation			
	Ver Ver	Ver Atch	Atch Atch	Atch Ver	Ver ₈₀₋₀₄ ₅₅₋₇₉	Ver ₅₅₋₇₉ ₈₀₋₀₄	Atch ₈₀₋₀₄ ₅₅₋₇₉	Atch ₅₅₋₇₉ ₈₀₋₀₄
<i>multiplicative, fixed, four-parameter</i>	0.37	-0.01	0.41	0.43	0.24	0.39	0.37	0.35
<i>multiplicative, fixed, two-parameter</i>	0.41	0.38	0.56	0.48	0.44	0.27	0.62	0.52
<i>univariate-W, fixed, two-parameter</i>	0.38	0.43	0.50	0.40	0.29	0.46	0.58	0.51
<i>multiplicative, filtered-W, four-parameter</i>	0.49	0.26	0.48	0.55	0.40	0.47	0.58	0.62
<i>multiplicative, filtered-W, two-parameter</i>	0.52	0.56	0.60	0.59	0.54	0.54	0.65	0.67
<i>univariate-W, filtered-W, four-parameter</i>	0.50	0.54	0.57	0.53	0.43	0.47	0.62	0.63
multiple regression T, W	0.38	0.34	0.42	0.46	0.34	0.32	0.50	0.39
multiple regression $W(m)$	0.46	0.24	0.53	0.31	-0.14	-0.30	0.15	0.36
simple regression ^A	0.31	0.36	0.43	0.33	0.56	0.36	0.52	0.41

^A For $W(m)$ or $T(m)$ of a single month, with month varying, for whichever provided best fit for the training chronology.

Figure Captions

Figure 1 Diagrammatic representation of VSL-Wet and the time scale at which calculations were performed, showing interactions of trapezoidal growth response functions to month-year water levels, $W(m,y)$, and temperatures, $T(m,y)$.

Figure 2 Map of study region in southern Louisiana, USA, with Lake Verret plots—Godchaux Canal (GC), Elm Hall Wildlife Management Area (EH), and Attakapas Landing (AT)—and Atchafalaya (Atch) plots in Grand Lake—Six Mile Lake (SM), Verdunville landing (VU), and Gray Horse Island (GH). Figure adapted with permission from Amos and Keim, 2012.

Figure 3 Site-specific hydrographs for (A) Lake Verret sites— Godchaux Canal (GC), Elm Hall Wildlife Management Area (EH), and Attakapas Landing (AT)—and (B) Atchafalaya sites—Six Mile Lake (SM), Verdunville landing (VU), and Gray Horse Island.

Figure 4 Distribution of 50-year monthly data (for GC, VU plots) and means of monthly water levels at all Verret plots (A) and Atchafalaya plots (B), and temperature (C).

Figure 5 Tree ring chronologies for the Verret (A-C) and Atch (D-F) plots, showing the normalized measured chronology (Norm) from ARSTAN, the raw ring widths (in mm), and one example of optimized VSL-Wet output (from *multiplicative, filtered-W, two-parameter* model).

Figure 6 Optimal water (W) growth response functions (red lines), as optimized for all six sites for *univariate-W, fixed, two-parameter* model (Verret plots in first column, Atch plots in second) and *multiplicative, fixed, two-parameter* model (Verret plots in third column, Atch plots in fourth). Bars compose histograms showing relative frequency of water levels.

Figure 7 Monte Carlo simulation of correlation coefficients showing sensitivity to w_2 and w_3 parameters for the *univariate-W, fixed, two-parameter* model, defining the water levels at which growth increases with water level (w_2) and after which growth decreases with water level (w_3); plots represent the six evaluation plots with Verret plots in left column and Atchafalaya plots in right column.

Figure 8 Monte Carlo simulation of correlation coefficients showing sensitivity to w_2 and w_3 parameters for the *univariate-W* model using *filtered* water levels and *two-parameter* curves model, defining the filtered water levels at to which growth increases with water level deviation (w_2) and after which growth decreases with water level deviation (w_3); plots represent the six evaluation plots with Verret plots in left column and Atchafalaya plots in right column.

Figure 9 Optimal temperature (T) growth response functions (red lines), as optimized for all six sites *univariate-T, fixed, two-parameter* model (Verret plots in first column, Atch plots in second) and *multiplicative, fixed, two-parameter* model (Verret plots in third column, Atch plots in fourth). Bars compose histograms showing relative frequency of temperatures.

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7

Figure 8

Figure 9