AN INTEGRATED HYDRO-BIOLOGICAL MODEL FOR SIMULATING THE ESTABLISHMENT OF FREMONT COTTONWOOD SEEDLINGS

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Abstract  The Riparian Habitat Establishment Model (RHEM) is an integrated hydro-biological model that dynamically simulates plant growth as a function of atmospheric and soil moisture conditions. RHEM consists of plant growth algorithms that are fully integrated into the variably saturated flow model HYDRUS 2-D. RHEM simulates the effects of soil water content on biomass production, partitioning of growth into roots and shoots, and depth distribution of roots. The capability to simulate the combined effects of atmospheric, soil, groundwater, and plant growth characteristics offers the potential for a more comprehensive assessment of riparian vegetation growth and survival than can be obtained from empirical models that employ establishment elevation and changes in water table depth over time as the principal factors for predicting riparian vegetation establishment and survival.

The plant growth algorithms used by RHEM employ a number of plant specific parameters. Consequently, we have performed controlled laboratory experiments, replicated field trials, and observational studies under natural conditions to determine representative parameter values for Fremont cottonwood growing in the riparian corridor along the Sacramento River in California. These cottonwood growth parameters along with representative soil properties were used to calibrate and validate RHEM to experimental results. RHEM was subsequently used to simulate conditions at several sites along the Sacramento River. These simulations demonstrated that RHEM could successfully reproduce the significantly different cottonwood growth outcomes that occurred at these sites.

Currently, we are performing additional laboratory and field experiments to further refine the cottonwood parameters used in RHEM as well as to improve the scientific understanding of other important factors affecting their growth and survival including seedling inundation, water temperature, dissolved oxygen, atmospheric carbon dioxide and soil nitrogen speciation. As this information becomes available, it is our intention to implement corresponding improvements in the capabilities of RHEM to simulate these factors.

INTRODUCTION

The Mid-Pacific Region of the U.S. Bureau of Reclamation operates the Central Valley Project (CVP) which includes about twenty percent of the State of California’s developed water supply. The CVP supplies water to approximately 3 million acres of farm land and 2 million urban users. The Sacramento River and its tributaries contribute a significant portion of these supplies. Currently, there are several on-going feasibility studies investigating how Reclamation can meet the needs of its many customers and the American public in the most environmentally and economically sound manner. As part of the feasibility study process, the affects of project operations on riparian habitat along the Sacramento River is being investigated between the cities of Red Bluff and Colusa. To address these goals, Reclamation’s Mid-Pacific Region and Technical Services Center staff have developed a suite of models that will allow for the analysis of fluvial geomorphological processes including sediment transport, river meandering, and river stage and flow velocity. Among other outputs, these models will provide an estimate of river bank erosion and point bar growth which is integral to the process of riparian forest regeneration. Building on these outputs is another module (SRH 1DV) which considers the survival of the pioneer riparian forest species Fremont Cottonwood. Using SRH 1DV, the growth and survival of seedlings are modeled for the entire 100 mile reach between Red Bluff and Colusa. During the development of SRH 1DV, it was determined that a more detailed analysis was required to provide information for parameterizing its seedling growth and survival algorithms. In response to this need, a multi-faceted program was developed that included field studies on the Sacramento River, seedling growth model development, controlled seedling growth experiments, and model calibration and validation. The computer model that was developed uses the well known HYDRUS 2-D code (Simunek, et al., 1999) to simulate variably saturated flow in the river sediments and a new dynamically coupled plant growth algorithm described in this paper to model initial seedling establishment and survival. The combined hydro-biological model is called the Riparian Habitat Establishment Model (RHEM). In this paper we will report on the controlled field experiments, RHEM algorithm development, and RHEM calibration.
Cottonwood Seedling Establishment
Along the Sacramento River, the establishment of cottonwood seedlings is an integral part of the bio-physical river and flood plain processes. During periods of wintertime high flow, erosion occurs on the outer banks of river bends. This process works to destroy existing forest in these locations. Conversely, on the inner bank of river bends, sediment is deposited and new point bars are formed. Under natural conditions, river stage typically decreases throughout the spring and summer months. Cottonwood seeds are generally released by adult trees during the months of May and June just as the newly deposited point bar sediment is exposed to the atmosphere. The seeds collect on this moist substrate and germinate. As time progresses, the river stage and the water table in the river bank recede. Cottonwood seedlings grow roots into the sediment and utilize the moisture left by the receding water table. Seedlings are established and other species such as willow also colonize the point bar. This begins the succession of tree species that populate riparian forests along the Sacramento River.

The operation of on-stream dams along with various land use practices that impact tributary flows may potentially disrupt these natural processes by: 1.) reducing the number and magnitude of sediment moving high flow events, 2.) causing rapid drops or increases in river stage, and 3.) creating unseasonably high- or low-flow events. On the Sacramento River it is typically rapid changes in flow during the spring and summer months that may lead to unsuccessful seedling establishment (Morgan and Henderson, 2005). These decreases in flow result in the water table decline rates that when combined with unfavorable physical conditions (ex. coarse sediment texture) and environmental factors (ex. high evapotranspiration rates) may result in seedling mortality. One of the reasons for the development of the suite of models discussed above is to provide improved tools and methods that may be used to evaluate the effects of the historical flow regimes and study potential alternative regimes to promote the long term health of riparian habitats along this reach of the Sacramento River. The development of RHEM allows for a more detailed analysis of the many factors that affect seedling survival including sediment texture, water holding capacity, atmospheric conditions, water table decline rates, and plant growth properties.

CONTROLLED EXPERIMENTS

Experiment Design
A system of 30 rhizopods was constructed on the University of California at Davis campus. Each rhizopod consisted of a 45 cm diameter PVC tube, open on one end, 154 cm in length, and filled with a fine sand that had a similar texture to that found along the Sacramento River. Additional tubes were installed in each rhizopod that allowed for the control of the water table, soil moisture observations, and extraction of intact seedlings. The rhizopods were placed in a pre-existing, rectangular, concrete lined pit. A wooden cover over the pit, which had cutouts for each rhizopod, minimized the exposure of the rhizopod sides to solar radiation (Figure 1).
The experiment consisted of 5 treatments: T1, T2, T3, T4, and T5. Each treatment had 5 replicates and each treatment had an “evaporation” rhizopod in which no seedlings were planted (5 treatments x 5 replicates + 5 evap. = 30 rhizopods), these rhizopods were used to measure the rate of bare soil evaporation.

At the beginning of the experiment the water table was maintained at 5 cm below the soil surface and cottonwood seeds collected from the Sacramento River were sown. Nine days after germination an initial harvest (H1) was done. Treatments were started 11 days after germination. Each treatment subjected the cottonwood seedlings to a different level of water stress. In T1 – T4, the water table was lowered at a rate of 1, 2, 3, and 4 cm/d, respectively. In T5 the seedlings were irrigated twice a day and the rhizopod was allowed to freely drain. Treatments T1, T2, and T3 were continued for a total of 40 days during which an additional 3 harvests were made of individual seedlings (H2 – H4). Treatment T4 had complete plant death within the first 16 days after the treatments began. Treatment 3 had complete death by H4, 40 days after germination. Following H4, treatments T1 and T5 were continued for another 30 days. Each harvest consisted of the extraction of 3 individual plants from each rhizopod. After each harvest, plant samples were processed to measure total dry biomass, shoot biomass, root biomass, leaf area, maximum root depth, and root distribution in 10 cm depth increments.

Experiment Results and Discussion
Differences between treatments were observed in overall biomass production, root depth, and plant survival (Figure 2, Tables 1, 2). Plants in all treatments grew at nearly the same rate through H2. However, by H3 the plants in T5 had grown larger than the others and the plants in T4 were smaller. By H4 the plants in T5 had grown to more than 60% and 40% larger than plants in T1 and T2, respectively. The T4 plants had died and the last surviving T3 plants were 50% the size of the plants in T1.

The different total biomass values observed between treatments is explained by a combination of water logging and drought stress. In the beginning of the experiment the sediments were equally saturated in all treatments and the similar biomass values recorded for H1 reflect this. Treatments were started two days after H1. By H2, there was still little difference between the treatments in terms of average plant biomass. However, the root depth was greatest for T4 as those plants attempted to grow into the moist sediment above the rapidly declining water table. By H3 the plants in T5 were clearly growing at the most rapid rate. This was due to the combination of good root aeration...
caused by the draining of the T5 rhizopods and ample supply of water supplied by twice daily irrigations. In contrast, the T1 and T2 plants had access to ample water but were experiencing water logging stress caused by the relatively slow water table decline rates. Plants in T3 and T4 were stressed by a lack of water and no T4 plants survived beyond H3. By the time of H4 the plants in T5 were continuing their relatively rapid growth. Plants in T3 were severely stressed by lack of water and almost completely dead. The plants in T2, while having produced more biomass than T1 plants, were suffering from drought stress and survival was rapidly declining (Figure 2).

Table 1. Total average per-plant biomass (mg).

<table>
<thead>
<tr>
<th>Harvest/Date</th>
<th>T1</th>
<th>T2</th>
<th>T3</th>
<th>T4</th>
<th>T5</th>
</tr>
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<tbody>
<tr>
<td>H1/June 27</td>
<td>2.64</td>
<td>3.14</td>
<td>2.28</td>
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<td>2.51</td>
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<td>H2/July 9</td>
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<td>12.06</td>
<td>9.23</td>
<td>13.04</td>
<td>12.00</td>
</tr>
<tr>
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<td>22.84</td>
<td>25.02</td>
<td>22.52</td>
<td>10.70</td>
<td>36.86</td>
</tr>
<tr>
<td>H4/July 28</td>
<td>31.51</td>
<td>36.22</td>
<td>16.54</td>
<td></td>
<td>52.31</td>
</tr>
</tbody>
</table>

Table 2. Total average maximum root depth (cm).

<table>
<thead>
<tr>
<th>Harvest/Date</th>
<th>H1</th>
<th>H2</th>
<th>H3</th>
<th>H4</th>
</tr>
</thead>
<tbody>
<tr>
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<td>8.50</td>
<td>7.50</td>
<td>7.50</td>
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<tr>
<td>H2/July 9</td>
<td>17.00</td>
<td>21.00</td>
<td>16.00</td>
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</tr>
<tr>
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<td>44.00</td>
<td>34.00</td>
<td>20.00</td>
</tr>
<tr>
<td>H4/July 28</td>
<td>44.29</td>
<td>59.09</td>
<td>40.00</td>
<td>43.13</td>
</tr>
</tbody>
</table>

Figure 2. Seedling survival during controlled water table decline experiments. T1 = 1 cm/d, T2 = 2 cm/d, T3 = 3 cm/d, T4 = 4 cm/d, and T5 was irrigated twice daily and allowed to freely drain.

MODEL DEVELOPMENT

Plant growth in RHEM is represented by a series of equations that are used to simulate dry matter or biomass production, the partitioning of growth between above ground (shoot) and below ground (root) biomass, and the depth distribution of roots in the root zone. Equations for potential and actual transpiration are used to estimate seedling water stress. Due to the importance of root zone water availability for the survival of cottonwood seedlings, particular attention was devoted to the distribution of root growth within the root zone. Initial inspiration for this model was derived from Adiku et al. (1996). The model assumes that potential stressors such as nutrients, heat, and shading are not a factor. Only water stress is considered.
Plant Growth

The first step in computing seedling growth is the calculation of potential growth assuming no water stress (Neitsch et al., 2005):

\[
\frac{dW_{g_{\text{max}}}(t)}{dt} = eS(1 - e^{-kL}) \tag{1}
\]

where \( W_{g_{\text{max}}}(t) \) is the dry matter per unit area under ideal conditions (kg m\(^{-2}\)), \( e \) is the radiation use efficiency (kg MJ\(^{-1}\)), \( S \) is the incident radiation (MJ m\(^{-2}\) s\(^{-1}\)), \( k \) is the light extinction coefficient, and \( L \) is the leaf area (m\(^2\) m\(^{-2}\)).

The radiation use efficiency was reduced under high vapor pressure deficit conditions using the following relationship (Neitsch et al., 2005):

\[
e = \begin{cases} 
  e_{vpd=1} - \Delta e_{act} \left( vp d - vpd_{thr} \right), & vp d > vpd_{thr} \\
  e_{vpd=1}, & vp d \leq vpd_{thr}
\end{cases} \tag{2}
\]

Where \( e_{vpd=1} \) is the radiation use efficiency when the vapor pressure deficit is 1 kPa, \( \Delta e_{act} \) is the rate of decline in the radiation use efficiency per unit decrease in the vapor pressure deficit (kg MJ\(^{-1}\) kPa\(^{-1}\)), \( vpd \) is the vapor pressure deficit (kPa), and \( vpd_{thr} \) is the threshold vapor pressure deficit above which the plant will have a reduced radiation use efficiency (kPa).

The actual growth rate is calculated as the potential growth rate limited by a factor that is a function of the degree of water stress:

\[
\frac{dW_{g_{a}}(t)}{dt} = fg \frac{dW_{g_{\text{max}}}(t)}{dt} \tag{3}
\]

where \( W_{g_{a}}(t) \) is the actual dry matter per unit area (kg m\(^{-2}\)), and \( fg \) is a growth reduction function based on the ratio of actual transpiration (Ta) to potential transpiration (Tp) where Tr is the threshold value of Ta/Tp. This ratio serves as a sign of drought stress since Ta is reduced relative to Tp as soil moisture conditions become limiting. For Ta/Tp values less than 1.0 growth is limited.

\[
fg = \begin{cases} 
  1.0, & \frac{T_a}{T_p} = 1.0 \\
  \frac{T_a}{T_p}, & \frac{T_a}{T_p} < 1.0
\end{cases} \tag{4}
\]

Once actual biomass production is calculated, biomass is partitioned to either the shoot or root system. Greenhouse observations have shown that cottonwood seedlings divert more energy to root growth when soil moisture conditions are limiting (Kranjcec, et al, 1998). In this model, dry matter growth is partitioned between roots and shoots as a function of the ratio Ta/Tp.

\[
\frac{dW_{s_{a}}(t)}{dt} = (1 - RMRatio) \frac{dW_{g_{a}}(t)}{dt} \tag{5a} \textbf{ Shoots}
\]

\[
\frac{dW_{r_{d}}(t)}{dt} = [RMRatio] \frac{dW_{g_{a}}(t)}{dt} \tag{5b} \textbf{ Roots}
\]

where \( W_{s_{a}}(t) \) and \( W_{r_{d}}(t) \) are the actual shoot and root dry matter, respectively (kg m\(^{-2}\)). The root-mass-ratio, RMRatio, is a partitioning factor and a function of Ta/Tp.
At $\frac{T_a}{T_p}$ values greater than $T_{src}$ the root-mass-ratio is equal to a minimum value, $RMR_{min}$. For decreasing values of $\frac{T_a}{T_p}$ less than $T_{src}$, plant growth is increasingly allocated to the roots until a maximum root-mass-ratio value is reached at the threshold value of $T_{mrc}$. For $\frac{T_a}{T_p}$ values less than $T_{mrc}$ the root-mass-ratio is equal to the maximum value, $RMR_{max}$.

Once the shoot biomass is calculated, a relationship between shoot biomass and leaf area can be used to calculate the change in leaf area relative to plant growth:

$$L(t) = f_L W_s(t) \quad [7]$$

Where $L$ is leaf area ($m^2$) and $f_L$ is a factor that converts shoot biomass to leaf area ($m^2$ leaf area/ kg m$^{-2}$).

**Root Growth**

After plant biomass is partitioned into roots and shoots, the root front is extended, the new root mass is distributed over the root zone, and the root mass is converted into root length for eventual use in the calculation of actual transpiration.

The root front velocity of cottonwood seedlings varies according to changing soil moisture conditions (Amlin and Rood, 2002). Under conditions of drought stress seedlings will increase the root front velocity. Presumably this is an effort by the plants to grow roots into sediment with more available water. In the coarse soils typically found along the Sacramento River ample supplies of soil water are only available in the zone of capillary rise close to the water table. In coarse soils, this zone is relatively thin whereas in finer grained soils the zone is thicker. Results from the controlled study indicate that seedlings extend the root front at a rate of $1 – 3.5$ cm/d. Additionally, it was observed that roots grow up to 15 cm below the water table. These two phenomena are captured in the following equation:

$$\frac{dDr(t)}{dt} = V_r fvr(\Psi) \quad [8]$$

where $Dr(t)$ is the depth of the root zone (cm) at time $t$, $V_r$ is the root front velocity (cm/h), and $fvr$ is a root front velocity reduction factor that is a function of the pressure head at the root front. The root front velocity is a function of the degree of water stress.

$$V_r = \begin{cases} 
V_{r_{max}}, & \frac{T_a}{T_p} < T_2 \\
V_{r_{max}} - \frac{\frac{T_a}{T_p} - T_2}{T_1 - T_2} (V_{r_{max}} - V_{r_{min}}), & T_2 \leq \frac{T_a}{T_p} \leq T_1 \\
V_{r_{min}}, & \frac{T_a}{T_p} > T_1
\end{cases} \quad [9]$$

The root front velocity reduction factor limits root growth into sediments where the pressure head is greater than 15 cm:

$$fvr = \begin{cases} 1.0, & \Psi < 15 \\
0.0, & \Psi \leq 15 \quad [10]
\end{cases}$$
Next, the root growth is distributed within the root zone. Adiku, et al (1996) address this issue with a model that predicts root growth as a function of the overall increase in root biomass and the moisture distribution with depth:

\[
\frac{\partial W_r(z,t)}{\partial t} = W_r(z,t)P_r\left[1-\frac{W_r(z,t)}{W_{r_{Am}}}\right]E_f(S_\theta) \tag{11}
\]

where \(W_r(z,t)\) is the root mass per unit area (kg m\(^{-2}\)) at depth \(z\) and time \(t\). \(W_{r_{Am}}\) is the maximum root mass of the plant (kg m\(^{-2}\)), \(P_r\) is the net root proliferation rate (s\(^{-1}\)), and \(E_f(S_\theta)\) is a function that limits root growth as a function of soil moisture where \(S_\theta\) is the soil saturation. This serves as a proxy for soil strength which increases as soil moisture declines and therefore limits root extension.

\[
E_f = \begin{cases} 
0.0, & S_\theta < S_L \\
\frac{S_\theta - S_L}{S_c - S_L}, & S_L \leq S_\theta \leq S_c \\
1.0, & S_\theta > S_c
\end{cases} \tag{12}
\]

Adiku et al (1996) present a method for solving Eq 10 without specifying the net root proliferation rate, \(P_r\). Using this method the right hand side of Eq 10 is solved for each depth increment assuming that \(P_r\) is constant with depth and time. These values are then divided by the sum of values for all depth increments in the root zone thereby creating a weighting factor that is used to distribute the total root growth over the depth increments and allowing for cancellation of \(P_r\):

\[
\Delta W_{r_{Ai}} = \frac{W_r(t-1)}{\sum_{j=1}^{N} W_r(t-1)} \frac{W_{r_{Am}}}{\sum_{j=1}^{N} W_{r_{Am}}} \Delta W_r(t) \tag{13}
\]

where \(\Delta W_{r_{Ai}}\) is the change in root mass per unit area at depth increment \(i\) during time step \(t\), \(W_r(t-1)\) is the root mass per unit area at depth increment \(i\) during the previous time step, \(S_{\theta_{Ti}}\) is the soil saturation in soil depth increment \(i\) during the previous time step, and \(N\) is the total number of depth increments in the root zone.

Finally, the increase in root dry matter per unit area, \(\Delta W_{r_{Ai}}\), is converted to root length per unit area for each depth increment in the root zone by multiplying by specific root length, \(c\) (m kg\(^{-1}\)), which is calculated as a function of the soil moisture conditions:

\[
\frac{dR_{r_{Ai}}(t)}{dt} = c(\theta(t)) \frac{dW_{r_{Ai}}(t)}{dt} \tag{14}
\]

where \(R_{r_{Ai}}(t)\) is the total root length per unit area (m m\(^{-2}\)) for root zone layer \(i\). The value of specific root length, \(c\) (m kg\(^{-1}\)) varies as a function of soil saturation in root zone layer \(i\):

\[
c = S_\theta * (c_{\text{max}} - c_{\text{min}}) + c_{\text{min}} \tag{15}
\]

where \(c_{\text{max}}\) and \(c_{\text{min}}\) are the maximum and minimum values of specific root length, respectively.
**Plant Transpiration**

Potential transpiration by a seedling is estimated using a modified version of the Penman-Monteith equation found in Zhang, et al. (1997).

\[
T_{p}^{t} = L \cdot A(t) \cdot \frac{sR_{n} + 0.93 \cdot \rho_{air} \cdot C_{p} \cdot D / \rho_{b}}{\lambda(s + 0.93 \gamma(2 + \rho_{s} / \rho_{b}))} \cdot \rho H_{2}O \quad [16]
\]

where \( T_{p}^{t} \) is the transpiration rate per unit leaf area (g m\(^{-2}\)s\(^{-1}\)), \( \lambda \) is the latent heat of vaporization of water (J g\(^{-1}\)), \( L \) is the total leaf area of the tree canopy (m\(^{2}\)), \( s \) is the slope of the saturation vapor pressure curve (kPa °C\(^{-1}\)), \( R_{n} \) is the net radiation absorbed per unit leaf area (W m\(^{-2}\)), \( \rho_{air} \) and \( C_{p} \) are the density (kg m\(^{-3}\)) and specific heat capacity (J kg\(^{-1}\) °K\(^{-1}\)) of air at constant pressure, \( D \) is the saturation vapor pressure deficit of the air (kPa), \( r_{s} \) is the leaf boundary layer resistance (s m\(^{-1}\)), \( \gamma \) is the psychrometric constant (kPa °C\(^{-1}\)), \( \overline{R}_{s} \) is the minimum stomatal resistance and \( \rho_{H_{2}O} \) is the density of water (g m\(^{-3}\)). In the approach used in RHEM, the stomatal resistance is set at a minimum value based on field observations of unstressed plants.

The actual transpiration is calculated using a two step process. First, maximum transpiration limited by the root’s ability to uptake water is calculated:

\[
T_{d}^{R} = \sum_{i=1}^{N} q_{i} R_{t}^{i-1} R W (\theta_{t}^{i-1}) \quad [17]
\]

where \( T_{d}^{R} \) is the root limited maximum transpiration rate for timestep \( t \) (m\(^{3}\) H\(_{2}O\) m\(^{2}\) t\(^{-1}\)), \( q_{i} \) is the maximum uptake of water per unit root length per unit time (m\(^{3}\) H\(_{2}O\) m\(^{-1}\) root t\(^{-1}\)), \( R W \) is a dimensionless factor that limits transpiration as a function of soil moisture content during the previous timestep, and \( T_{d}^{R} \) is the root limited maximum transpiration for depth increment \( i \). The \( R W \) function limits transpiration when pressure head, \( \Psi \), is either below a threshold value, \( P_{2} \), (water limiting) or above a threshold value, \( P_{1} \), (water logging) (Feddes, et al., 1978, Simunek, et al. 1999). For values of \( h \) below the wilting point (h\(_{wp}\)), transpiration ceases (Figure 6).

\[
RW = \begin{cases} 
0.0, & \Psi < P_{3} \\
\frac{\Psi - P_{3}}{P_{2} - P_{3}}, & P_{3} \leq \Psi \leq P_{2} \\
1.0, & P_{2} \leq \Psi \leq P_{1} \\
\frac{\Psi - P_{1}}{P_{0} - P_{1}}, & P_{1} \leq \Psi \leq P_{0} \\
0.0, & \Psi > P_{0} 
\end{cases} \quad [18]
\]

The second step in calculating the actual transpiration is to compare the maximum transpiration that can be supported by the roots, \( T_{d}^{R} \), to the potential atmospheric transpiration demand, \( T_{p} \), for the current timestep. When \( T_{d}^{R} \) is greater than or equal to \( T_{p} \) the transpiration is partitioned into the root zone depth increments using the following equation.

\[
T_{a} = T_{p} / T_{d}^{R} (T_{d}^{R}) \quad [19a]
\]

Otherwise, the transpiration in each root zone depth increment is given by:

\[
T_{a} = T_{d}^{R} \quad [19b]
\]
MODEL CALIBRATION

During calibration the first step was to set all parameters to values observed during the controlled experiments or found in the literature. These included most of the parameters in the model (Table 3). The next step was to run the model and determine if HYDRUS 2-D was solving properly. This process required adjusting the time step controls and the minimum allowable pressure head at the soil surface, hCritA, which is used to calculate the atmospheric flux boundary condition. For finer grained soils this value is often on the order of -10,000 cm, however, in this case a sand was modeled and use of such small values resulted in numerical instability. Using recommendations found on the HYDRUS user forum, a pressure head with a water content equivalent to 2% of the pore space was used. This value was -50 cm. The next step of the process was to adjust parameters relating to water logging, drought stress and root growth until simulated values matched observed values. This was done in several steps:

1. The potential growth parameters from Equation 2, $e_{vpd=1}$, $\delta_{edcl}$, $vpd_{thr}$ were set using literature values. The light extinction coefficient, $k$, was adjusted so that simulated total plant biomass for T5 equaled the observed value at H4. The calibrated value was 0.64 which is very close to the commonly used value of 0.65 (Neitsch et al., 2005). During this step the observed biomass for T5 was the target based on the assumption that plants in this treatment grew at nearly the potential rate.

2. The water logging parameters $P_0$ and $P_1$ from Equation 18 were adjusted until the simulated biomass value for T1 matched the observed value at H4. These values were set at -18 and -21 cm, respectively. These parameters were adjusted using the plants in T1 as the target because this treatment had the largest amount of water logging stress due to it having the slowest rate of water table decline.

3. The drought stress parameters $P_2$ and $P_3$ from Equation 18 were adjusted until the simulated biomass value for the plants in T2 matched the observed value for H4. These values were set at -39 and -42 cm, respectively.

4. The root growth parameters $T_1$, $T_2$, $S_{th}$, and $S_{fl}$ from Equations 9 and 12 were adjusted until the root front velocity and root mass depth distribution matched the observed values. Their values were 0.95, 0.85, 0.25, and 0.1, respectively.

Results from the calibration show the model simulated the observed biomass and maximum root depth values from H4 (Tables 4 and 5). All values were within 5% of the observed values for T1, T2, and T5 which were the calibration targets. The simulated values for T3 were less accurate with the biomass value over predicted by 20% and the maximum root zone depth over predicted by 89%. These results suggest the root front velocity algorithm (Equation 8) does not contain some necessary features. It may be that the root front extension rate, while initially increasing during periods of drought stress, may be limited during periods of severe stress which would explain the relatively low observed value at H4.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Value</th>
<th>Equation</th>
<th>Variable</th>
<th>Value</th>
<th>Equation</th>
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<td>2</td>
<td>$\Delta_{edcl}$</td>
<td>0.0008 kg MJ$^{-1}$ kPa$^{-1}$</td>
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</tr>
<tr>
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<td>2</td>
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<td>6</td>
</tr>
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<td>6</td>
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<td>$T_{src}$</td>
<td>0.9</td>
<td>6</td>
<td>$f_{L}$</td>
<td>0.015 m$^2$ leaf area/ kg m$^{-2}$</td>
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<tr>
<td>$T_1$</td>
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<td>9</td>
<td>$T_2$</td>
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<td>9</td>
</tr>
<tr>
<td>$V_{r \min}$</td>
<td>0.075 cm/d</td>
<td>9</td>
<td>$V_{r \max}$</td>
<td>0.235 cm/d</td>
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<tr>
<td>$c_{max}$</td>
<td>300,000 m kg$^{-1}$</td>
<td>15</td>
<td>$c_{min}$</td>
<td>100,000 m kg$^{-1}$</td>
<td>15</td>
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<th>Equation</th>
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<td>$T_5$</td>
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<tr>
<td>$T_2$</td>
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<td>$T_3$</td>
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Table 3. Model parameters set using observations or literature.

Table 4. Observed and simulated per-plant biomass (mg) at H4.
Table 5. Observed and maximum root depth (cm) at H4.

<table>
<thead>
<tr>
<th></th>
<th>T1</th>
<th>T2</th>
<th>T3</th>
<th>T4</th>
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<td>59.09</td>
<td>40.00</td>
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<tr>
<td>Simulated</td>
<td>41.78</td>
<td>59.56</td>
<td>75.56</td>
<td>44.87</td>
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As the main purpose of the model is to predict cottonwood seedling survival under drought stress, another metric by which the accuracy of the calibrated model can be judged is to compare predicted drought stress to observations of seedling stress and death. To do this, a plot was made of an average daily drought stress factor which represents the value of $\frac{Ta}{Tp}$ when drought stress reduces the transpiration below potential (Figure 3). From this plot it can be seen that the simulated plant in T4 experienced drought stress starting July 7. By July 15 the stress factor had reached a value of less than 0.4. This coincides with the observed death of all seedlings in T4 (Figure 2). In the case of T3 the drought stress factor reached a value of 0.4 by July 28 which corresponds with the observation of complete plant death for this treatment (Figure 2). The simulated plant in T2 started to experience drought stress on July 14. This stress increased through the end of the month and this corresponds with the decreasing plant survival observed for T2 (Figure 2). This agreement between simulations and observations of drought stress and seedling death provides confidence that the model is simulating these processes well.

Figure 3. Daily average reduction in potential transpiration due to drought stress.

**CONCLUSIONS**

Results from the controlled experiments show that cottonwood seedlings established in sands are unlikely to survive an average water table decline rate in excess of 2 cm/d over a period of 30 days or more. However, this conclusion is based on several factors. First, the soil type used in the controlled experiment was sand. In coarser soils such as gravels, cottonwood survival during a water table recession would be more difficult due to a more limited zone of capillary rise and a relatively lower plant available soil water holding capacity associated with coarser sediments. In contrast, soils with more silt and clay content would have a relatively thicker capillary zone and more soil water holding capacity above the capillary rise zone. Atmospheric conditions also exert important effects on plant survival. If the vapor pressure deficit had been lower than what was observed during the controlled experiments, it is possible that the seedlings would have been able to withstand more rapid water table decline rates. Based on these factors, it is reasonable to conclude that atmospheric conditions, water table decline rates and the length of time that plants experience these conditions determine their survival in a particular geomorphic setting.
REFERENCES


