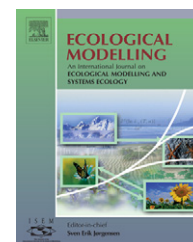


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Developing a dynamic model to predict the recruitment and early survival of black willow (*Salix nigra*) in response to different hydrologic conditions

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ABSTRACT

Disruption of the natural flood regime in floodplain-river ecosystems can decrease plant diversity and lead to dominance by one or a few species that can tolerate the altered conditions. Restoration of native plant communities requires naturalization of the flood regime, to prevent dominance by one species and to promote germination and growth of a variety of native species. Black willow (*Salix nigra*), cottonwood (*Populus deltoides*) and silver maple (*Acer saccharinum*) are native, flood-tolerant trees that often form monocultures and shade out moist-soil plants (e.g., millets) in waterfowl management areas and restoration sites on floodplains along the Illinois River and some portions of the Upper Mississippi River. Since the moist-soil plants provide ecological goods and services that are not provided by pioneering tree species alone, such as food for migratory waterfowl, wetland managers try to limit recruitment of these pioneering tree species with herbicides, disking and mowing. Other natural resource managers value the same species for reducing bank erosion or as potential sources of rapidly growing biomass for generation of electricity. From either perspective, it is important to identify characteristics of flooding regimes that might encourage these tree species or keep them in check. We developed a dynamic simulation model to predict the recruitment and seedling growth of one of these pioneering trees (black willow, *Salix nigra*) in response to flood timing and duration over three growing seasons following germination. Tree germination and survival respond to capillary water depth, flood duration, length of growing season and timing of seed dispersal. The model was tested over a range of elevations (132.3–132.9 m) that were observed on aerial photos as the tree line in the vicinity of River Km 201 along the Illinois River. The model was validated to the extent that it simulated establishment of black willow at the elevation of the observed tree line and variability of seedling growth in response to the flooding regime (i.e., poor or no survival or growth at elevations below the tree line where floods were longer-lasting and more frequent). Although more experimental or field-based information on seedling physiology should be gathered to refine the model, the prototype model is useful for exploring effects of alternative water level regimes. The model provides a framework for simulating any pioneering tree species that colonizes floodplains, if the required species-specific physiological information is available.

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1. Introduction

Disruption of the natural flood regime in floodplain-river ecosystems can decrease plant diversity and lead to dominance by one or a few species that can tolerate the altered conditions (Middleton, 1999, 2002). In the floodplains of the Illinois River and the Upper Mississippi River, changes in disturbance patterns from presettlement times to the present probably contributed to dramatic shifts observed in vegetation patterns (Nelson et al., 1998). According to data recorded in 1817 by surveyors from the U.S. General Land Office at the confluence of the Illinois and Mississippi rivers, upstream of St. Louis, prairies covered 46% of the floodplain and trees covered 35% (Nelson et al., 1998). The term “prairies” would have included low-lying, open areas without trees that were occupied by what today are termed “wet prairies” or “moist soil plant communities”. Today, 56.5% of the floodplain in the same area is developed, mostly for agriculture and trees occupy three times more of the remaining area (18.6%) than do the prairies (5.6%). The contemporary forest in the lower Illinois River is dominated (44.9%) by just one species (*Acer saccharinum*, silver maple), whereas the presettlement forest had a more even distribution of abundance among species and *A. saccharinum* only ranked seventh in relative dominance (5.8%; Nelson et al., 1994).

Nelson et al. (1998) attribute the presettlement prevalence of prairies in the floodplains and the species diversity of the forests to a combination of two disturbances: fire in the higher elevations and flooding in the lower elevations. They recommend a return to an intermediate level of disturbance (*sensu* Connell, 1978); i.e., prescribed flooding and fire regimes to restore plant communities on floodplains managed by state and federal agencies, but they do not specify what these regimes should be in terms of frequency, intensity and seasonal timing. Plant models that respond to flooding would be useful in predicting the effects of alternative disturbance regimes. As described next, waterfowl managers and conservationists along the middle Illinois River and portions of the Upper Mississippi regard black willow (*Salix nigra*) and cottonwood (*Populus deltoides*) as major problems, although the relative dominance of the remaining floodplain forests by willows, at least along the lower Illinois River, was actually less in 1992 (5.3%) than in 1817 (8.3%) and dominance by cottonwood was likewise less (4.7% in 1992 versus 10.1% in 1817; Nelson and Sparks, 1998). The differences in the pioneering tree species that currently dominate particular river reaches within the same climatic zone may be attributable to differences in the regulated water regimes within and among reaches that favor one species over another (Yin and Nelson, 1996). The problem with the three pioneering tree species mentioned above (silver maple, black willow and cottonwood), from a natural resource manager's point of view, has less to do with dominance in the remaining floodplain forests than with competition with the moist-soil plant community.

The moist-soil plant community includes at least one federally listed threatened species (the decurrent false aster, *Boltonia decurrens*) and several state-listed species (Smith et al., 2005). This plant community also provides ecological goods

and services that are not provided by the pioneering tree species alone (e.g., the millets, *Echinochloa* sp., provide food for migratory waterfowl). Once established, these pioneering trees are persistent and expensive for managers to control. For example, tens of thousands of dollars are spent annually in individual wildlife refuges in Illinois and Missouri trying to control black willow by spraying with herbicide and disking and mowing (Laubhan and Hamilton, 1988; personal communication with Ross Adams at The Chautauqua National Wildlife Refuge, Havana, Illinois). “Naturalization” of the flood regime (defined as an approximation of the presettlement flood regime, to which the native plant communities were presumably adapted), by modifying dam operations or using gates to control inundation in leveed areas of the floodplain, might provide an alternative to physical and chemical control. However, the exact flooding requirements are not known and would have to be specified in areas where water levels are now controlled. In contrast to the view that black willows, cottonwoods and silver maple need to be controlled, others regard these same species as potential sources of biomass for energy production. Douglas Blodgett, the Great Rivers Area Director for The Nature Conservancy (personal communication), believes that some parts of the floodplain might be restored and other parts might be used for commercial production of flood-tolerant species for fuel, while still accommodating floods and providing some degree of moist-soil habitat for wildlife. The power station on the Illinois River at Havana, and some other power stations along the Mississippi River, are capable (with some modifications of operation) of burning wood or other renewable fuel sources, as well as fossil fuels. Black willow is a good candidate for biomass for energy production (Kuzovkina and Quigley, 2005). A model that predicts responses of candidate species to water levels would be a useful tool for site selection and water management to optimize production.

Here, we report the development of a dynamic simulation model to predict the recruitment and seedling growth of one of the pioneering trees mentioned above, black willow, in response to flood timing and duration over three growing seasons following germination. The prototype model is akin to and intended to supplement the moist-soil plant model developed by Ahn et al. (2004b). We apply the model to a representative site along the Illinois River, near Havana, Illinois, where there are state and federal wildlife refuges and hunting and fishing areas, and where The Nature Conservancy is converting an agricultural drainage and levee district back to a floodplain.

2. Site description

During the past 100 years, the hydrologic regime of the Illinois River has been altered by urban and agricultural development of the watershed; locks and dams for commercial navigation; levees that protect floodplain agriculture from flooding; water diversion from Lake Michigan (Sparks et al., 1998; Schneider, 2000). Recently, public interest in the conservation and recovery of natural services has prompted major public and private investments along the Illinois River in habitat rehabilitation

and enhancement, stream bank stabilization and conversion of former agricultural drainage and levee districts back to functioning floodplains. Two non-governmental organizations, The Nature Conservancy and the Wetlands Initiative, have acquired three agricultural drainage and levee districts along the Illinois River and are currently in the early stages of restoring their natural functions. Both organizations see these projects as models for floodplain naturalization in the entire Upper Mississippi Basin. The largest of these projects is The Nature Conservancy's 3046-ha Emiquon Floodplain Restoration Project, where gates will be used to manage the reconnection of the river to its floodplain. Here and at other sites throughout the Upper Mississippi Basin, the development and use of predictive models, including the black willow model we describe, should assist in designing and managing these reconnections.

3. Methods

3.1. Simulation methods

This model predicts the early development of the black willow population for a 1-m² floodplain patch at a given land elevation, based on the flooding regime and duration of seed dispersal with respect to the growing season. It explicitly models seedling survival and growth, without attempting to model vegetative reproduction and/or competitive exclusion. The water level is based on the river stage hydrograph and the height of the capillary fringe (Mahoney and Rood, 1998). The capillary fringe is the zone above the water table wherein moisture is conducted upward between soil particles and is available for plant uptake. The level of available water determines success in germination and tree growth, in connection with seedling height and root depth. Seedling mortality occurs when the water level either inundates the trees or drops below the root depth (Table 1). The differential equations of the model were integrated using the modeling software STELLA™ (v.8.1.1), a high-level visual-oriented programming and simulation language for use on personal computers (Richmond and Peterson, 1997). Euler's method was used as the integration method, with a time step of 1 day, for a simulation period of 3 years (1095 days).

3.2. Model assumptions and description

In our model, flooding directly or indirectly affects: (1) germination, production and mortality of willow seedlings; (2) additions or subtractions from the seed bank due to dispersal into or out of the simulated 1-m² floodplain patch (Fig. 1). The differential equations used in the dynamic model are included in Table 1, and state variables, forcing functions and parameters/coefficients of the model are described in Table 2. The assumptions used in the model follow, with references:

1. Early black willow seedling growth is a linear function of time (Donovan et al., 1988; Pitcher and McKnight, 1991).
2. Black willow seedling growth ceases during complete inundation, then resumes (Hosner, 1960).

3. Total number of growing season days for first-year seedlings is 120, starting 15 June and ending 13 October, based on Ahn et al. (2004a,b).
4. Standing water level is the difference between the water level elevation and the elevation of the floodplain patch being modeled (Table 1; Fig. 2).
5. Belowground water level is the difference between the elevation of the floodplain patch and the sum of the river level plus the capillary fringe (Mahoney and Rood, 1998). This measure becomes relevant only when the river level drops below the elevation of the floodplain patch by more than the dimension of the capillary fringe.
6. Black willow seedlings have varying sensitivity to drought and inundation depending on growth stage (Hosner, 1958, 1960).
7. Seedling mortality depends on duration of either inundation or drought conditions during the growing season (Hall and Smith, 1955; Hosner, 1958, 1960; Mahoney and Rood, 1998; Karrenberg et al., 2002).
8. Seedlings that survive resume growth the following growing season at the same point they left off (i.e., no mortality outside the growing season assumed).
9. Competition with other plants, and different sedimentation and nutrient levels have no impact on the growth of black willow.

3.3. Seedling growth stages

The model tracks black willow seedlings by seedling cohorts, which are initiated in each time step during seed dispersal. Because a cohort has a distinct age in days and must be followed over time, the state variable *Tree* is a conveyor object (Richmond and Peterson, 1997). Seedlings are modeled as having three major potential growth stages (G1–G3), corresponding to three seasons' growth. A G2-stage seedling is treated as in its second year of growth. These annual stages are divided into substages to allow the seedling height and root depth to be treated in finer detail, and to ensure that the effects of short-duration flood/drought events that might occur within a year are reflected in the model (Table 3). The growing season length may be varied within the model; as a consequence, the annual stages do not indicate age precisely; due to the potential variability in growing season and seed dispersal periods, a seedling cohort might start its third growing season in substage G2c, for example, or a cohort in substage G3a might be near the end of its second growing season. For this reason, the length of substage G3c has been extended to accommodate modeling longer growing seasons (Table 3).

The model makes *arrays* for state variables and parameters (Fig. 2). In STELLA, arrays provide a very powerful mechanism for managing the visual complexity associated with repetitive model structures, thus making it possible to easily construct and modify very detailed models (Richmond and Peterson, 1997). Arrays are defined to keep track of multiple instances (i.e., several stages of seedling growth in our model) or levels of similar objects. In the model, a single array (*DevStage*) is defined to allow certain parameters and variables to vary by growth stage; an example is the variable for flood tolerance (*FloodTolerance*), which has higher values for later growth

Table 1 – Differential equations used in the black willow model

$dTree[DevStage]/dt = germ[DevStage] + adv2[DevStage] - adv1[DevStage] - Mort[DevStage]$ where	
$dTree[DevStage]$	Number of trees at a given growth stage [DevStage]
$germ[DevStage]$	Germination of seeds. As follows for stage G1s (all other stages are zero). $germ[G1s] = \text{if SeedDispersal} = 0 \text{ then } 0 \text{ else if WaterLevel} < 5 \text{ and WaterLevel} > 0 \text{ then Seeds else } 0$
$adv2[DevStage]$	Passes tree cohort up to next array level (zero for G1s). $adv2[DevStage] = adv1[prevDevStage]$
$adv1[DevStage]$	Removes tree cohort from a given array level. $adv1[G1s] = \text{CONVEYOR OUTFLOW ARREST IF } GS = 1$
$Mort[DevStage]$	Tree mortality (conveyor leakage function). $Mort[DevStage] = \text{LEAKAGE OUTFLOW // LEAKAGE FRACTION} = \text{if } GS = 0 \text{ then } (DroughtKill[DevStage] + FloodKill[DevStage]) \text{ else } 0 \text{ // NO-LEAK ZONE} = 0$
SeedDispersal	Timing of seed dispersal as a function of start and duration. $SeedDispersal = \text{if TIME} \geq (0 + DispStart) \text{ and TIME} \leq (0 + DispStart + DispLength) \text{ then } 1 \text{ else. If TIME} \geq (365 + DispStart) \text{ and TIME} \leq (365 + DispStart + DispLength) \text{ then } 1 \text{ else. If TIME} \geq (730 + DispStart) \text{ and TIME} \leq (730 + DispStart + DispLength) \text{ then } 1 \text{ else } 0$
DroughtKill[DevStage]	Drought mortality condition per growth stage. $DroughtKill[DevStage] = \text{if (ContDrought[DevStage]} > \text{DroughtTolerance[DevStage]) then } 1 \text{ else } 0$
FloodKill[DevStage]	Flood mortality condition per growth stage. $FloodKill[DevStage] = \text{if (ContInund[DevStage]} > \text{FloodTolerance[DevStage]) then } 1 \text{ else } 0$
WaterLevel	$WaterLevel = \text{if (Hydrograph} \times 100) > \text{Elevation then (Hydrograph} \times 100) - \text{Elevation else. if ((Hydrograph} \times 100) + \text{CapF}) > \text{Elevation then } 0 \text{ else (Hydrograph} \times 100) + \text{CapF} - \text{Elevation}$
GS	Growing season off/on (1/0), used to arrest conveyors. $GS = \text{if TIME} \geq (0 + GSstart) \text{ and TIME} \leq (GSstart + GSlength) \text{ then } 0 \text{ else. If TIME} \geq (365 + GSstart) \text{ and TIME} \leq (365 + GSstart + GSlength) \text{ then } 0 \text{ else. If TIME} \geq (730 + GSstart) \text{ and TIME} \leq (730 + GSstart + GSlength) \text{ then } 0 \text{ else } 1$
$dContDrought[DevStage]/dt = DrCount[DevStage]$ where	
$DrCount[DevStage]$	Bi-flow resetting counter for continuous days of drought. $DrCount[DevStage] = \text{if } GS = 0 \text{ then, if WaterLevel} < \text{RootDepth[DevStage]} \text{ then } 1, \text{ else } -\text{ContDrought[DevStage]}, \text{ else } -\text{ContDrought[DevStage]}$
$InCount[DevStage]$	Bi-flow resetting counter for continuous days of flood inundation. $InCount[DevStage] = \text{if } GS = 0 \text{ then, if WaterLevel} > \text{TreeGrowth[DevStage]} \text{ then } 1, \text{ else } -\text{ContInund[DevStage]}, \text{ else } -\text{ContInund[DevStage]}$
$RootDepth[DevStage]$	Root depth determined from ratio to tree height. $RootDepth[DevStage] = -\text{RootRatio} \times \text{TreeGrowth[DevStage]}$
$dTreeGrowth[DevStage]/dt = Hadv2[DevStage] - Hadv1[DevStage]$ where	
$Hadv1[DevStage]$	Function removing tree cohort height by growth stage. $Hadv1[DevStage] = \text{CONVEYOR OUTFLOW // ARREST IF } GS = 1$
$Hadv2[DevStage]$	Replacement function for tree cohort height. As follows for stage G1a. $Hadv2[G1a] = \text{if } Hadv1[G1s] = 0 \text{ then } 0, \text{ else if } adv1[G1s] = 0 \text{ then } 0, \text{ else } (0 \times \text{SeedDispersal}) + (Hadv1[G1s] + \text{DryGrowDays[G1s]} \times \text{PerDiemGrowth})$
$dCohortsPerStage[DevStage]/dt = Cadv2[DevStage] - Cadv1[DevStage]$ where	
$Cadv1[DevStage]$	Function removing tree cohort height by growth stage. $Cadv1[DevStage] = \text{CONVEYOR OUTFLOW // ARREST IF } GS = 1$
$Cadv2[DevStage]$	Replacement function for tree cohort counter. As follows for stage G1a. $Hadv2[G1a] = \text{if } adv1[G1a] = 0 \text{ then } 0 \text{ else, } 0 \times \text{SeedDispersal} + \text{Cadv1[G1a]}$
$dDryGrowDays[DevStage]/dt = \text{StandWater[DevStage]} - \text{PassingDay[DevStage]}$ where	
$\text{StandWater[DevStage]}$	Water at or above tree height condition. $\text{StandWater[DevStage]} = \text{if WaterLevel} > \text{TreeGrowth[DevStage]} \text{ then } 0 \text{ else } 1$
$\text{PassingDay[DevStage]}$	Removes standing water day counter from array. $\text{PassingDay[DevStage]} = \text{CONVEYOR OUTFLOW // ARREST IF } GS = 1$
$dTotalGerm/dt = \text{GermCount}$ where	
GermCount	Counts total number of seeds germinated for simulation. $\text{GermCount} = \text{germ[G1s]}$

stages than for early ones. The array DevStage thus defines the 10 growth substages; any arrayed parameter in the model, then, has 10 values associated with it, each corresponding to a growth substage. In the case of conveyor objects (e.g., Tree, TreeHeight, etc.), there are 10 “belts” on the conveyor, each of which has its own transit time. For the first annual growth stage (G1), the transit times are scaled up from 8 days in substage G1s to 64 days in G1c. This is to ensure that the initial seedling stage (G1s) represents the critical time length for germinating seedlings, particularly with regard to desiccation (McLeod and McPherson, 1973). The doubling of stage lengths for the remainder of the G1 stages ensures that the earliest seedling development is modeled the most closely, particularly since early seedling mortality is often high (Karrenberg et al., 2002).

3.4. Flooding regime

The water level for the floodplain patch is determined both for the purposes of assessing standing water height and for determining the depth to water below ground when there is no standing water. When there is no standing water, the below-ground level is river height plus capillary fringe (parameter CapF; Table 2). The capillary fringe will vary for different substrate soil types. When the river level (from the hydrograph) exceeds the elevation of the floodplain patch, there is standing water and the WaterLevel parameter is positive (Table 1). When the river level is at or below the elevation of the floodplain patch, the depth of available water is determined by adding the height of the capillary fringe to the river level (not to exceed the floodplain elevation), and WaterLevel is zero or

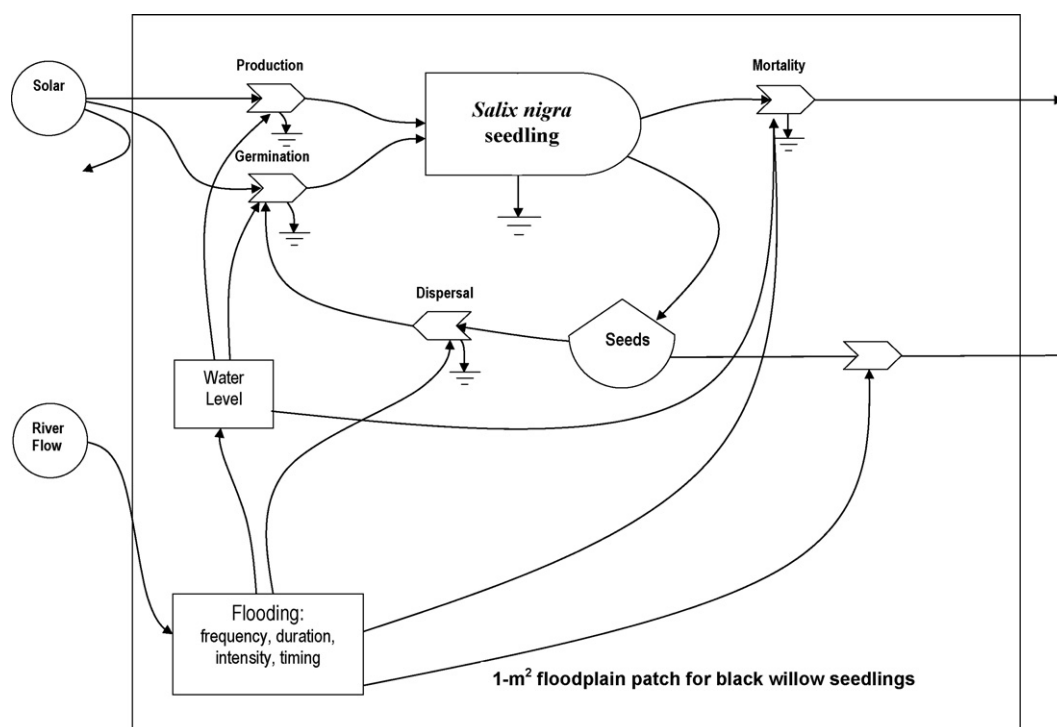


Fig. 1 – Conceptual model of black willow seedlings in a floodplain patch. The model focuses on the recruit and seedling growth of black willow. The seed and seedling of black willow respond to water level, flow regime and sunlight. Symbols are from Odum (1983).

negative (Table 1). The water level thus rises or falls with the hydrograph, but the available water level in the soil is always at or higher than the river level.

3.5. Germination and survival

Seed germination is modeled as a function of seed dispersal, which is a simple function of time. Dispersal is treated as a binary condition (occurrence, non-occurrence) for each time step, depending on the start time (DispStart) and duration of the seed release period (DispLength) (Table 2). Since black willow seeds remain viable only a short time, any seed cohort failing to germinate within a day is considered not to be viable (Brinkman, 1974; Karrenberg et al., 2002). The number of germinating seeds per dispersal day, parameter Seeds (Table 2), is an estimate based on the maximum seedling density ($\# \text{ m}^{-2}$, all species) observed in demography plots and the overall proportion of seedlings accounted for by black willow in a multi-year study of riparian seedling recruitment (Dixon, 2003). Once a seed cohort has germinated, the cohort is counted in the CohortsPerStage state variable and the number of individual seedlings is tracked in the Tree state variable (Table 2). As discussed previously, these arrayed variables are conveyor objects with associated transit times for each growth substage. Each seedling cohort enters/exits at a different time, and simple return function (e.g., adv1 and adv2 for Tree) passes the cohort from the end of one conveyor level to the start of the next (Table 1). For the Tree state variable, the mortality function Mort is a conveyor leakage function, which removes seedlings from the conveyor (Tables 1 and 2).

Seedling mortality is modeled as due to drought or inundation. Whenever either condition has persisted beyond the tolerance for the given growth stage (Table 3), the entire stage of seedling cohorts is lost. For each growth stage, the number of continuous drought or inundation days is calculated in ContDrought and ContInund, depending on water level and seedling height/root depth (Tables 1 and 2). For ease in interpretation, a number of output variables present aggregate values for the major stages (e.g., TotalG1, TotalG2, TotalG3, see Table 2).

3.6. Seedling growth

Seedling growth is a linear function of elapsed time in the growing season minus no-growth days (i.e., during inundation conditions). The state variable DryGrowthDays is the counter used to track the elapsed growth time (Table 2). The growth function computes the height for each extant cohort and the height is accumulated through the duration of a stage and stored as the variable TreeGrowth. Dividing TreeGrowth by CohortsPerStage computes the average height for the stage, TreeHeight, an arrayed parameter used for the mortality functions to determine whether or not a drought or inundation condition exists (Tables 1 and 2). In the case of drought, where root depth is the concern, the arrayed parameter RootDepth is a simple fraction of TreeHeight (Table 2). Calculated this way, the root depth probably becomes unrealistic for the late seedling stages, but the importance of the root depth to the model diminishes in later stages because a later-stage tree is very

Table 2 – State variables, forcing functions and parameters used in the black willow model

Symbol	Name	Value/units	Source
State variables			
Tree	Number of trees per growth stage	Trees	Calculation
TreeGrowth	Tree cohort heights by stage (sum)	cm	Calculation
CohortsPerStage	Conveyor/counter for seedling cohorts	Cohorts	Calculation
DryGrowDays	Number of days of normal tree growth by growth stage	Time (days)	Calculation
ContDrought	Length of current drought condition by growth stage	Time (days)	Calculation
ContInund	Length of current inundation condition by growth stage	Time (days)	Calculation
Forcing functions			
Hydrograph	River stage elevation, various years used (HydroXXX, selected by Hystart)	m	Ahn et al. (2004a,b)
Elevation	Elevation of floodplain	cm	Input variable
CapF	Capillary fringe height	65 cm	Mahoney and Rood (1998)
GSstart	Growing season start day	166	Ahn et al. (2004a,b)
GSlength	Growing season duration	120	Ahn et al. (2004a,b)
Seeds	Number of germinating seeds per day	3 m ⁻²	Estimated based on Dixon (2003)
DispStart	Starting day of year for seed dispersal	166	Dixon (2003)
DispLength	Length of seed dispersal period	30 (days)	Dixon (2003)
WaterLevel	Level of available water relative to floodplain elevation	cm	Calculation
Parameters and coefficients			
FloodTolerance	Number of survivable consecutive days inundation by growth stage	Time (days)	Hosner (1958, 1960), Hall and Smith (1955)
DroughtTolerance	Number of survivable consecutive days drought by growth stage	Time (days)	McLeod and McPherson (1973) and estimate
PerDiemGrowth	Normal amount of growth per day by growth stage	0.834 cm day ⁻¹	Linear regression from Donovan et al. (1988)
RootRatio	Ratio of root length to tree height	0.6	Estimate based on McLeod et al. (1986); Mahoney and Rood (1998)
DaysPerStage	Number of days in each growth stage	Time (days)	Assigned
Symbol	Name	Value/units	
Model output parameters			
PercentSuccess	Percent survival of germinated seeds	%	
TotalPop, TotalG1-3	Total population counts for all stages	Trees	
TotalMort	Conveyor leakage sum, all stages	0–9.8	
TotalPDK, TotalPFK	Summed drought/flood kill coefficients	0–10	

Table 3 – Seed germination and seedling growth stages developed for black willow model to divide the growing season each year for the 3-year simulation period

Stage	Substage (DevStage array name)	Days in stage (GS days total)	Tolerance, drought/ flood (days)
G1	G1s	8(8)	3/7
	G1a	16(24)	5/8
	G1b	32(56)	7/30
	G1c	64(120)	30/30
G2	G2a	40(160)	30/90
	G2b	40(200)	30/90
	G2c	40(240)	30/90
G3	G3a	40(280)	30/90
	G3b	40(320)	30/90
	G3c	240(560)	30/90

G1 presents a stage for seed germination and the first-year seedling growth. G2 and G3 are stages for the second and the third-year growth, respectively. Seed and seedling tolerances for drought and flooding used in the model are given.



The model has been designed to run over a 3-year time frame. Several sets of 3-year period hydrographs at or near River Km 201, the mid point of the La Grange reach of the Illinois River, were obtained from a U.S. Geological Survey (USGS) gauging station at Havana, Illinois, where the record began in 1887 (Table 4). Since consecutive years were not always available, the 3-year series used were: 1946–1948, 1951/57/58, 1961/63/64, 1964/66/67, 1971–73 and 1984/85/87 (Table 4). The

output parameters, TotalPop and PercentSuccess, which represent the total seedling population surviving through the simulation period and the percentage of successfully germinated seeds, were evaluated as indicators of successful establishment of black willow seedlings at a given range of floodplain land elevations, including the projected treeline elevations (132.3–132.9 m). Total seedling population was also evaluated for multiple runs of the model along a range of land elevations for each of the hydrographs, and compared against similar runs changing the parameters, such as capillary fringe and timing of seed dispersal to see how sensitively the model responds to those changes. Since there is a lack of information available on seedling physiology and growth some param-

Table 4 – Three-year mean water levels and their variation at River Km 201 along the Illinois River used for multi-year simulations

Simulation	Year(s)	Mean water level	Variation (CV) in water levels
1	1887	131.11	0.62
2	1946–48	132.25	0.88
3	1951/57/58	132.49	0.83
4	1961/63/64	131.69	0.55
5	1964/66/67	132.03	0.78
6	1971–73	132.78	1.00
7	1984/85/87	132.84	1.10
8	1987	132.99	1.30

ter values were obtained through reasonable, literature-based assumptions in the simulations.

4. Results

4.1. Qualitative test of the model

We used a total of eight sets of 3-year hydrographs to test the model (Table 4). Both the mean values and variation (coefficient of variation, CV) in water levels have increased through time, due to many factors, including construction of navigation dams to maintain water levels for barge traffic during the summer low flow season (Koel and Sparks, 2002). Water levels were nearly 2 m higher in 1987 than 100 years earlier, and the variation (CV) more than twice as great (Table 4).

At the elevation of the tree line (132 m), seedling populations were produced each of the 3 years and populations produced in the first and second years survived into the third year (Fig. 3). Since black willows do grow and survive at the tree line, this result is a qualitative validation of the model.

4.2. Sensitivity to capillary fringe and start of seed dispersal

When we increased the capillary fringe from 65 to 100 cm, with no change in the start of seed dispersal, the total population of each growth stage increased significantly (Fig. 3c). When we kept capillary fringe at 65 cm, but started seed dispersal earlier, on day 151 instead of day 166, recruitment was poor and total seedling population decreased markedly (Fig. 3d).

The same combinations of capillary fringe and start date for seed dispersal were next run at several land elevations, starting just above the tree line elevation (133.9 m) and decreasing in 10-cm decrements to an elevation below the tree line (131.0 m). Capillary fringe and start date had the same relative effects on total population as in the previous simulation at the tree line elevation. For most of the six 3-year hydrographs we used, populations were greatest within an elevation range of 131.0–132.5 m, but with capillary fringe increased to 100 cm, populations occurred at higher (and presumably, drier) elevations in some years (the 1951 set, which included 1951, 1957 and 1958, due to missing data between 1951 and 1957; Fig. 4b). We also conducted multiple simulations with the same modifications of capillary fringe and the start of seed dispersal as we changed land elevations for 10 cm increments over the elevation interval 131–133.9 m, which includes projected treeline elevation range (132.3–132.9 m) at the location

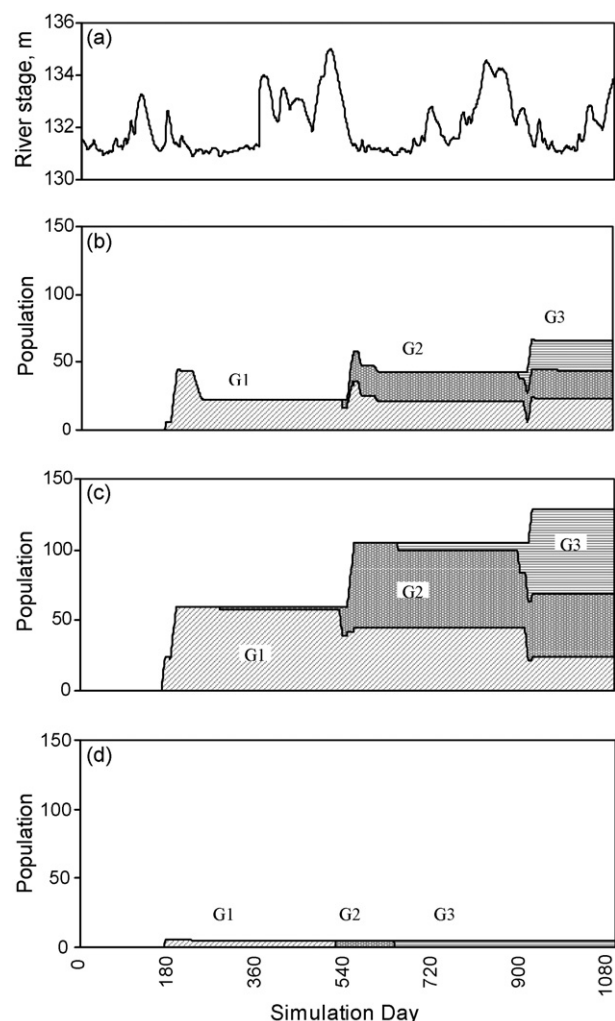


Fig. 3 – Model output for the simulation with 3-year hydrograph (1964/66/67) at River Km 201 along the Illinois River. The figures show total population for stages G1–G3, as well as hydrograph. All simulations were run at near projected treeline elevation of 132 m. Shown are (a) hydrograph used for simulation; (b) output using capillary fringe (CapF) set equal to 65 cm, start of seed dispersal (DispStart) set equal to day 166; (c) CapF = 100 cm, DispStart = day 166; (d) CapF = 65 cm, DispStart = day 151.

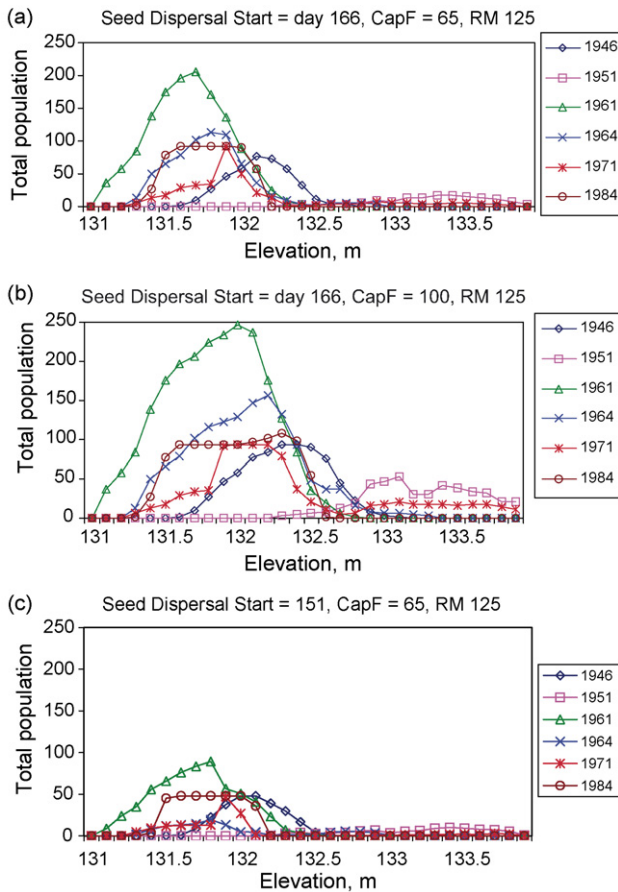


Fig. 4 – Simulation results with varying capillary fringe and the start of seed dispersal. The legends show the starting year of 3-year period hydrographs (see Table 4) used in the model. The figures show total seedling population (TotalPop) over the range of floodplain land elevation (131–133.9 m) with (a) capillary fringe (CapF) set equal to 65 cm, start of seed dispersal (DispStart) set equal to day 166; (b) CapF = 100 cm, DispStart = day 166; (c) CapF = 65 cm, DispStart = day 151.

of the river. The model predicts that black willow seedlings will do well at elevations below the tree line, where they are known to compete with the moist-soil plant community. However, no or little germination occurred and so no or little populations established at the lower and upper ends of the elevation range, which were outside the projected treeline elevation range (132.3–132.9 m). These elevations were presumably too wet or too dry, given the drought and flood tolerances of black willow seedling built into the model.

5. Discussion

The peak population densities achieved in the simulations were generally high (as high as 280 seedlings/m²), compared to those observed for black willow seedling plots in some studies (Dixon, 2003). On the Wisconsin River, within quadrats placed in seedling patches, Dixon (2002, 2003) shows average fall densities of first year black willow seedlings of 5.9 seedlings/m²

(standard deviation, S.D. = 34.5, n = 80, range = 0–300). The range of seedling density was quite wide in that study. Densities of older seedlings (mostly second year) were 3.8 (S.D. = 15.7, n = 58, range = 0–111) for spring samples, 2.5 (S.D. = 8.0, n = 81, range = 0–57) for summer and 4.6 (S.D. = 9.0, n = 15, range = 1–33) for fall. Density information for *Salix* spp. (*S. amygdaloides* and others) is also available along the Platte River, Nebraska. Across about 18 years of demography data (Johnson, 2000), average fall densities of the first growing season seedlings were about 4.5 seedlings/m² (S.D. = 98, range = 0–103). If one only looks at plots with seedlings, mean densities were 8.8 (S.D. = 12.2). Seedling densities by fall of the second year were 7.7 (range = 0–120) for all measured plots and 9.5 for only pots with seedlings present. Average densities by third, fourth and fifth years were 7.8, 1.9 and 6.3 seedlings/m². However, maximum third, fourth and fifth year densities were 97, 27, 19 m⁻², based on progressively smaller sample sizes, showing much higher density. Overall, maximum seedling density of black willow found is 300 seedlings/m² by the end of the first growing season (additional information provided by Mark Dixon and Carter Johnson).

Based on the limited information our model estimates for total seedling population densities seem close to maximum seedling density observed in the field. Currently, there is a lack of information available on the seedling density of black willow in the Illinois river floodplain. The model prediction will become more realistic with more information being garnered in the future. Also, it seems that some of the assumptions of the model may be too generous, and it is likely that some of the parameters applied, parameters Seeds and CapF in particular (Table 2), do not fit well the actual conditions for the Illinois River floodplain. Many of the parameters used in this model may demand calibration against more appropriate field data. Nonetheless, the model served its original purpose of predicting a range of elevations where black willow will achieve a successful early growth and shade out moist-soil plants (Ahn et al., 2004a,b).

With a change in the capillary fringe parameter to 100 cm, the recruitment range overlapped the observed treeline (mainly within 131.3–132.7 m, see Figs. 3c and 4b), as was expected since the level of available water increased by 35 cm. The population counts were also higher for the increased CapF scenario, as would be expected, due to lower drought-induced mortality. These results illustrate the importance of the CapF parameter, which ideally would have been determined from field observations of Illinois River floodplain soils, rather than from literature values based on other rivers (Mahoney and Rood, 1998).

Under the 2-week-early seed dispersal scenario (day 151, Figs. 3d and 4c), the range of recruitment was reduced and shifted somewhat for each simulation, particularly apparent for the 1964 series, where it was 131.6–132.0 m, roughly half the range for day 166 seed dispersal simulation (Fig. 4c). The total populations reached for the early dispersal scenario were also lower. These results suggest the sensitivity of seedling recruitment and survival to the timing of the seed dispersal.

The model predicted recruitment of black willow at elevations lower (within 131.3–132.3 m) than that of the observed treeline (132.3–132.9 m; Fig. 4a), and thus encroaching into moist-soil plant territory theoretically (Ahn et al., 2004a,b),

which might change as the conditions of the model gets modified with more information on the responses of black willow seedlings to drought and flooding available. The next step would be to fine-tune the model and then to estimate the critical range of floodplain elevation that is ecohydrologically indicative of achieving a certain level of black willow population with various hydrologic patterns at a certain target location along the river. Then, the model prediction for a range of elevation for black willow can be analyzed along with that of moist-soil plants to provide useful information to recover moist-soil plants (Ahn et al., 2006).

Whereas the model currently predicts seedling recruitment at lower elevations than the observed treeline, the treeline reflects the cumulative impact of flood disturbance in a way not incorporated in the model, including catastrophic disturbance and non-growing season mortality. Though the model results otherwise appear reasonable, the model has not yet been subjected to extensive testing. The model is not particularly complex, but it would benefit from analysis to identify and correct any model artifacts leading to unwelcome errors.

5.1. Factors excluded from the model

For the purpose of keeping the model relatively simple, a number of factors influencing seedling success have been excluded. Since the model does not address mortality outside the growing season or beyond drought and inundation, factors, such as ice scouring during winter flows (Auble and Scott, 1998; Mahoney and Rood, 1998), catastrophic disturbance (Sparks and Spink, 1998; Yin, 1998) or others are underrepresented. The model also lacks any intra- or inter-species competitive effects, even though canopy cover surely would affect seedling recruitment. Nor does this model address soil substrate composition, except insofar as it is reflected in the capillary fringe height, even though sediment texture influences germination and growth (McLeod and McPherson, 1973; Schaff et al., 2003). As it is not a spatial model, this model cannot address the effects of erosion and sedimentation, even though these influence and are influenced by the establishment of willow stands in alluvial rivers (Johnson et al., 1976; Shafroth et al., 1998; Sparks and Spink, 1998). This model only looks at the early development of black willow populations, but longer-term establishment of black willow likely depends upon large-scale disturbance (Romme et al., 1998; Sparks and Spink, 1998; Yin, 1998).

5.2. Application of the model

The model could be used to prescribe management procedures either to encourage, or to discourage colonization and growth of black willow. As mentioned in Section 1, black willow might be a candidate species for fuel for power plants along the river. The model can be used to predict more precisely (than with the previously developed moist-soil plant model alone, Ahn et al., 2004b) where the tree line will develop on restoration sites, such as Emiquon. The predictions are useful in planning at what elevations to plant trees and where to plant or encourage more inundation-tolerant species. At sites, where water level management is possible, flooding can be prescribed that maintains species diversity.

The model provides a framework for modeling other tree species. The only requirement is data on the inundation tolerance, germination temperatures and times, and other physiological information that may be available in the literature. If not, the information needs to be collected in field or laboratory experiments. The model could readily be extended to longer time periods than 3 years and to other floodplains by specifying the growing season and seed dispersal dates. The growth stages in the array (DevStage, Table 2) could also be changed easily should better growth categories be identified. The model would benefit from a more sophisticated growth regression function, however, based on more extensive data.

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