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A DYNAMIC MODEL TO PREDICT RESPONSES OF MILLETS (*ECHINOCHLOA* SP.) TO DIFFERENT HYDROLOGIC CONDITIONS FOR THE ILLINOIS FLOODPLAIN–RIVER

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ABSTRACT

Millets grow on floodplain mud flats exposed when seasonal floods recede, and the seeds of this plant are an important food source for waterfowl during their spring and autumn migrations in the Mississippi Flyway. Productivity of millets along the Illinois River has declined because of unnaturally frequent floods that inundate the mud flats and drown the plants during the summer growing season. These small floods are caused by operation of the navigation dams on the main channel and by alterations of the floodplain and tributary watersheds and channels. Predictive models are needed to evaluate the most cost-effective combination of approaches for restoring plant productivity. We developed a moist-soil plant model that simulates millet growth on 1 m^2 in response to daily water levels during the summer growing season. The model responds to daily water depth, flood timing (within the growing season), and flood duration, and was qualitatively verified using historical (1938–1959) water levels and plant coverage for three areas along the Illinois River. In the absence of untimely floods, the model predicts net aboveground primary productivity of $\sim 500\,g\,m^{-2}\,yr^{-1}$ and plant heights of up to 130 cm by the end of the growing season. As expected, growth declines with decreasing land elevation or with more frequent flooding (or a shorter duration of the dry period) at the same elevation. A dry period of > 85 days is required to achieve at least 50% of maximum production during the growing season, which is somewhat longer than the 70-day recommendation based on reported field observations. The model predictions of plant success or failure agree with historical observations, indicating that water regime is a major factor limiting plant success.

KEY WORDS: millets; moist-soil plant; floodplain restoration; hydrology; river restoration; Illinois River; ecological modelling; wetland

INTRODUCTION

Like many rivers in developed countries, the hydrologic regime of the Illinois River has been substantially altered by locks and dams, floodplain levees, upland drainage, channelization of tributaries, and water diversion (Sparks *et al.*, 1998, 2000; Schneider, 2000). A significant problem on the Illinois River is that low water levels that naturally occurred for several weeks or longer in the summer season have been artificially raised (and incidentally destabilized) to benefit commercial navigation.

The higher water level and more frequent flooding profoundly affect many plants that thrive in the Illinois floodplain–river ecosystem, particularly moist-soil plants that grow on mud flats when seasonal floods recede. The seeds, rhizomes and tubers of these plants are an important food source for waterfowl during the spring and autumn migrations in the Mississippi Flyway (Bellrose *et al.*, 1979; Fredrickson and Taylor, 1982; Havera, 1999). Moist-soil sites also provide diverse habitats that support a variety of wildlife species. In some moist-soil units, over 80% more species can be found than on adjacent row crops (Fredrickson and Taylor, 1982). Herons, rails, prairie and marsh passerines, upland game birds and mammals that are rare or lacking on agricultural fields commonly use moist-soil sites. Inundation of floodplain areas for an extended period during germination and early seedling development is detrimental to establishment of moist-soil plants. In addition, black willow and cottonwood will quickly colonize and dominate floodplains if water recedes too early (Toner and Keddy, 1997).

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Dynamic models approximate the response of a system to time-variable changes (Hannon and Ruth, 1997). They have been commonly applied in studies of wetland biogeochemistry and nutrient retention (Mitsch and Reeder, 1991; Kadlec, 1997; Wang and Mitsch, 2000), floodplain forests (Phipps, 1979; Phipps and Applegate, 1983; Pearlstine *et al.*, 1985), and vegetation dynamics in semi-permanent prairie wetlands (Poiani and Johnson, 1993). No simulation model to our knowledge has been developed to describe the effects of different flooding conditions on moist-soil plant growth. In this paper, we describe a model developed to evaluate effects of alternative inundation regimes on millets, a group of moist-soil plants preferred by waterfowl in the floodplains of the Upper Mississippi Basin. The model predicts the response of millet growth to flood timing and duration over the growing season. We also discuss the applicability of the model to other plant species and other floodplain–river ecosystems.

Illinois River and hydrology

The Illinois River, with a drainage area of 75 156 km^2, is a major tributary of the Mississippi River. For thousands of years, the flood pulse of the Illinois River had a predictable pattern of a spring flood followed by a summer low flow (Junk *et al.*, 1989). Even today, despite the presence of navigation dams and levees, the lower Illinois River retains a seasonal flood and summer low flows on about 50% of its original floodplains. The National Research Council (1992) judged that it was one of three large floodplain–river ecosystems in the USA with high potential for further recovery. However, the natural flow pattern of the Illinois River has become erratic due to hydrologic effects of development (Sparks, 1995; Sparks *et al.*, 2000; Koel and Sparks, 2002) (Figure 1). The pre-dam period before the 1890s may be considered representative of the relatively undisturbed condition of the river. The river now has unnaturally high water levels in the summer, often with several ‘little’ floods in mid-summer.

Millets

Moist-soil plants tolerate saturated soils and seasonal flooding, but must have a dry period to germinate (Bellrose *et al.*, 1979, 1983; Ellison and Bedford, 1995). In the Illinois floodplain–river system, they typically grow in areas that are flooded in spring, but are dry in summer. Several species of millets (*Echinochloa* sp.) grow on moist sites throughout the Illinois River valley. These include Duck millet (*Echinochloa crus-galli* (L.) Beauv.), Japanese millet (*Echinochloa frumantacea* (L.) Beauv.), and Walter’s millet (*Echinochloa walteri* (Pursh) Heller). These summer annuals grow up to 1.5 m tall and single plants can produce up to 20 000 seeds (Keeley and Thullen, 1989). They prefer wet, but not flooded soils, and warm temperatures to germinate. Although millets have been studied as weeds competing with rice plants in rice-growing regions (Dickerson, 1964; Ahmadi, 1979; Keeley and Thullen, 1989), Japanese millet is commonly planted in floodplain areas along the Illinois River that are managed for waterfowl (personal communication with R. Adams, manager, Chautauqua National Wildlife Refuge (NWR),

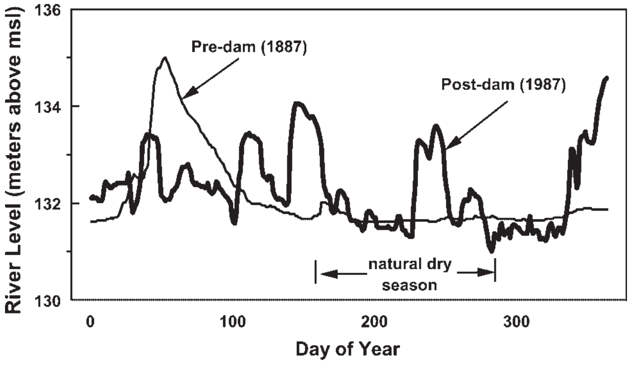

Figure 1. The natural water level pattern of a spring flood followed by a summer low flow on the Illinois River has been replaced since navigation dams were built by unnaturally rapid fluctuations year-round (msl: mean surface level). The 1887 water levels are representative of the pre-dam pattern and the 1987 levels are representative of the post-dam pattern, although there are year-to-year variations in both periods. Hydrographs were provided by the Illinois State Water Survey

Havana, Illinois). The seeds and vegetative parts of the millet species are eaten by 17 species of waterfowl, upland game birds and many non-game birds (Bauder, 1999; Fredrickson and Taylor, 1982; Laubhan and Hamilton, 1988). Rabbits, muskrats and deer also consume the leaves and seed heads. Flowering and seed production occur from June to October. Once millets germinate, Fredrickson and Taylor (1982) recommend that they not be reflooded until the plants are at least 15 cm tall to avoid mortality and poor seed production.

METHODS

Simulation methods

We developed a model to predict responses of millets to daily water depth. Two submodels were developed: hydrology and plant growth. The hydrology model calculated water depths (difference between daily river water elevations and land elevation of the floodplain) and number of flooding days in the floodplain at various land elevations. Water depth and flooding days determined plant response to daily water regime as the plant germinated and grew through its assigned growth stages (see Plant growth stage simulation). A set of non-linear, ordinary differential equations was used to describe the submodels. The model was integrated using the software STELLA$^{\text{TM}}$ VII, a high level visual-oriented programming and simulation language for use on PC (Richmond and Peterson, 1997). Euler's method (Richmond and Peterson, 1997) was used as the integration method with a time step of 1 day. Simulations ran over a 1-year period (from 1 January to 31 December).

Growth requirements for the model were obtained from previous literature on millets (Dickerson, 1964; Ahmadi, 1979; Fredrickson and Taylor, 1982) and limited field observations in the Illinois floodplain–river system (personal communication with R. Adams, Chautauqua NWR). We fine-tuned the model by adjusting selected parameters (e.g., plant solar efficiencies in each stage of plant growth) to make the simulation of plant growth follow a logistic growth equation (Table I).

Plant growth stage simulation

A logistic equation was developed to describe millet height after the seedling stage (5–7 cm assumed) as a function of growing days, based on literature (Sung *et al.*, 1987; Keeley and Thullen, 1989; Caton *et al.*, 1999).

$$\text{Plant height (cm)} = \frac{150}{[1 + 25 \times \exp(-0.1 \times \text{day})]}$$

This equation divides the 120-day growing season of millets (Bellrose *et al.*, 1979) into four successive stages of specific durations, thus making the model sensitive to hydrologic conditions several times during plant growth. Millets begin to germinate when soil temperature reaches 17°C (Bellrose, 1941; Bellrose *et al.*, 1979), and reach 150 cm tall, a maximum height for the species, about 90 days later (Table I). The four growth stages (GS1–GS4)

Table I. Logistic growth of millet plants developed to divide the growing season (120 days)[a] in modelling

Growing day[b]	Height (cm)[a]	% of maximum growth[c]
0	6	seedling
21	37.5	25
32	75	50
43	112.5	75
89	149.5	100
120	150	100

[a] Calculated based on an equation: Plant height = 150/[1 + 25 × exp(−0.1 × growing day)].
[b] Growing day corresponding to different stages of millet plant growth during the growing season; note that the plant reaches full growth on day 89 within a 120-day growing season as it follows an S-type growth pattern.
[c] Maximum known height of the plant species (e.g. 150 cm for *Echinochloa* sp.).

represent 25, 50, 75, and 100% of maximum plant growth (Table I). For our model we chose days 166 to 285 as a typical growing season and divided it as follows:

Growing season: 120 days from day 166 to day 285 (Bellrose *et al.*, 1979)
Seedling: germination starts when soil temperature reaches 17°C through to day 165
GS1: day 166 to day 186
GS2: day 187 to day 198
GS3: day 199 to day 209
GS4: day 210 to day 285

Model assumptions and description

A conceptual model of a moist-soil plant community in a floodplain patch is shown in Figure 2. Differential equations used for the model are presented in Table II and state variables, forcing functions, and parameters are summarized in Table III. The model is described in detail below. Several assumptions were made in developing the moist-soil plant model since limited information is available on plant responses to water regime.

1. Plants follow an S-type logistic growth curve with a maximum height of 150 cm (Sung *et al.*, 1987; Keeley and Thullen, 1989; Caton *et al.*, 1999).
2. Total number of growing days for plants is 120 days (Bellrose *et al.*, 1979).
3. Growing season for plants begins 15 June and ends 13 October (Bellrose *et al.*, 1979).
4. First killing frost is approximately 15 October.
5. Water depth in a floodplain patch is simulated as the difference between river water elevation and floodplain land elevation.
6. Minimum duration of the dry period for plant maturation and seed production is 70 days (Bellrose *et al.*, 1979).
7. Plants resume their germination or growth when floods recede unless the plants are overtopped or a lethal flood duration occurs.
8. Sensitivity of the plants to the flooding regime varies with each of their growth stages (Table II).

Hydrology submodel

The hydrology submodel uses daily water elevations at a chosen elevation of the floodplain to calculate several state variables. State variables, Days of F0 to F4 (Table II, Figure 3), are the number of flooding days (when water level of a unit floodplain > flooding tolerance of plants) during each stage of plant growth (1–4). Other hydrologic variables were calculated, including duration of dry period in each stage of plant growth and total number of dry days during the growing season (from day 166 to day 285) to investigate how they are associated with plant performance (Table II, Figure 3).

Relatively high land elevations, projected as tree lines by Wlosinski and Wlosinski (2001), were used in calibrating the model. Several other simulations were conducted as we decreased the elevation from the tree line by 10–30 cm until the model predicted zero biomass and plant height. Those simulations allowed us to calculate how plant heights and productivity change with decreasing elevations (or with more frequent flooding).

Plant growth submodel

The plant growth submodel simulates productivity and growth in height of millet plants in each of the four growth stages (GS1–GS4). This submodel is initiated when seeds germinate at a certain soil temperature (>17°C at the depth of 5 cm assumed) and terminated upon the death of the plants when the first frost occurs. Soil temperature is known to be a forcing function for seed germination (Sung *et al.*, 1987; Keeley and Thullen, 1989; Galatowitsch and Budelsky, 1999). The soil temperature equation used a cosine function (Table II), which was calibrated with mean monthly soil temperature data in central Illinois from March to September: simulated soil temp. (°C) $= 0.6808 \times$ observed soil temp. (°C) $+ 7.8265$, $R^2 = 0.9528$.

After germination the plant follows its S-type growth curve if not interrupted by flooding. The plant grows and produces biomass (Biom 1) at the first stage of growth modeled (Table II). Flood duration and water depths in the

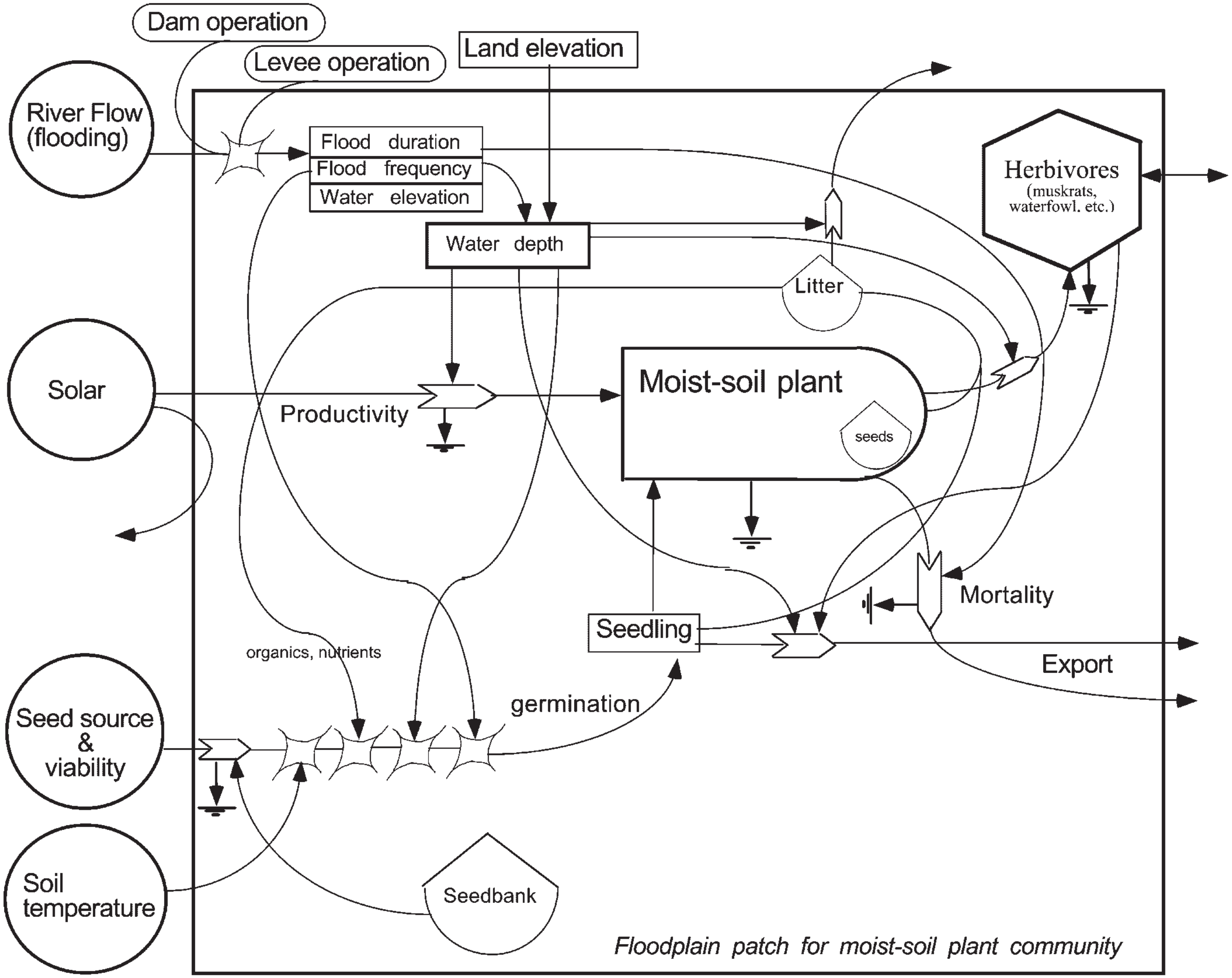

Figure 2. Conceptual model of a moist-soil plant community in a floodplain patch. The moist-soil plants respond to natural and man-made water level and flow fluctuations, light, temperature, availability of propagules from within and outside the patch, and to consumption by herbivores (including muskrats and waterfowl). Symbols are from Odum (1983)

Table II. Differential equations used in the plant model (based on the simulation for Quiver Lake, 1938)

Hydrology submodel	
FWD	Floodplain water depth (cm) If Hydroyear = 1938 then (WL1938-F_elevation) × 100
F_elevation	Floodplain elevation being assumed (m)
WL1938	Hydroyear 1938, the year for an annual hydrograph used in the model Annual hydrograph of the Illinois River in 1938 at Quiver Lake (provided by Illinois Water Survey)
dDays_of_F0–F4/dt = FD0–FD4	
Where	
Days_of_F0–F4	Accumulated number of flooding days in each period from germination through stage 4 (day)
FD0–FD4	Number of flooding days (day). If time >133 and time <165.5 and WD > 0 then 1 else 0 for FD0; If time >165.5 and time <186.5 WD > 0 then 1 else 0 for FD1; If time >186.5 and time <198.5 and WD > 0 then 1 else 0 for FD2; If time >198.5 and time <209.5 and WD > 0 then 1 else 0 for FD3; If time >209.5 and time <286.5 and WD > 0 then 1 else 0 for FD4
Time	Calendar days out of 365 days (day)
WD	Floodplain water depth (= FWD) (cm)
dDays_of_d1–d4/dt = dd1–dd4	
Where	
Days_of_d1–d4	Accumulated number of dry days in each stage from stage 1 to 4 (day)
dd1–dd4	Number of drawdown days (day), if time >165.5 and time <186.5 and Biom1>0 then 1 else 0 for dd1; If time >186.5 and time <198.5 and Biom2 >0 then 1 else 0 for dd2; If time >198.5 and time <209.5 and Biom3 >0 then 1 else 0 for dd3; If time >209.5 and time <286 and Biom4 >0 then 1 else 0 for dd4
Number of drawdown days	Total number of dry days (day), if time > 166 and time < 286 then Days_of_d1 + Days_of_d2 + Days_of_d3 + Days_of_d4 else 0
Plant growth submodel	
dSeedling/dt = germination - G1 - S_Mort	
dBiom1/dt = G1 + Grow1 - G2 - Mort1	
dBiom2/dt = G2 + Grow2 - G3 - Mort2	
dBiom3/dt = G3 + Grow3 - G4 - Mort3	
dBiom4/dt = G4 + Grow4 - Death - Mort4	
Where	
Seedling	Plant biomass produced during seedling stage (g m^{-2})
Biom 1–4	Plant biomass produced in each stage from Biom1 to Biom 4 (g m^{-2})
Germination	Seed germination (g day^{-1}). If time < 166 and Stemp > 17 and WD < 0.01 then Solar × Se/(R × 52) else 0
Grow1–4	Plant productivity at growth stage 1 . . . 4 (g day^{-1}), If G1 > 0 and WD < 0.1 then Solar × Se1 × GS1_/(R × 20) else if G1 = 0 and WD < 0.1 then Solar × GS1 × ((Se + Se1)/2)/(R × 20) else 0 for Grow1; If G2 > 0 and WD < 0.1 then Solar × Se2 × GS2_/(R × 11) else if G2 = 0 and WD < 0.1 then Solar × ((Se1 + Se2)/2) × GS2_/(R × 11) else 0 for Grow2; If G3 > 0 and WD < 0.1 then Solar × Se3 × GS3/(R × 10) else if G3 = 0 and WD < 0.1 then Solar × ((Se2 + Se3)/2) × GS3/(R × 10) else 0 for Grow3; If G4 > 0 and WD < 0.1 then Solar × Se4 × GS4/(R × 40) else if G4 = 0 and WD < 0.1 then Solar × ((Se3 + Se4)/2) × GS4/(R × 40) else 0 for Grow4
G1–G4	Biomass transfer from seedling to Biom 1 (g day^{-1}), seedling × trans1 for G1; Biom1 to Biom 2, Biom1 × trans2 for G2; from Biom 2 to Biom 3, Biom2 × trans3 for G3; from Biom 3 to Biom 4 (g day^{-1}), Biom3 × trans4 for G4
S_Mort	Seedling mortality due to hydrologic condition, If WD > 0 or Days_of_F0 > 1 then seedling else 0
Mort1–4	Mortality from Biom 1–4 due to hydrologic condition of each stage (g day^{-1}). If WD > 0.3 × H2 or Days_of_F1 > 2 then Biom1 else 0 for Biom1; If WD > 0.3 × H3 and Days_of_F2 > 3 then Biom2 else 0 for Biom2;

Continues

Table II. Continued

	If WD $> 0.5 \times$ H4 and Days_of_F3 > 3 then Biom3 else 0 for Biom3; If WD $>$ H5 and Days_of_F4 > 3 then Biom4 else 0 for Biom4
Stemp	Soil temperature (°C day^{-1}), 13–11 × cosine (1.7 × π × (time)/365)
Solar	Amount of solar energy flowing into the floodplain plot (kcal $\mathrm{m}^{-2}\,\mathrm{day}^{-1}$), 4000–2000 × cosine (2 × π × (time)/365)
Se–Se4	Plant solar efficiency at seedling stage through stage 4
GS1–4	Growing season for growth stage 1–4 (day), 166 to 186 out of 365 days for GS1; 187 to 198 out of 365 days for GS2; 199 to 209 out of 365 days for GS3; 210 to 255 for GS4
R	Plant energy/biomass ratio (kcal g^{-1})
trans1–trans4	Pulse function that occurs on day 166, day 187, day 199, and 210, respectively
H1	Corresponding seedling height calculated by regression (cm)
H2–H5	Corresponding plant height calculated by regression at 25%, 50%, 75% and 100% of maximum growth (cm)
Death	Death of biomass due to frost (g day^{-1}), Biom4 × (0.0001 + Frost)
Frost	Pulse function that occurs as the first frost on day 288 (15 October), terminating the biomass produced

floodplain relative to plant height determine whether the plant grows successfully in that stage, and in the following stages (Table II). Flooding tolerance assigned to each stage of plant growth is somewhat different. The plant becomes more flood-tolerant as it grows (based on Fredrickson and Taylor, 1982). For example, the plant does not survive if the water level in the floodplain is higher than one-third its height for more than two days for growth stage 1 (GS1) (Table II). In growth stage 4 (GS4), the plant survives unless it is completely covered with water for more than three days (Table II). Once the plant passes the flooding constraints in one step successfully, the biomass produced is transferred to the next step through a pulse function and the plant continues to grow (Table II, Figure 3). However, if the plant fails because of the hydrologic conditions nothing is transferred. In that case, the plant dies and the biomass starts from zero and grows in the current step, but with lower solar use efficiency (the average between the previous and current growth stages; Table II) to catch up with the growth it did not complete in the previous stage due to the unfavourable flooding conditions. The same routine repeats in each growth stage until stage 4 (GS4) completes the annual growth of the plant. At the end of the growing season the first frost kills all the biomass produced in the model. Plant height was based on a regression equation developed from a literature survey (Dickerson, 1964) and field measurements in Chautauqua NWR (Plant Height (cm) = 7.05 × Biomass (0.4654) $\mathrm{g\,m}^{-2}$).

Qualitative test

We compared model predictions of millet success at the tree line (where floodplain forest normally grows because the flooding during the summer is relatively infrequent) within the floodplain with historic moist-soil plant cover observations in three bottomland lakes. We chose 95% of maximum productivity as a criterion for millet success because any value less than 95% at the relatively high elevation of the tree line would indicate almost certain failure at the lower elevations where millets typically occur naturally. All three lakes, Clear, Quiver, and Crane, were connected to the Illinois River in the past (Bellrose *et al.*, 1979). Millet plant coverage from those bottomland lakes was recorded by Bellrose *et al.* (1979) during two different periods, 1938–1941 and the 1950s. The units of measurement are not the same (plant coverage as a percentage of total moist-soil area versus biomass m^{-2}), so this comparison is not a rigorous validation of the model; however, it provides a qualitative evaluation.

RESULTS

Simulation results—effects of pre-dam and post-dam hydrographs

Using the 'natural' (1887; Figure 1) hydrograph prior to dam construction, the model predicted a millet biomass of $\sim 500\,\mathrm{g\,m}^{-2}$ and growth to 130 cm tall by the end of the growing season (mid-October) (Figure 4a). However,

Table III. State variables, forcing functions and parameters for the plant model

Symbol	Name	Value/units	Source
State variables			
Days_of_F0	Accumulated number of flooding days during potential germination period	day	Calculation
Days_of_F1–F4	Accumulated number of flooding days during growth stages 1–4	day	Calculation
Days_of_d1–d4	Accumulated number of dry days during potential growth stages 1–4	day	Calculation
Seedling	Biomass produced during seedling stage	$g\,m^{-2}$	Calculation
Biom1–4	Biomass produced during growth stages 1–4	$g\,m^{-2}$	Calculation
Forcing functions			
WD	Estimated water level of the simulated floodplain plot based on river water elevation and floodplain land elevation	$cm\,day^{-1}$	
F_elevation	Floodplain elevation	m	
Stemp	Soil temperature	$°C\,day^{-1}$	
Solar	Amount of solar energy flowing into the floodplain plot	$kcal\,m^{-2}\,day^{-1}$	
Parameters and coefficients			
Se	Plant solar efficiency at seedling stage	0.003	Estimate/calibration
R	Plant energy/biomass ratio	$19.2\,kcal\,g^{-1}$	Caton *et al.* (1999)
trans1–4	Pulse functions that occur on days 166, 187, 199, and 210	1 pulse	Calculation
GS1–GS4	Growing season for growth stage 1–4	0.0–1.0 range	Odum (1971)
Se1	Plant solar efficiency at growth stage 1	0.095	Estimate/calibration
Se2	Plant solar efficiency at growth stage 2	0.3	Estimate/calibration
Se3	Plant solar efficiency at growth stage 3	0.7	Estimate/calibration
Se4	Plant solar efficiency at growth stage 4	0.97	Estimate/calibration
Frost	Pulse function that occurs as the first frost on day 288 (15 October)	1.5 pulse	Calibration

the post-dam (1987; Figure 1) hydrograph, which has several small summer floods, damaged the millet plants in several stages (Figure 4b). Two high peaks of the post-dam hydrograph in the second half of the natural dry season (Figure 1) prevented millet plants from starting their final growth stage (Biom4) (Figure 4b).

Comparison of post-dam simulation results with historical observations

In general, the model correctly predicted moist-soil plant success or failure in all of the cases tested (Table IV), indicating that the model captures millet responses to flooding condition fairly well. Few millet plants were observed in 1938 in Quiver Lake, and the model predicted only 71% of maximum plant productivity at the elevation of the tree line (Table IV) due to unfavourable flooding conditions during the early stage of plant growth (GS2) in that year; therefore the year 1938 was reasonably judged a ‘failure’. Model predictions for Clear Lake matched observations through all the years tested. No moist-soil plants were observed in 1938 and 1939 in Crane Lake, and the model predictions for each corresponding year were 28 and 78% of maximum plant productivity, much lower than the chosen criteria for success (>95%) (Table IV).

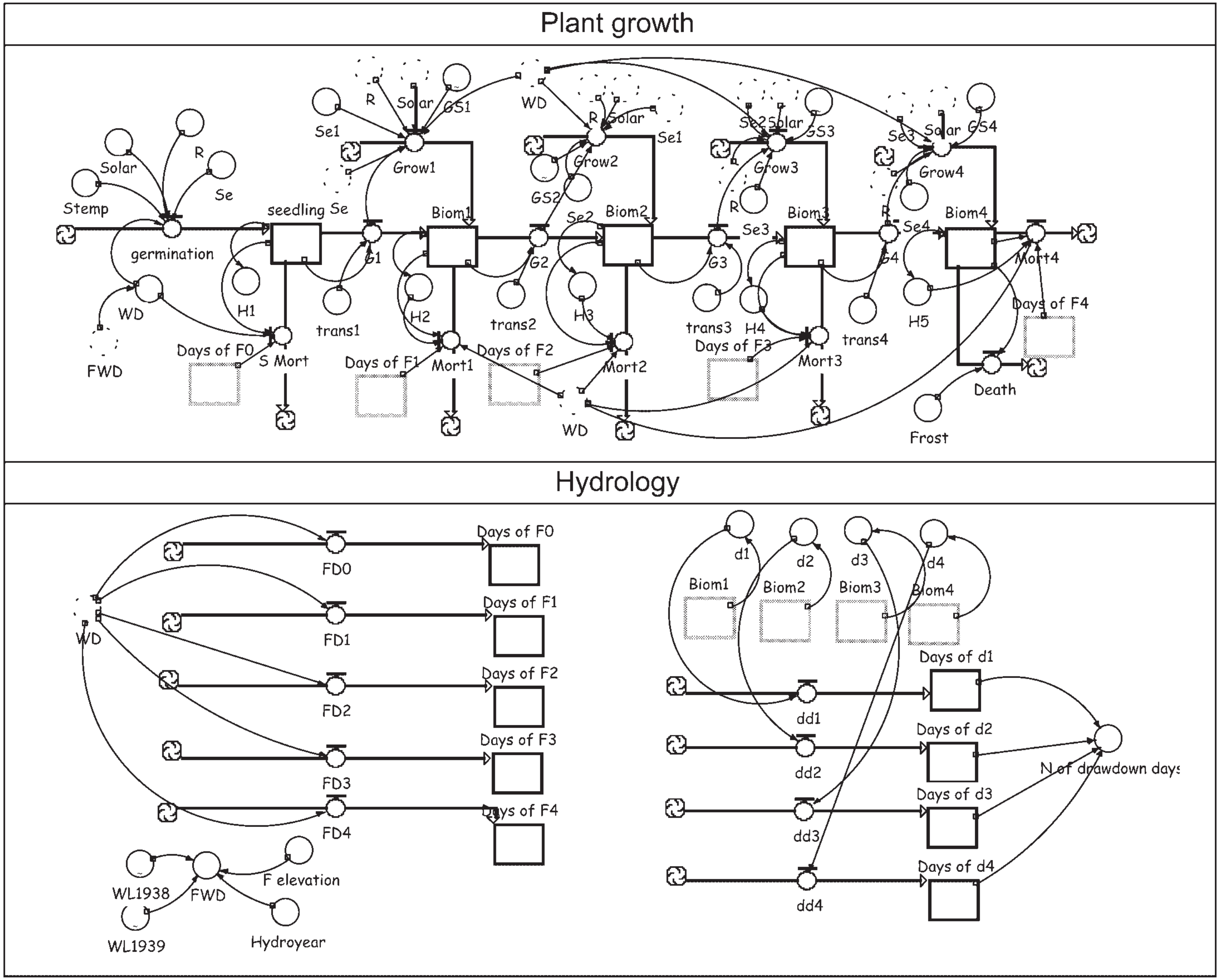

Figure 3. STELLA^{TM} diagrams of the moist-soil plant model. All variable legends are described in Tables II and III

Table IV. Comparison between model predictions and plant coverage in three bottomland lakes in La Grange pool of the Illinois River

Lake[a]	Year	Millet plant observation[b]		Model prediction[c] (% of max. productivity)	Qualitative agreement (Yes/ No)
		Biomass	Number of species		
Quiver	1938	failure	0	failure (71)	Yes
	1939	success	2	success (100)	Yes
	1940	success	4	success (100)	Yes
	1941	success	1	success (100)	Yes
Clear	1938	failure	0	failure (81)	Yes
	1939	success	5	success (100)	Yes
	1940	success	6	success (100)	Yes
	1941	success	2	success (100)	Yes
	1944	success	5	success (100)	Yes
	1950	success	2	success (97)	Yes
	1955	success	7	success (100)	Yes
	1956	success	7	success (100)	Yes
	1959	success	2	success (100)	Yes
Crane	1938	failure	0	failure (28)	Yes
	1939	failure	0	failure (78)	Yes
	1940	success	3	success (100)	Yes
	1941	success	4	success (100)	Yes
	1955	success	7	success (97)	Yes
	1956	success	7	success (100)	Yes

[a] Quiver, Clear and Crane lakes were described as connected to the Illinois River during the period of historic observation (1938–1959) (Bellrose *et al.*, 1979).

[b] Plant coverage (based on Bellrose *et al.*, 1979 and data from Forbes Biological Station, Havana, Illinois, USA). 'Success' means plant cover observed whereas 'failure' indicates no plant cover observed.

[c] Simulated at tree line land elevations (Wlosinski and Wlosinski, 2001); 131.4 m for Quiver lake, 131.8 m for Clear lake, and 130.5 m for Crane lake. Values in parentheses are percentages of the maximum plant productivity for a moist-soil plant simulated in the model ($\approx$524 g DW m^{-2}). Less than 95% of the maximum productivity is judged as a 'failure' since plant growth was simulated at relatively high land elevations.

Simulations with decreasing land elevations

We also investigated effects of decreasing land elevations on millet productivity through a series of simulations conducted for Quiver Lake with the 1939 river hydrograph (Table V). At the tree line elevation (131.4 m), millets developed fully, producing $\sim 500\,\mathrm{g\,m^{-2}\,yr^{-1}}$. As expected, plant growth declined with decreasing land elevation because flooding frequency increases as land elevation decreases (Table V). Maximum growth dropped about 50% as elevation dropped by 1.5 m (131.4 m to 129.9 m: Table V).

Effects of duration of dry period on moist-soil plants in simulations

The effect of *duration* of dry period during the growing season on millet productivity was simulated for Quiver Lake using the 1939 river hydrograph (Table VI). The dry period becomes shorter as land elevation decreases, resulting in gradually decreasing plant productivity in general (Table VI). However, a precipitous decrease of biomass production occurred when the duration of the dry period dropped from 88 days to 85 days, indicating a possible threshold for successful plant growth during the growing season. Table VII compares successful and failing years for moist-soil plants at three bottomland lakes. The duration of the dry period among successful cases that resulted in at least 50% of maximum plant productivity was 86 days on average, while failing years had a shorter dry period of 78 days (Table VII). Both were more than the minimum dry period, 70 days, recommended by Bellrose *et al.* (1979) for moist-soil plants. Species richness also increased with duration of the dry period in stage 3 and stage 4 where flooding conditions are critical for the full growth of plants (number of dry days in stage 3 and stage 4 $= 0.8892 \times$ species richness $+ 79.058$, $R^2 = 0.5152$, $p < 0.001$: Figure 5).

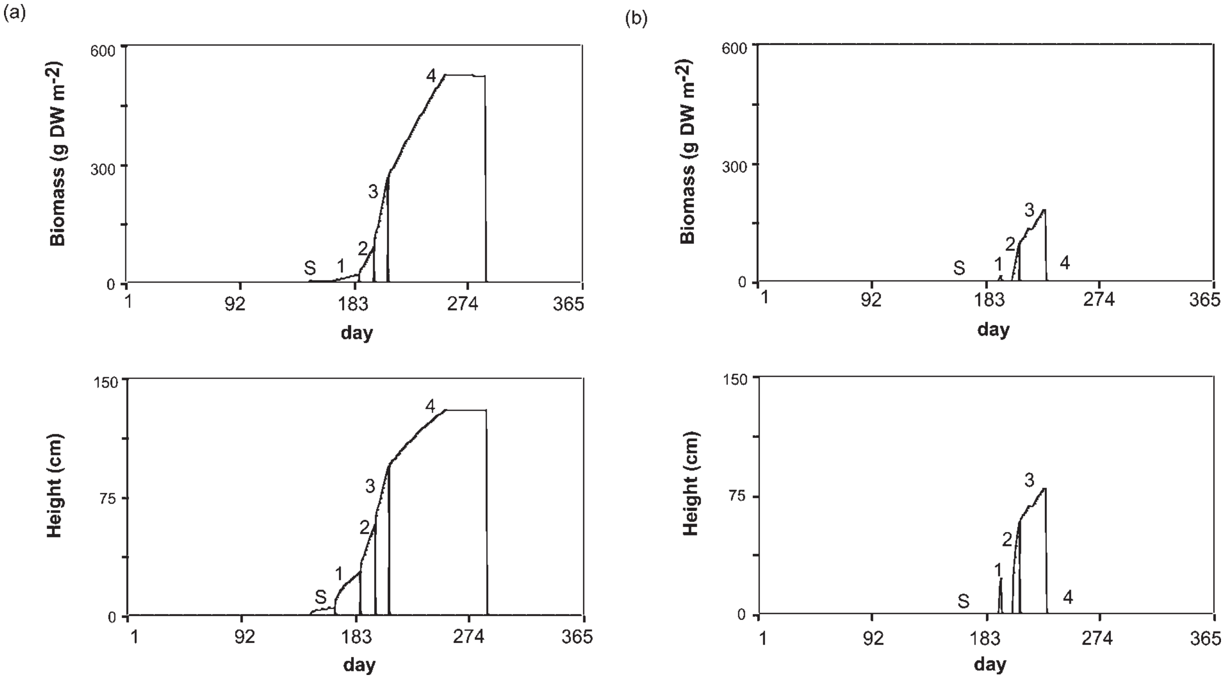

Figure 4. Simulated biomass (seedling, S, to Growth Stage 4, GS4, in g DW m^{-2}) and height (seedling, S, to Height stage 4, H4, in cm) of a moist-soil plant in response to two water regimes: (a) a representative pre-dam hydrograph (1887), and (b) a representative post-dam hydrograph (1987), both shown in Figure 1

Table V. Modelling effect of floodplain land elevation on plant growth in Quiver Lake, 1939

Lane elevation (m)	Biomass (g DW m^{-2})	Percentage of maximum growth modelled (%)
131.4	523.9	100
131.1	523.8	100
130.8	522.8	99.8
130.5	491	93.7
130.2	420	80.1
129.9	263	50.2

Table VI. Modelling effects of duration of dry period on plant growth in Quiver Lake, 1939

Land elevation (m)	Duration of dry period[a] (days)	Biomass (g DW m^{-2})
131.4	115	523.9
130.8	115	522.8
130.5	97	491
130.2	88	420
129.9	85	263

[a] Total number of dry days counted during the growing season (day 166 to day 286) in a year.

Table VII. Duration of dry period calculated during the growing season by the model simulations in three bottomland lakes for both 'success' and 'failure' cases of plants[a]

	Lake/year	Duration of dry period[b] (days)	Mean (days)
Success	Quiver, 1939–41	83	
	Crane, 1940–56	87	
	Clear, 1939–59	89	
			86
Failure	Quiver, 1938	78	
	Crane, 1938–39	80	
	Clear, 1938	76	78

[a] It shows that qualitatively 85 days might be the threshold duration for reasonable plant success (based on at least 50% of maximum plant productivity).

[b] Average of the annual values during the period of years.

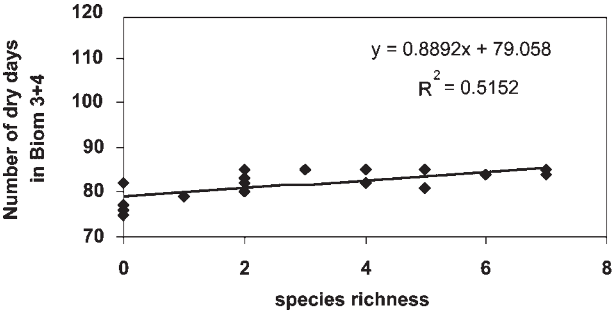

Figure 5. Relationship between number of dry days in later two stages of the growing season (GS3 and GS4) and species richness of moist-soil plants found in three bottomland lakes connected to the Illinois River (1938–1959)

DISCUSSION

Applicability of the model

Optimum conditions for moist-soil plants and for feeding ducks are generally well known and no model is needed to make management decisions in an environment that is controlled to produce moist-soil plants and attract ducks. However, if the management goal is to reconnect the river and its floodplain, in order to recover hydraulic functions of flood conveyance and storage and to provide suitable habitats for migratory fishes and birds, managers will not have the same control as in impoundments. The model described in this paper is useful in predicting responses of a group of important moist-soil plants, the millets, to *any* water level fluctuations, including: (1) natural fluctuations; (2) dam operations on the mainstem river that might be instituted to benefit floodplain vegetation; (3) moderating effects of soil-and-water-conserving practices in tributary watersheds on extreme flows in the main river; or (4) combinations of approaches. Since millets attract birds (and birders and hunters), there is a link between the success of these plants, use by wildlife, and value to humans that can be incorporated in evaluations of probable benefits and costs of river management alternatives. For example, it would be helpful for decision-makers to know whether it is more cost-effective to restore floodplain vegetation by building and operating impoundments on the floodplain, by modifying dam operations on the mainstem river, or some optimal combination of both approaches.

The model described in this paper can be easily adapted to simulate growth of other species of floodplain vegetation, provided that flood tolerances and other information (e.g. maximum plant heights) are obtained to parameterize the model. Also, if better information on millets is developed from field or laboratory experiments, it could be easily incorporated in the model. However, critical restoration decisions are being made now and in the near future that would benefit from simulation models, such as ours, that incorporate the best information currently available. (The STELLA^{TM} VII version of the model is available on CD at cost upon request to the corresponding author.) Since the model simulates millet growth on 1 m^2 at a particular floodplain elevation, it can easily be incorporated in spatial-dynamic models, i.e. it could run in each cell of a cellular or mesh model of the type developed by Costanza *et al.* (1990) and Sklar *et al.* (2001).

The basic structure of the model (five successive stages of plant growth that vary in sensitivity to flood depth and duration) reflects a fundamental characteristic of floodplain vegetation: species differ in flood tolerance, and even within the same species, different life history stages are differentially sensitive to flooding (or actually may require flooding). The model incorporates our understanding of zone and patch structure of vegetation in floodplains, i.e. small differences in elevation within floodplains (on the order of 10–18 cm) govern flood timing, frequency, and duration, which in turn govern plant germination, survival, and growth. Many responses are not linear; rather, there are thresholds (e.g. for duration of the dry period; Bellrose *et al.*, 1979). Timing is critically important: a killing flood in late spring may have little or no effect in late summer—even though the flood depth may be the same, the plants are taller and therefore more resistant to flooding later in the growing season (Fredrickson and Taylor, 1982).

We did not find it necessary to include other environmental factors such as nutrient availability, soil structure, or sedimentation rates in the model to explain historical variations in plant success in our study reach of the Illinois River. The Illinois River floodplain is in the US corn belt, where soils are fertile and nutrients are applied annually, so nutrients in river water and in deposited sediments on the floodplain exceed plant requirements (Spink *et al.*, 1998). However, these factors may be important in other floodplains and would need to be modelled (Sluis and Tandarich, in press; Wassen *et al.*, 2002). Nutrients may be limiting in some floodplains, requiring an annual subsidy in the form of nutrient-rich sediments deposited by floods. Conversely, excessive sedimentation could bury seeds and winter buds or other plant parts that need to regrow following dormancy.

CONCLUSIONS

The simulation model developed in this work provided insights on the dynamics between possible hydrologic manipulations being planned for restoration and millet plant growth. The model confirms the importance of maintaining a certain dry period for millets during the growing season so they will be able to grow fully and set seeds. The model also indicated that there is a threshold: productivity drops markedly when the dry period is less than 86 days. Field observations indicated that a minimum duration of 70 days is necessary, but the model results suggest that longer dry periods (>86 days) would increase production substantially.

More information and understanding of the physiology of millets and other moist-soil plants are necessary to strengthen the existing model and test the prediction that species richness also increases with length of the dry period. The predictions of our model mostly matched historical field observations of millet plant success, and these results indicate that the altered water regime is a major environmental factor currently limiting plant productivity in the Illinois floodplain–river ecosystem.

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