STOCHASTIC FLOOD AND PRECIPITATION REGIMES AND THE POPULATION DYNAMICS OF A THREATENED FLOODPLAIN PLANT

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Abstract. *Boltonia decurrens* is an endangered plant restricted to the Illinois River Valley. Its complex life cycle has evolved in response to the dynamics of the historic flood regime, which has changed dramatically in the last century due to the construction of navigation dams and agricultural levees. To explore the effects of these changes, we developed deterministic and stochastic matrix population models of the demography of *Boltonia*. We used periodic matrix models to incorporate intra-annual seasonal variation. We estimated parameters as a function of the timing of spring flood recession (early or late) and of growing season precipitation (high or low). Late floods and/or low precipitation reduce population growth (λ). Early floods and high precipitation lead to explosive population growth. Elasticity analysis shows that changes in floods and precipitation alter the life history pathways responsible for population growth, from annual to biennial and eventually clonal pathways. We constructed and analyzed a stochastic model in which flood timing and precipitation vary independently, and we computed the stochastic growth rate (log λ_s) and the variance growth rate (σ^2) as functions of the frequency of late floods and low precipitation. Using historical data on floods and rainfall over the last 100 years, we found that log λ_s has declined as a result of hydrological changes accompanying the regulation of the river. Stochastic elasticity analysis showed that over that time the contribution of annual life history pathways to log λ_s has declined as the contributions of biennial and clonal pathways have increased. Over the same time period, σ^2 has increased, in agreement with observations of large fluctuations in local *B. decurrens* populations. Undoubtedly, many plant and animal species evolved in concert with dynamic habitats and are now threatened by anthropogenic changes in those dynamics. The data and analyses used in this study can be applied to management and development strategies to preserve other dynamic systems.

Key words: Boltonia decurrens; conservation; elasticity; floodplain; flood regime; LTRE; matrix population model; periodic matrix model; stochastic elasticity; stochastic environment; stochastic matrix model; threatened species.

INTRODUCTION

All environments are subject to stochastic disturbances, some more so than others. Species adapt to this stochasticity, often by modifications of the life cycle that synchronize biological processes with conditions favorable to these processes. These adaptations are not to a single condition, but to the statistical properties of the stochastic environment (e.g., the frequency of fires or floods, the probability distribution of the severity of hurricanes, etc.). Therefore, changes in those statistical properties can have dramatic impacts on populations. In extreme cases, a change in the statistics of a disturbance regime could render large areas uninhabitable for a disturbance-adapted species, without any apparent change in the landscape.

Floods in large river systems are stochastic disturbances on a massive scale. For example, the 1993 flood in the upper Mississippi River system affected a third of the United States, lasted for 244 days, and caused 52 deaths and $18 billion in damages (Changnon 1996). Between 26 June and 14 September, 5.5×10^7 metric tons of sediment and 1.4×10^{11} m³ of water (enough to cover the states of Missouri and Illinois to a depth of 43 cm) passed St. Louis, Missouri (U.S. Army Corps of Engineers [USACE] 1994). In spite of the intensity of such disturbances, a variety of ancient and endemic species have evolved to take advantage of the natural cycle of flooding and have thrived in the Illinois river–floodplain system (Sparks 1995, Sparks et al. 1998, Smith and Mettler 2002). Human activities, however, have caused major changes in the timing and severity of flooding of the Illinois River. In this paper, we use stochastic population models to explore the consequences of these changes for the population dynamics of *Boltonia decurrens* (Torrey and Gray 1841) Wood

PLATE 1. Cluster of flower heads of *Boltonia decurrens* in a variety of stages of development (fully expanded disk and ray flowers, upper right; ray flowers senescing, upper left; and maturing seed head, center right). Each flower head produces about 250 disk flowers and 50 ray flowers, which produce dimorphic seeds. Photo credit: Nancy Parker.

(Asteraceae), a threatened plant of the Illinois River valley.

Populations of *B. decurrens* are restricted to a narrow band of floodplain along the lower Illinois River (U.S. Fish and Wildlife Service [USFWS] 1990) (Fig. 1). The number of populations, which fluctuates annually, has declined over the past 100 years (Schwegman and Nyboer 1985, USFWS 1990, Smith 1995, 2002). In the 19th and early 20th centuries *B. decurrens* was abundant in wet prairies, shallow marshes, and open shores of lakes of the Illinois River (Torrey and Gray 1841, Hus 1908, Turner 1934, 1936). Since the 1970s, it has been collected only from disturbed alluvial ground (Morgan 1980) and open, muddy edges of floodplain forests (Kurz 1981, Schwegman and Nyboer 1985). Although settlers in the late 1800s changed the prairie landscape in Illinois by cultivating the fertile upland areas (Allen 1870, Nelson et al. 1994), the wetland prairies that formed the habitat for *B. decurrens* were safe from settlement, due to their frequent flooding,

until the 1930s when the system of agricultural levees and navigation dams was completed (Yaeger 1949, Scarpino 1985, Thompson 1989).

In 1988, the U.S. Fish and Wildlife Service placed *B. decurrens* on the federal list of threatened species; it is currently listed as a ''species of concern'' in Missouri (Missouri Department of Conservation 1999) and as threatened in Illinois (Herkert 1991). Although it is the consensus of federal, state, and private conservation agencies that alterations of the flood regime have caused the threatened status of *B. decurrens* (USFWS 1990, Missouri Department of Conservation 1999, Smith and Mettler 2002), the inference has not been tested until the present study.

The species and its habitat

Although commonly classified as a perennial, *B. decurrens* may complete its life cycle as a winter annual, or more rarely, as a facultative biennial (Smith and Mettler 2002; see Plate 1). Plants flower from August through October, and seeds, which mature from September to November, exhibit conditional dormancy (Baskin and Baskin 2001). Some seeds germinate in the fall and overwinter as rosettes; others overwinter
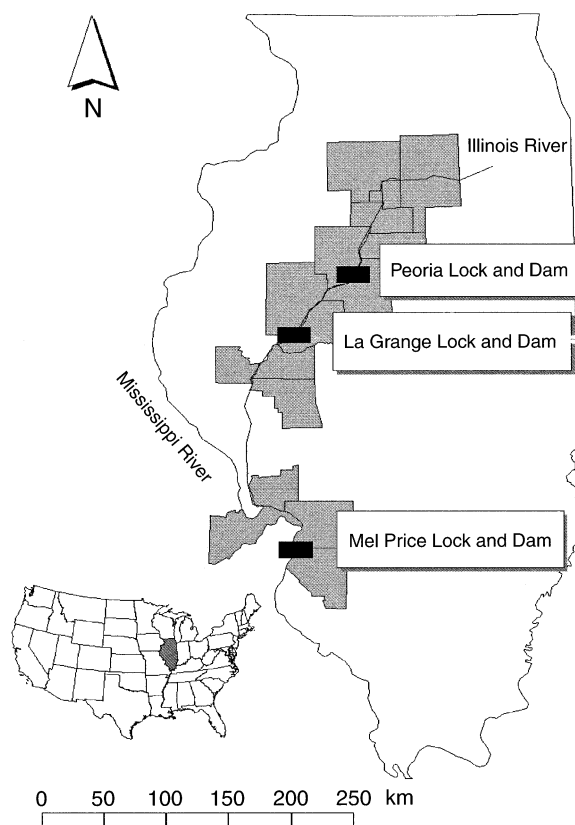

FIG. 1. Map of Illinois showing the historical distribution of *Boltonia decurrens* (counties shaded in gray); and locks and dams on the Illinois and Mississippi Rivers that control the water levels at all *B. decurrens* sites (black rectangles).

as seeds and produce seedlings the following spring. Summer flowering plants may arise from spring-germinating seedlings or overwintering rosettes, with large differences in size and seed production. As seeds are forming, senescing plants produce basal rosettes that flower the following season. Regardless of origin (rosette or seedling) or time of germination (fall or spring), all plants die during the season they flower, leaving no overwintering root.

Boltonia decurrens' life cycle is intimately linked to the annual regime of flooding. It is a fugitive species (sensu Hutchinson 1951), depending on disturbance to create habitat suitable for colonization and population growth. As we will show, the key to the disturbance process is a flood of appropriate timing early in the year followed by sufficient rainfall during the growing season later in the year. After such disturbances, *B. decurrens* colonizes and grows rapidly, dominating the vegetation in the short term. Without subsequent disturbances, the population crashes within three to five years (Schwegman and Nyboer 1985, USFWS 1990, Smith et al. 1998).

The Illinois River has been modified to control its hydrology. A series of locks and dams on the Illinois River (Fig. 1) was completed by 1939 with the primary goal of keeping the river navigable for barge traffic by maintaining a 2.7 m navigation channel (Waller 1972, Tweet 1984). The locks and dams created a series of navigation pools (the stretch of river impounded by each navigation structure) in which water levels are manipulated by the U.S. Army Corps of Engineers (USACE) to maintain the necessary channel depth. A network of 54 levee districts constructed during the early 1900s constricted the river channel, raising water depth and increasing the velocity of flow (Thompson 1989, Sparks et al. 1998). The combination of water level manipulation and channelization has drastically altered the historic hydrologic cycle, creating chaotic flood conditions that shorten the summer growing season for floodplain plants (Fig. 2). In addition, many areas that formerly provided habitat for *B. decurrens* are now either isolated from the river, permanently inundated, or experience severe flooding during the growing season (Sparks 1995, Sparks et al. 1998, Smith and Mettler 2002).

Demographic analysis

It is widely believed that the decline in range, number of populations, and population size of *B. decurrens* and other Illinois floodplain species is primarily due to alteration of the river's hydrology (Schwegman and Nyboer 1985, Nelson et al. 1996, Smith and Mettler 2002). If this is true, the demography of the species should vary in response to the characteristics of floods and other environmental factors. Thus, we have developed a demographic model for *B. decurrens* in a dynamic flood and precipitation environment. The life cycle of *B. decurrens* includes processes operating
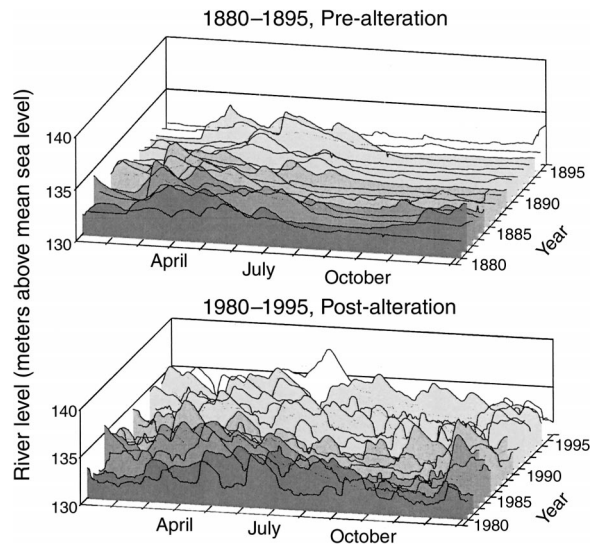

Fig. 2. Daily water-level hydrographs (meters above mean sea level) from 1880 to 1895 and from 1980 to 1995 measured at a USACE gage station located in the La Grange navigation pool, 220.11 km above the confluence of the Illinois and Mississippi Rivers.

within a single year (germination of seeds and growth and flowering of seedlings) as well as between years (overwintering of seeds and vegetative rosettes). Together, these within-year and between-year processes determine population growth on a multi-year time scale. The periodic matrix model approach to annual life cycles (Caswell 2001, Section 13.2) was developed for just such cases.

We developed demographic models to explore the interacting effects of two environmental factors: the timing of spring flood recession and the amount of precipitation during the growing season. When floodwaters recede late, seed germination is delayed, the growing season is shortened, flowering plants are smaller, and seed production is reduced. When precipitation during the growing season is low, the survival and growth of seedlings and rosettes, and the production of seeds and rosettes, are reduced.

As a first approximation to an environment-dependent model, we estimated population projection matrices for all four combinations of early and late flood recession and high and low growing season precipitation. We refer to these as the condition-specific matrices.

With the condition-specific matrices, we projected population growth under (hypothetical) constant environmental conditions, and used life table response experiment (LTRE) analysis to determine the contribution of each of the vital rates to the effects of flood timing and precipitation on population growth.

Such projections are hypothetical, because real environments are not constant, so we used the condition-specific matrices to build a stochastic model, charac-

FIG. 3. A seasonal life cycle graph for *Boltonia decurrens*. Each horizontal row represents a season of the year. Each circle represents a stage (SR = small rosette, LR = large rosette, SFP = small flowering plant, LFP = large flowering plant). Small and large rosettes in the fall (f) may overwinter, and seeds may overwinter and germinate as seedlings in the spring (s). From spring to summer (u), small and large rosettes may flower, producing large flowering plants. Spring seedlings may remain vegetative as small rosettes or may flower. Summer small rosettes, if they survive, remain as small rosettes in the fall. Flowering plants in the summer produce seeds and basal rosettes (small or large) in the fall.
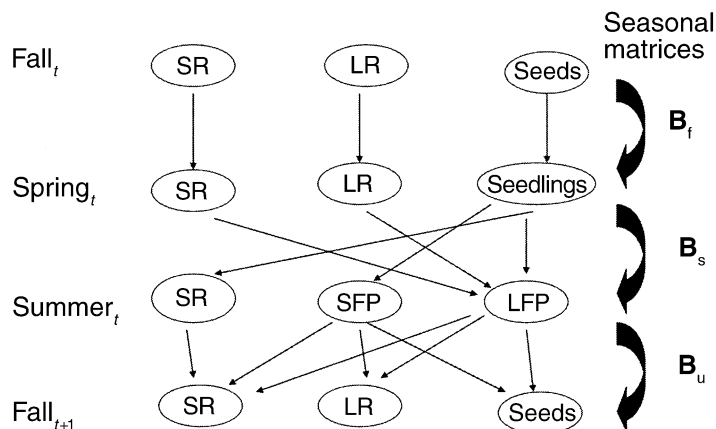
terizing the environment by the frequency of early and late floods and high and low precipitation. The results show how the stochastic properties of the environment affect the long-term growth rate of *B. decurrens* and its probability of quasi-extinction. Such stochastic models have been used before, particularly to explore the consequences of dynamic fire regimes (Canales et al. 1994, Caswell and Kaye 2001, Satterthwaite et al. 2002). We have been able to integrate historical changes in the flood and precipitation regime into the stochastic model, permitting us to evaluate the hypothesis that these environmental changes could be responsible for the threatened status of *B. decurrens*.

A DEMOGRAPHIC MODEL FOR *B. DECURRENS*

We will begin with a seasonal life cycle graph, from which we construct a periodic matrix model (Caswell 2001, Section 13.2). The graph is constructed by choosing a set of time points, or phases, within the year (spring, summer, and fall in our case). They need not be evenly spaced. At each phase of the cycle, we choose a set of stages into which to classify individuals. The stages need not be the same at each phase. We represent the stages by circles on a horizontal row, one row for each phase in the cycle (Fig. 3). The starting point of the cycle has no effect on population growth rate, the seasonal cycles of stage distribution and reproductive value, or the sensitivity and elasticity of population growth to the seasonal vital rates. A copy of the first phase is added at the bottom to complete the cycle. Arrows between rows show how stages at one phase contribute to the next. In general, the arrows from phase h to phase $h + 1$ define a matrix $\mathbf{B}_h$ that projects the population from phase h to phase $h + 1$.

Population growth over an annual cycle of p phases, starting at phase 1, is given by a periodic product:

$$\mathbf{A}_1 = \mathbf{B}_p \cdots \mathbf{B}_2 \mathbf{B}_1. \qquad (1)$$

The population growth rate per cycle is given by the dominant eigenvalue λ of $\mathbf{A}_1$. The stable stage distribution (at phase 1) is given by the corresponding right eigenvector $\mathbf{w}$. The reproductive value distribution is given by the left eigenvector $\mathbf{v}$. The stable-stage distribution and reproductive value at other phases of the cycle are given by the eigenvectors of the appropriate cyclic permutations of the $\mathbf{B}_i$; e.g., those at phase 2 would be obtained from

$$\mathbf{A}_2 = \mathbf{B}_1 \mathbf{B}_p \cdots \mathbf{B}_2. \qquad (2)$$

The life cycle

We used three phases: fall (the period when seeds are formed and vegetative rosettes are produced), spring (the period immediately following flood recession when seedlings emerge and fall rosettes resume growth), and summer (the time at which plants bolt and begin flowering).

At each phase, we classified individuals as seeds, seedlings, small rosettes, large rosettes, small flowering plants, or large flowering plants. Rosette size was based on diameter at the widest point (small rosettes <15 cm, large rosettes ≥15 cm); all our studies indicated that rosette size is related to survival. Flowering plant size was defined by height (small flowering plants, <46 cm; large flowering plants, ≥46 cm); plant height is positively related to seed production. *Boltonia decurrens* is a prolific seed producer (Smith and Keevin 1998), and up to 15 vegetative ramets can originate from the base of each large senescing plant in the fall (Redmond 1993, Baker 1997). This reproductive potential, however, is seldom realized. Seedling establishment is often low or lacking entirely, particularly in established populations (USFWS 1990, Moss 1997, Smith et al. 1998). Vegetative rosettes are not produced in years when late summer and fall precipitation is below normal (M. Smith, *unpublished data*) or when succession has been uninterrupted for several years (Schwegman and Nyboer 1985, USFWS 1990, Cochran 2002). Larger rosettes, whether produced from seedlings or vegetative ramets, produce taller plants, more inflorescences and seeds, and suffer lower mortality (Redmond 1993, Baker 1997, Tofari 2000). Although mortality in new seedlings is significantly higher than in vegetative ramets (Baker 1997, Moss 1997), once rosettes have become

established (approximately 4 weeks after germination), mortality is independent of rosette type (Redmond 1993, Tofari 2000, Cochran 2002).

Seasonal and annual projections

Seasonal projections are described by matrices $\mathbf{B}_f$ (from fall to spring), $\mathbf{B}_s$ (from spring to summer), and $\mathbf{B}_u$ (from summer to fall). All three annual matrices constructed from these seasonal matrices give the same population growth rates, so we will focus on $\mathbf{A}_f = \mathbf{B}_u\mathbf{B}_s\mathbf{B}_f$, which projects from fall in year t to fall in year $t + 1$.

Parameter estimation

Data used in the construction of the projection matrices were collected from two populations on the Illinois River and two populations in the area of confluence with the Mississippi River (Fig. 1). These sites encompass approximately 60% of the historical range of *B. decurrens* (USFWS 1990).

1) Rice Lake, Fulton County, Illinois. Three 10-m transects were established in 1997; two additional transects were established in 1998; and two more were established in 2000 to monitor rosette survival, plant biomass, and inflorescence production. From 1997 to 2000, nine 1-m² plots randomly spaced along the three original transects were established to monitor seedling survival.

2) Gilbert Lake, Jersey County, Illinois. In August, 1994, four 10-m transects were established and rosette survival was monitored through August 1996. In April 1995, four 1-m² plots were established on a fourth transect, and germination and seedling survival were monitored from April through August in 1995 and 1996. Three 10-m transects were established in 1997 and rosette survival was monitored until 2000. From May through July 1996, nine 25 × 25 cm plots were established at regular intervals along three new 10-m transects to monitor germination and seedling survival.

3) Horseshoe Lake, Madison County, Illinois. In August 1994, eight 1-m² plots were established along four 10-m transects and rosette survival, height, and inflorescence production were monitored through August 1996. Three 10-m transects were established in 1997 and rosette survival, biomass, and inflorescence production were monitored through 1999. Seed germination and seedling survival were monitored on 30, 25 × 25 cm plots on three additional transects from November 1998 through August 1999.

4) West Alton, St. Charles County, Missouri. Fourteen 20-m transects were established and monitored from 1990 to 1992 for rosette and seedling survival, plant height, and inflorescence and rosette production. Seed germination and seedling survival were monitored from March through November 2000 on 36 plots, each 25 × 25 cm, located at regular intervals on nine 30-m transects.

Over the 10 years of this study (1990–2000), survival was followed on more than 5000 individually tagged plants. Line transects were established by burying a 46-cm length of metal conduit pipe at each end and marking the locations with 2.5-m metal poles covered in plastic. Rosettes were marked using metal tags attached to 21-cm metal plant stakes, and sampling plots for seedlings were marked at two corners in the same manner. To minimize the loss of metal tags and stakes, tags were inserted level with the soil surface and located using a metal detector.

Rosette survival was monitored monthly, provided the site was not flooded, until the individual flowered and senesced. All seedlings were marked with 9-cm plastic cocktail picks and survival was monitored monthly from germination through the end of the growing season. Transects that lost their above ground metal poles were re-established by using a metal detector to locate the buried conduit pipe. In some years (e.g., 1993, 1995, and 1997), flooding was so severe that many tags and plots were swept away or buried under thick layers of silt. If the plant population survived at the site, transects and plots were re-established along the original transect lines. When rosettes were plentiful, they were tagged following a random number system, otherwise every rosette on each transect was marked. As rosettes were tagged, the maximum diameter of each was measured and the rosette determined to be either a small rosette (SR) or a large rosette (LR). When possible, equal numbers of rosettes in each size class were tagged at each site. At anthesis, plant height was measured and flowering plants were assigned to one of two groups: small flowering plants (SFP) or large flowering plants (LFP).

We estimated seed production from inflorescence number. The number of inflorescences increases with plant height, but seed number per inflorescence does not (Smith et al. 1993, Moss 1997, Cochran 2002); therefore, we used the average number of inflorescences for each size class, multiplied by seed production per inflorescence, to estimate seed production. The seed to seedling transition was calculated as the density of seedlings established following flood recession as a percentage of the estimated seed density in the preceding fall.

To evaluate the possibility of a seed bank, we measured germination of seeds from soil cores at two of our sites. Although Baskin and Baskin (2002) reported that ~90% of the seeds of *B. decurrens* unearthed from potted soil in an unheated greenhouse germinated after 88 months, we found germination rates of only 0–6% in seeds recovered from the soil cores (Redmond 1993; M. Smith, *unpublished data*). It is not surprising that *B. decurrens* lacks a significant seed bank, even though it lives in a disturbed environment. Light is required for germination (Baskin and Baskin 1988, Smith and Keevin 1998) and the disturbance provided by flooding leaves a thick layer of sediment as flood waters recede, rendering a seed bank useless. In addition, seeds of *B. decurrens* have a permeable seed coat and may have

TABLE 1. Values of deterministic population growth rate λ from condition-specific matrices.

Flood condition	High precipitation	Low precipitation	Averaged
Early flood	$\lambda^{(11)} = 5.0313$	$\lambda^{(12)} = 0.240$	$\lambda^{(j\cdot)} = 2.6012$
Late flood	$\lambda^{(21)} = 0.5345$	$\lambda^{(22)} = 0.0264$	$\lambda^{(2\cdot)} = 0.2905$
Averaged	$\lambda^{(\cdot i)} = 2.3288$	$\lambda^{(\cdot 2)} = 0.1246$	$\lambda^{(\cdot\cdot)} = 1.2174$

Notes: Superscripts denote environmental conditions: (i, j) denotes flood condition i and precipitation condition j. Dots indicate growth rates calculated from seasonal matrices averaged over flood or precipitation conditions.

little protection against soil microbes. For these reasons, a seed bank was not included in the model.

More information on the data utilized in the model can be found in a series of theses, papers and agency reports, including the following: seed production of small and large flowering plants (Smith and Keevin 1998, Tofari 2000, Cochran 2002); seed viability and germination (Redmond 1993, Moss 1997, Smith and Keevin 1998); seed dormancy and contribution of the seed bank (Redmond 1993, Baskin and Baskin 2002); transition of small and large rosettes to small and large flowering plants (Tofari 2000, Cochran 2002; J. Brooks, *unpublished data*); seedling survival (Redmond 1993, Moss 1997, Mettler-Cherry 2004); and survival of small and large flowering plants and the number of basal rosettes produced by each (Redmond 1993, Baker 1997, Tofari 2000).

Following the fate of marked individuals is a standard technique in plant ecology, but in our case it was challenging due to the sheer magnitude of flood disturbances. In the 1993 flood, levees were breached in many areas, including our West Alton site. The resulting uncontrolled flooding left scour holes 15–21 m deep and up to 0.8 km wide (USACE 1994). Tons of sand and silt were deposited in areas beyond the broken levee, covering tagged plants and seedling plots with layers up to 46 cm deep. Flooding on the upper Illinois River was even more severe in 1995 and 1997 than in 1993, and many levees were breached or overtopped. To minimize our losses, we established transects and sampling plots at several widely separated population sites, and developed a system that allowed us to locate stakes and tags under silt layers that obscured our markers, but often left plants alive and well.

Despite these efforts, our data are not as well balanced as they would have been in a more benign environment. However, we were able to obtain estimates of the major seasonal life cycle transitions under different environmental conditions. None of our conclusions, we believe, would be changed by better luck with the flooding of a major river.

Condition-specific matrices

In constructing the condition-specific matrices, we defined flood recession as early or late depending on whether floodwaters receded before or after 1 June; we will refer to these as ''early floods'' and ''late floods.'' We defined precipitation as high or low depending on

whether rainfall during the growing season (June through October) was greater or less than the 100-yr average during that period at the nearest weather station. Because we believe that low precipitation during the growing season does not affect environmental conditions during the subsequent winter, we used the same fall matrix for both high and low precipitation years. The range of sites used in this study sometimes enabled us to collect data on plant survival under different flood and precipitation regimes within a single year.

Basic Demographic Analyses

The condition-specific matrices characterize the response of *B. decurrens* to flood and precipitation conditions, following the standard logic of population projection (Keyfitz 1972, Caswell 2001). That is, analysis of the matrix for, say, early flood and high precipitation projects what *would happen if* early flood and high precipitation conditions occurred every year. Since they do not, this projection cannot forecast future growth; rather it is a way to characterize the effects of the environment on *B. decurrens*. Such projections are essential for interpreting stochastic models that include environmental variability. The seasonal matrices on which the analyses are based are available in the Appendix.

Population growth rate and structure

We use superscripts to denote environmental conditions, so that $\mathbf{A}^{(ij)}$ is the projection matrix, and $\lambda^{(ij)}$ the population growth rate, under flood condition i and precipitation condition j. Table 1 shows the effects. With early floods and high precipitation, *B. decurrens* would be capable of explosive population growth ($\lambda^{(11)} = 5.03$) (Table 1). Under conditions of late flood recession or low precipitation, the population would be unable to persist because $\lambda < 1$.

Flood timing has a major impact on population structure, especially in the summer (Fig. 4a–d). Under early flood conditions, the summer population would eventually be dominated by small and large flowering plants. Under late flood conditions, the summer population would be dominated by small rosettes, with a few large flowering plants.

Sensitivity and elasticity analysis

To evaluate the effect of changes in the vital rates, we computed the elasticities of λ to the entries of each
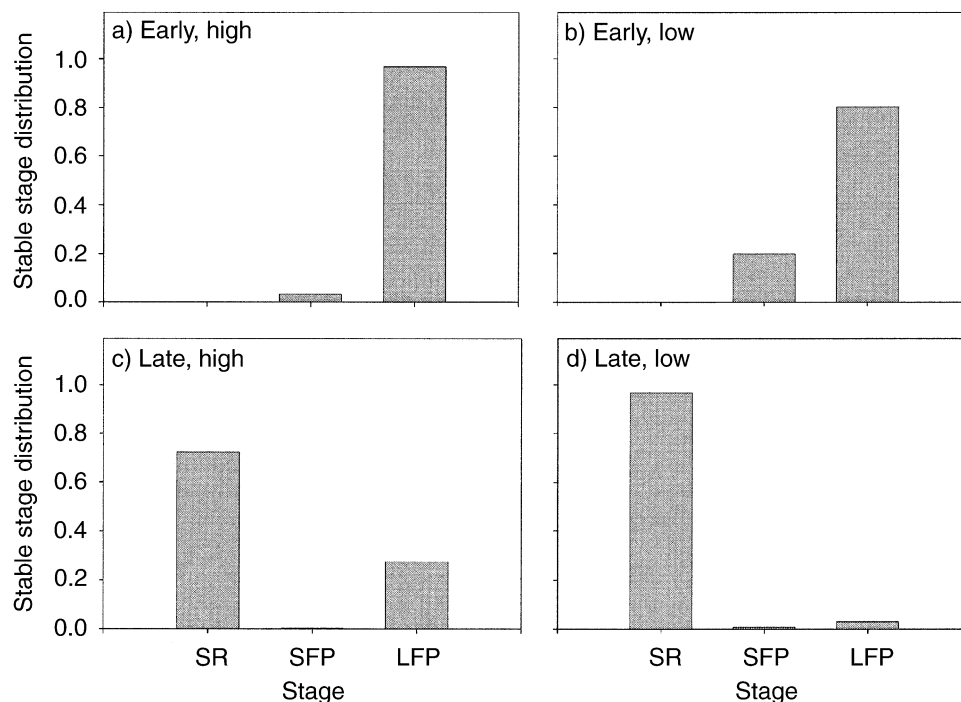
FIG. 4. Summer stable population structure for *Boltonia decurrens* under (a) early flood and high precipitation, (b) early flood and low precipitation, (c) late flood and high precipitation, and (d) late flood and low precipitation. Stable stage distributions calculated from the matrix $\mathbf{A}_f^{(ij)} = \mathbf{B}_u^{(ij)}\mathbf{B}_s^{(ij)}\mathbf{B}_f^{(ij)}$ for the appropriate flood and precipitation conditions.
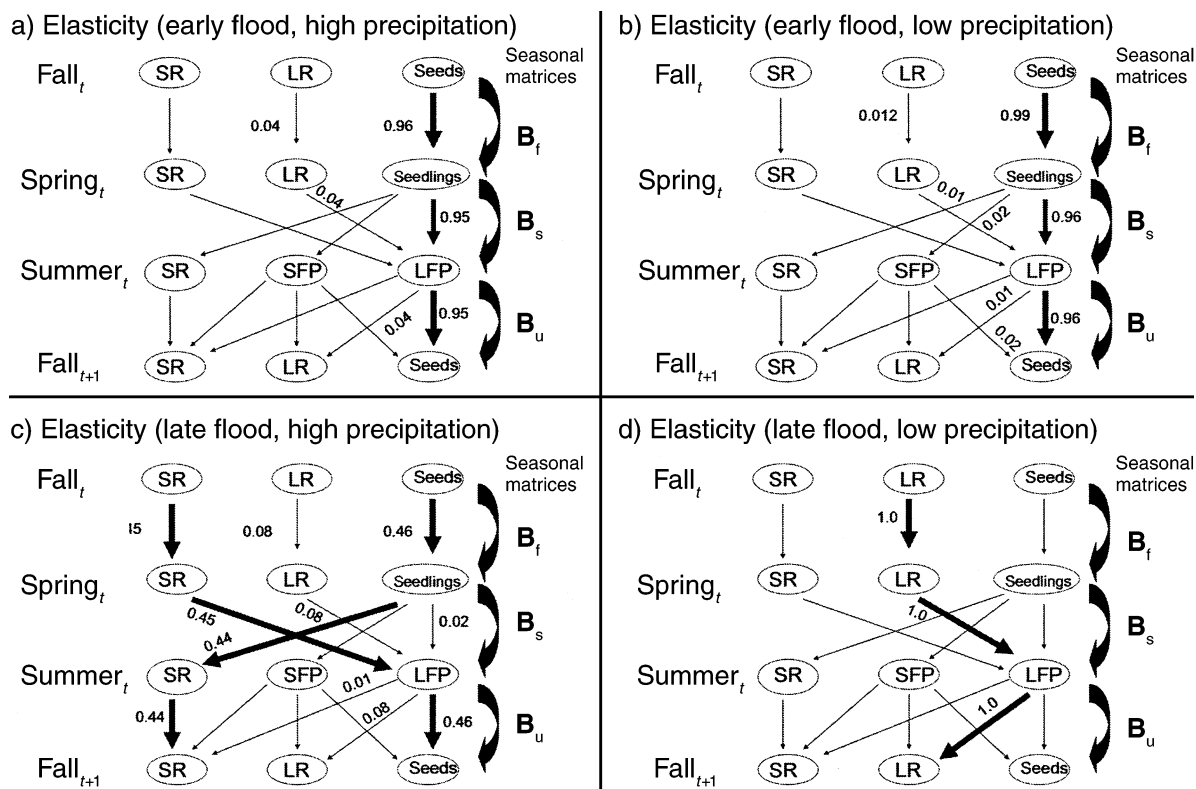

FIG. 5. Elasticities of λ (population growth) to changes in the entries of the seasonal matrices in each environment: (a) early flood and high precipitation, (b) early flood and low precipitation, (c) late flood and high precipitation, and (d) late flood and low precipitation. Only elasticities ≥0.01 are shown. Bold arrows indicate pathways with elasticities ≥0.1.

of the seasonal matrices, using the approach of Lesnoff et al. (2003). Let $\mathbf{S_A}$ be the sensitivity matrix for $\mathbf{A}$ (i.e., the matrix whose (i, j) entry is $\partial\lambda/\partial a_{ij}$). In general, suppose that there are p matrices in a seasonal cycle, $\mathbf{B}_1, \ldots, \mathbf{B}_p$. To calculate the sensitivity of λ to the entries of the mth of these matrices, $\mathbf{B}_m$, write $\mathbf{A}$ as

$$\mathbf{A} = \mathbf{F}_m\mathbf{B}_m\mathbf{G}_m \qquad (3)$$

where

$$\mathbf{F}_m = \begin{cases} \mathbf{B}_p \cdots \mathbf{B}_{m+1} & m \neq p \\ \mathbf{I} & m = p \end{cases}$$

$$\mathbf{G}_m = \begin{cases} \mathbf{B}_{m-1} \cdots \mathbf{B}_1 & m \neq 1 \\ \mathbf{I} & m = 1. \end{cases} \qquad (4)$$

The sensitivity matrix $\mathbf{S}_{\mathbf{B}_m}$ whose entries are the sensitivities of λ to $b_{ij}^{(m)}$ is

$$\mathbf{S}_{\mathbf{B}_m} = \mathbf{F}_m^{\mathsf{T}}\mathbf{S_A}\mathbf{G}_m^{\mathsf{T}}. \qquad (5)$$

The elasticity matrix $\mathbf{E}_{\mathbf{B}_m}$ is

$$\mathbf{E}_{\mathbf{B}_m} = \frac{1}{\lambda}\mathbf{B}_m \circ \mathbf{S}_{\mathbf{B}_m} \qquad (6)$$

where ''$\circ$'' denotes the Hadamard, or element-by-element, matrix product.

The elasticities $e_{ij}^{(m)}$ sum to 1 within each season, so they can be interpreted as proportional contributions of the seasonal vital rates $b_{ij}^{(m)}$ to population growth. The elasticities of the condition-specific matrices thus show the life cycle pathways responsible for population growth under a given set of flood and precipitation conditions.

The results reveal dramatic shifts in the seasonal life cycle pathways responsible for population growth under the four different environmental conditions:

1 and 2) Early floods, high or low precipitation (Fig. 5a and b). Over 95% of λ is accounted for by an annual life history pathway, from seeds in year t to seedlings to large flowering plants to seeds in year $t + 1$. Although many other transitions occur in the life cycle, this pathway accounts for almost all population growth.

3) Late floods, high precipitation (Fig. 5c). When the growing season is shortened by late flood recession, over 90% of λ is accounted for by a biennial life history pathway. Seeds in year t produce seedlings and small rosettes in year $t + 1$, which overwinter to form large flowering plants in year $t + 2$.

4) Late floods, low precipitation (Fig. 5d). This combination of conditions leads to precipitous population decline ($\lambda = 0.0264$), and the meager rate of population growth is accounted for by a very different pathway involving clonal reproduction. Large rosettes overwinter and flower the next summer, but their only contribution to population growth comes from the vegetative production of large rosettes.

Only a seasonal model coupled with elasticity analysis could detect these shifts in life history pathways within the year. The extent to which similar shifts occur in other species is an interesting question.

LTRE analysis

The effects of flood timing and precipitation on λ (Table 1) are mediated through effects on the vital rates at each season. We decomposed the contributions of each seasonal rate to the overall effect on λ via a LTRE analysis (Caswell 1989, see Caswell 2001 for a complete description). We used a 2×2 factorial design, with two levels of floods and two levels of precipitation. We describe the main effects of these factors by averaging the seasonal matrices and calculating all other quantities from them. For example, denoting means by dots, the matrix describing flood condition i is $\mathbf{A}_f^{(i\cdot)} = \mathbf{B}_u^{(i\cdot)}\mathbf{B}_s^{(i\cdot)}\mathbf{B}_f^{(i\cdot)}$ where $\mathbf{B}_f^{(i\cdot)} = 1/2\ \Sigma_{j=1}^{2}\ \mathbf{B}_f^{(ij)}$, etc. We write a linear model for $\lambda^{(ij)}$ as

$$\lambda^{(ij)} = \lambda^{(\cdot\cdot)} + \alpha^{(i)} + \beta^{(j)} + \alpha\beta^{(ij)} \qquad (7)$$

where $\alpha^{(i)}$ is the main effect of level i of flooding, $\beta^{(j)}$ is the main effect of level j of precipitation, and $\alpha\beta^{(ij)}$ is the interaction effect. We found the interaction effects to be negligible, and report only the main effects here.

The main effects can be written, to first order, as a sum of contributions from each of the vital rates at each season. To keep track of matrix elements, environmental conditions, and seasons, let $b_{kl}^{(ij,f)}$ be the (k, l) element of the matrix $\mathbf{B}_f$ in the (ij) treatment combination, and similarly for the other seasons. Then,

$$\alpha^{(i)} = \underbrace{\sum_{k,l}(b_{kl}^{(i\cdot,f)} - b_{kl}^{(\cdot\cdot,f)})\frac{\partial\lambda}{\partial b_{kl}^{(f)}}\bigg|_{\frac{A^{(i)}+A^{(\cdot)}}{2}}}_{\text{fall contributions}}$$

$$+ \underbrace{\sum_{k,l}(b_{kl}^{(i\cdot,s)} - b_{kl}^{(\cdot\cdot,s)})\frac{\partial\lambda}{\partial b_{kl}^{(s)}}\bigg|_{\frac{A^{(i)}+A^{(\cdot)}}{2}}}_{\text{spring contributions}}$$

$$+ \underbrace{\sum_{k,l}(b_{kl}^{(i\cdot,u)} - b_{kl}^{(\cdot\cdot,u)})\frac{\partial\lambda}{\partial b_{kl}^{(u)}}\bigg|_{\frac{A^{(i)}+A^{(\cdot)}}{2}}}_{\text{summer contributions}} \qquad (8)$$

$$\beta^{(j)} = \underbrace{\sum_{k,l}(b_{kl}^{(\cdot j,f)} - b_{kl}^{(\cdot\cdot,f)})\frac{\partial\lambda}{\partial b_{kl}^{(f)}}\bigg|_{\frac{A^{(\cdot j)}+A^{(\cdot)}}{2}}}_{\text{fall contributions}}$$

$$+ \underbrace{\sum_{k,l}(b_{kl}^{(\cdot j,s)} - b_{kl}^{(\cdot\cdot,s)})\frac{\partial\lambda}{\partial b_{kl}^{(s)}}\bigg|_{\frac{A^{(\cdot j)}+A^{(\cdot)}}{2}}}_{\text{spring contributions}}$$

$$+ \underbrace{\sum_{k,l}(b_{kl}^{(\cdot j,u)} - b_{kl}^{(\cdot\cdot,u)})\frac{\partial\lambda}{\partial b_{kl}^{(u)}}\bigg|_{\frac{A^{(\cdot j)}+A^{(\cdot)}}{2}}}_{\text{summer contributions}} \qquad (9)$$

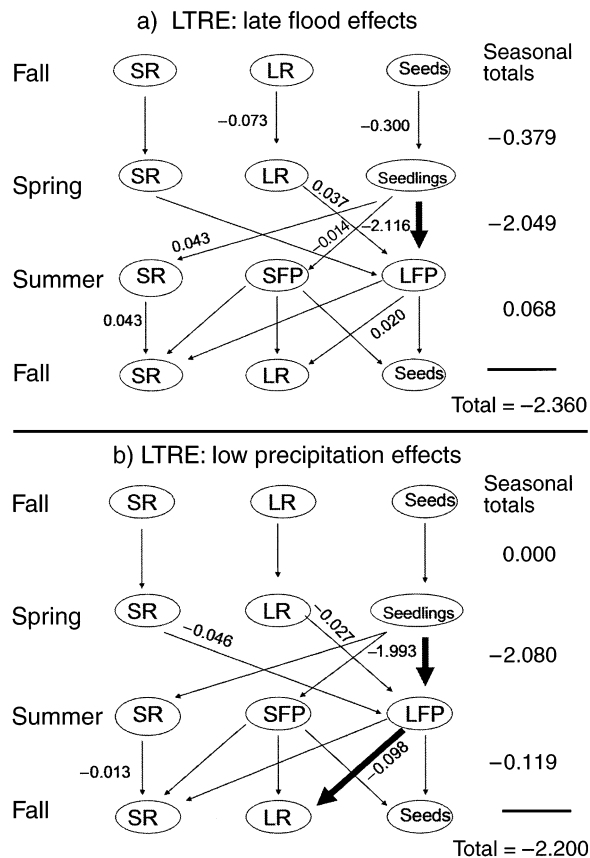Because there are only two levels of each treatment, we present the results in terms of the effect of late

FIG. 6. LTRE (life table response experiment) analysis of (a) late flood effects on λ and (b) low precipitation effects on λ. The numbers on each arrow show the contribution of differences in that vital rate to the effect on λ. Only contributions greater than 0.01 in absolute magnitude are shown. In both (a) and (b) the seasonal totals and the overall total contributions are shown.

relative to early floods ($\alpha^{(2)} - \alpha^{(1)}$) and of low relative to high precipitation ($\beta^{(2)} - \beta^{(1)}$).

The values of λ calculated from the various average matrices are shown in Table 1. Fig. 6a and b show the contributions of each of the seasonal vital rates to these effects. Late floods reduce λ mainly by reducing the probability that spring seedlings will grow to large flowering plants in the summer; this reflects the shortened growing season. There is also a small contribution from reduced seed germination due to the longer period of flood coverage. Low precipitation also reduces λ by reducing the growth of spring seedlings to large flowering plants and the vegetative production of large rosettes in the fall. Thus, the combination of a late flood and low precipitation delivers a double insult to the transition from spring seedlings to summer large flowering plants. The seasonal totals of the contributions effects show that late floods and low precipitation affect λ almost exclusively through processes operating from spring to summer (Fig. 6a and b).

The accuracy of the linear approximations in Eqs. 8 and 9 can be judged by comparing the sum of all the contributions (-2.360 for the late-flood effect; Fig. 6a; -2.200 for the low-precipitation effect; Fig. 6b) with the observed effects of late floods and low precipitation on λ (-2.311 and -2.204, respectively; Table 1). The LTRE contributions capture the effect of late floods to within 2.1% and the effect of low precipitation to within 0.2%, so the approximation, using only the main effects, is excellent.

BOLTONIA DECURRENS IN A STOCHASTIC ENVIRONMENT

Boltonia decurrens lives in a stochastic environment, in which flood timing and precipitation vary from year to year. To explore the consequences of that variation, we require a model in which we can vary the stochastic properties of the environment and obtain their consequences for population growth, fluctuation, and potential extinction.

A stochastic model for the environment

A stochastic population model begins with a model for the environment. Here, we used the simplest possible description of the flood and precipitation regime. We assume that the late and early floods occur independently from year to year, with probabilities p and $1 - p$, respectively. Low and high precipitation years occur independently from year to year with probabilities q and $1 - q$, respectively. We assume no temporal autocorrelation in the flood and precipitation regimes, and no cross-correlation between flooding and precipitation (remember that the model describes precipitation after floods have receded).

Stochastic population growth

At each year t, a population projection matrix $\mathbf{A}_t$ is chosen at random from one of the four condition specific matrices $\mathbf{A}^{(ij)}$ using the probabilities p and q. The population grows according to

$$\mathbf{n}(t + 1) = \mathbf{A}_t \mathbf{n}(t). \tag{10}$$

Two facts about stochastic demography are relevant here. First, with probability 1, the population eventually grows at the stochastic growth rate given by

$$\log \lambda_s = \lim_{T \to \infty} \frac{1}{T} \log \|\mathbf{A}_{T-1} \cdots \mathbf{A}_0 \mathbf{n}(0)\| \tag{11}$$

(Cohen 1976, Tuljapurkar and Orzack 1980). The stochastic growth rate is the relevant measure of population growth. It is the eventual long-term growth rate of any population experiencing the specified environmental probabilities. It is the relevant measure of fitness in a stochastic environment, and it helps to determine the probability of quasi-extinction.

Second, if $N(t)$ is the total population size, then log $N(t)$ is asymptotically normally distributed with a mean that grows at the rate log λ_s and a variance that grows at a rate σ^2 (Tuljapurkar and Orzack 1980). The mean

of $N(t)$ grows at a rate $\log \mu$, which, for the independent and identically distributed environment model used here, is given by the log of the dominant eigenvalue of the average matrix,

$$\bar{\mathbf{A}} = (1 - p)(1 - q)\mathbf{A}^{(11)} + (1 - p)q\mathbf{A}^{(12)}$$
$$+ p(1 - q)\mathbf{A}^{(21)} + pq\mathbf{A}^{(22)}. \tag{12}$$

The variance growth rate σ^2 can then be estimated by

$$\sigma^2 = 2(\log \mu - \log \lambda_s). \tag{13}$$

The quantity σ^2 shows how fast uncertainty increases when projecting population growth in the face of environmental fluctuations.

Fig. 7a shows $\log \lambda_s$ as a function of the frequency of late floods and low precipitation. In the lower left corner, the environment is constant with early floods and high precipitation, and

$$\log \lambda_s = \log \lambda^{(11)} = \log 5.03 = 1.62. \tag{14}$$

In the upper right corner, the environment is constant with late floods and low precipitation, and

$$\log \lambda_s = \log \lambda^{(22)} = \log 0.026 = -3.63. \tag{15}$$

Between these limits, $\log \lambda_s$ declines as the frequency of either late floods or low precipitation increases. The contour where $\log \lambda_s = 0$ defines critical combinations of late flood and low precipitation frequency beyond which the population cannot persist.

In most of the region of parameter space within which $\log \lambda_s > 0$, the variance growth rate σ^2 is in the range of 0.5–2.0 (Fig. 7b). These are very high values; for comparison, an analysis of the prairie perennial plant *Lomatium bradshawii* found σ^2 values less than about 0.07 (Caswell and Kaye 2001) and a hypothetical example of the desert tortoise (*Gopherus agassizii*) yielded values on the order of 0.01 (Caswell 2001). As we will see, the high value of σ^2 for *B. decurrens* has implications for the precision of population projections and the risk of population decline.

Quasi-extinction

If $\log \lambda_s \leq 0$, the population will eventually become extinct with probability 1. Even if $\log \lambda_s > 0$, however, the population may fluctuate to low values. Quasi-extinction is defined as a decline to a fraction θ of the initial population size (Ginzburg et al. 1982). The quasi-extinction threshold θ can be chosen either as representing a risk of genuine extinction, or as a reduction that is a management concern.

The probability of quasi-extinction with a threshold θ is calculated using the following diffusion approximation to the stochastic matrix model (Tuljapurkar and Orzack 1980, Lande and Orzack 1988, Dennis et al. 1991):

$$P_q(\theta) = \begin{cases} 1 & \log \lambda_s \leq 0 \\ \exp\left(\dfrac{2 \log \lambda_s \log \theta}{\sigma^2}\right) & \log \lambda_s > 0. \end{cases} \tag{16}$$

All else being equal, $P_q(\theta)$ is higher the smaller $\log \lambda_s$ and the larger the variance.

Fig. 8a shows $P_q(\theta)$ as a function of late flood frequency, for reductions to 10%, 50%, and 90% of current population size (i.e., $\theta = 0.1, 0.5, 0.9$), for a fixed probability of low precipitation $q = 0.1$. The quasi-extinction probabilities are quite high, as a result of the high variance exhibited by *B. decurrens*. For example, when $p = 0.3$ the population is still able to grow rapidly ($\log \lambda_s = 0.47$, an average growth rate of over 60% per year). But there is a 23% chance that it will decline to 10% of its initial size, a 64% chance of shrinking to 50% of its initial size and a 93% chance of declining to 90% of its current population size.

$P_q(\theta)$ gives the asymptotic probability of quasi-extinction as $t \to \infty$, but the results are still relevant for short-term calculations. Fig. 8b shows the conditional probability distribution of the time to quasi-extinction (calculated from Eq. 14.143 of Caswell 1989), for $\theta = 0.1$. Most of the quasi-extinction events happen within 20, or even 10 years.

Historical trends in floods and precipitation

Water levels on the Illinois River are measured daily at a network of gage stations maintained by the USACE. We analyzed daily gage readings for the period of 1877–2000 at the gage station at Copperas Creek (Banner, Illinois) located at river mile 136.8 on the Illinois River (34°40′28″ N, 18°89′53″ W). We classified each year as early or late depending on whether floods receded before or after 1 June.

We obtained precipitation data for the months of June–October from 1895–2000 from the U.S. National Climatic Data Center, Illinois Region 6. Since we are interested in precipitation during the growing season, we classified an early flood year as having high or low precipitation depending on whether rainfall was above or below average between 1 June and 31 October. Late flood years were classified in the same way based on rainfall during the period 1 July–31 December.

We used a Gaussian kernel smoother (a moving average in which the data surrounding each point are weighted by a Gaussian distribution with specified standard deviation; see Copas 1983) to calculate and plot the frequencies of late-flood years and low-precipitation years (Fig. 9a). The data show a clear increase in the frequency of late floods over the last century. The frequency of low precipitation years has oscillated between about 0.3 and 0.5, without any apparent trend.

This historical trajectory of flood and precipitation frequency is indicated on the contour plot of $\log \lambda_s$ and σ^2 (Fig. 7). That trajectory has carried *B. decurrens* from a regime supporting positive stochastic growth to

a) Stochastic growth rate log λ_s

b) Variance growth rate σ^2
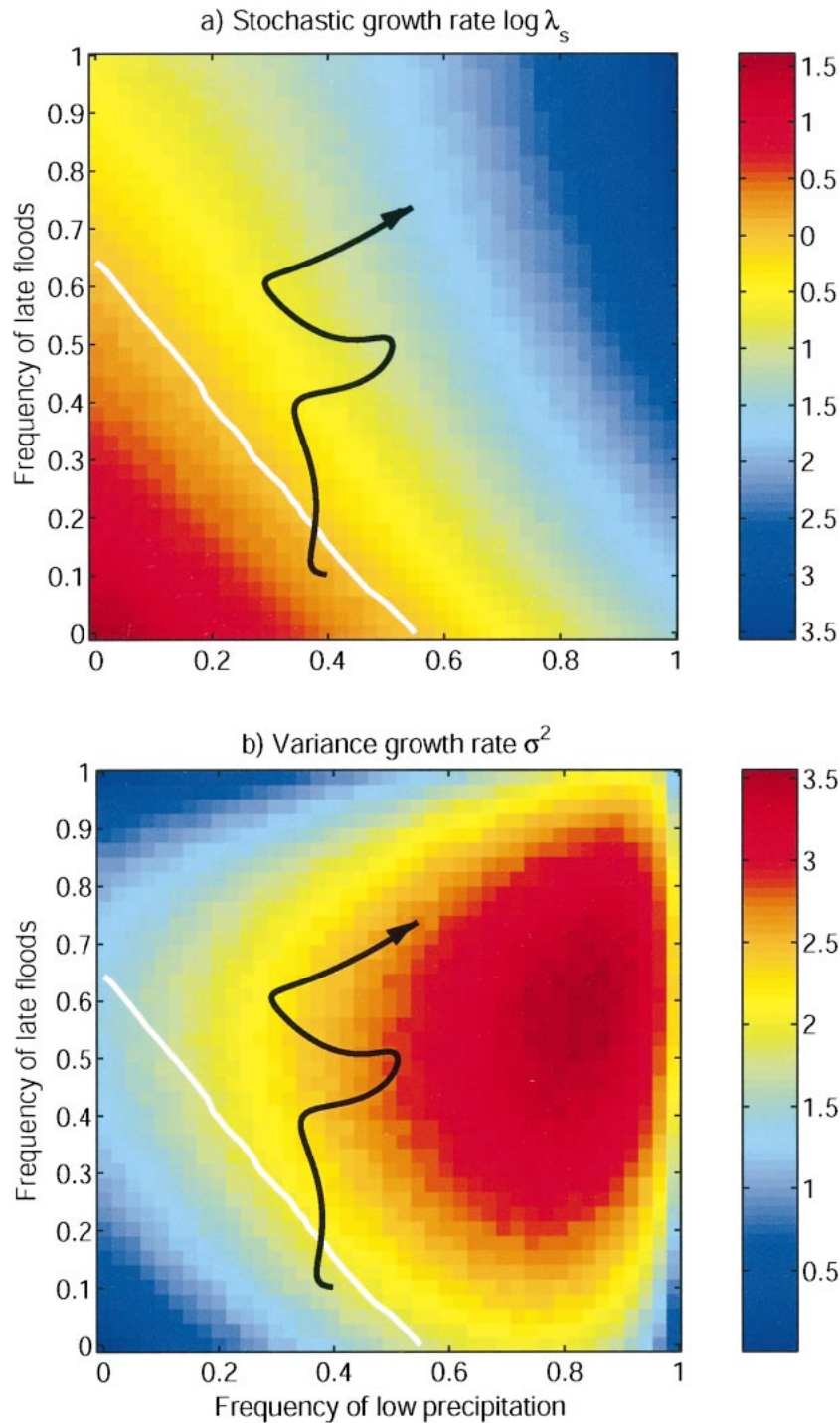

FIG. 7. (a) The stochastic growth rate log λ_s as a function of the frequency of late floods and low precipitation. The contour identifies frequencies of late floods and low precipitation leading to log $\lambda_s = 0$. The arrow shows the observed historical trajectory of late flood and low precipitation frequencies between 1895 and 2000, from Fig. 9a. (b) The growth rate σ^2 of the variance in log population size as a function of the frequency of late floods and of low precipitation.

one in which log λ_s is negative, implying that the population cannot maintain itself. The same trajectory has also increased σ^2, from about 1.8 to about 2.6. In Fig. 9b, we plot log λ_s as a function of the historical tra-

jectory of late flood frequency (holding the frequency of low precipitation at its 1895 value, which is also approximately the mean value), of the trajectory of low precipitation frequency (holding the frequency of late
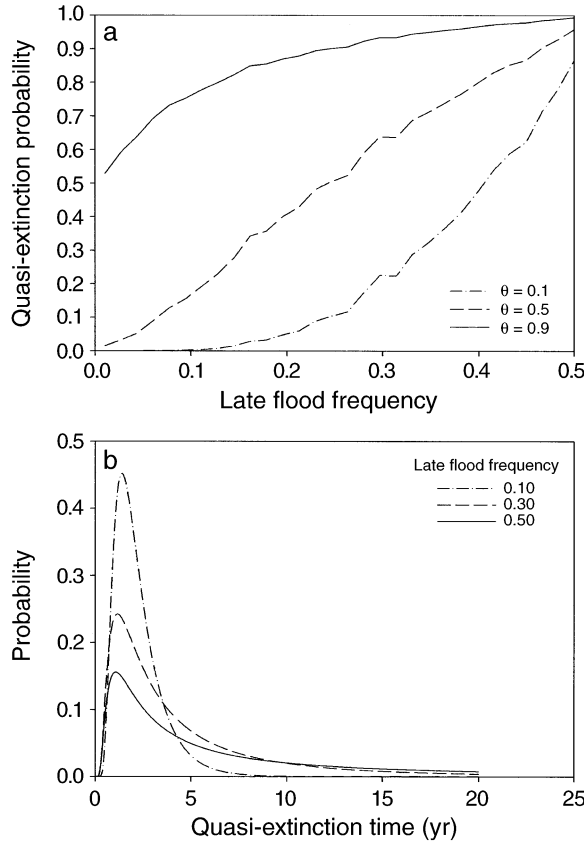
FIG. 8. (a) The quasi-extinction probability $P_q(\theta)$ as a function of the threshold θ and the frequency of late floods, with the frequency of low precipitation fixed at 0.1. (b) The probability density of the time to quasi-extinction.

floods at its 1895 value) and of both trajectories. The decline in $\log \lambda_s$ is due primarily to the historical changes in the frequency of late floods. The changes in precipitation impose oscillations on the downward trend in $\log \lambda_s$, but by themselves would not have produced any trend in population growth rate.

Elasticity of the stochastic growth rate

We calculated the elasticity of λ_s to the entries of each of the seasonal matrices using an extension of Tuljapurkar's (1990) perturbation analysis to seasonal models (Caswell 2005). We use the stochastic environment model to generate a sequence of projection matrices $\mathbf{A}_0, \mathbf{A}_1, \ldots, \mathbf{A}_{T-1}$ for some large value of T. Then, starting with an arbitrary initial vector $\mathbf{w}(0)$, with $\|\mathbf{w}(0)\| = 1$, we generate a stochastic sequence of stage distribution vectors

$$\mathbf{w}(t+1) = \frac{\mathbf{A}_t \mathbf{w}(t)}{\|\mathbf{A}_t \mathbf{w}(t)\|} \qquad t = 0, \ldots, T-1 \quad (17)$$

and one-step growth rates

$$R_t = \frac{\|\mathbf{A}_t \mathbf{w}(t)\|}{\|\mathbf{w}(t)\|}. \quad (18)$$

Starting with an arbitrary final vector $\mathbf{v}(T)$, with $\|\mathbf{v}(T)\| = 1$, we generate a sequence of reproductive value vectors

$$\mathbf{v}^\top(t-1) = \frac{\mathbf{v}^\top(t)\mathbf{A}_t}{\|\mathbf{v}^\top(t)\mathbf{A}_t\|} \qquad t = T, \ldots, 1. \quad (19)$$

Then, writing $\mathbf{A}_t = \mathbf{A} = \mathbf{F}_m \mathbf{B}_m \mathbf{G}_m$ as in Eq. 3, the elasticity of λ_s to the entries of $\mathbf{B}_m$ is given by

$$\frac{\partial \log \lambda_s}{\partial \log b_{ij}^{(m)}} = \lim_{T \to \infty} \frac{1}{T} \sum_{t=0}^{T-1} \frac{b_{ij}^{(m)}(t)\mathbf{v}^\top(t)\mathbf{f}_{.i}(t)\mathbf{g}_{j.}(t)\mathbf{w}(t)}{R_t \mathbf{v}^\top(t+1)\mathbf{w}(t+1)} \quad (20)$$

where $\mathbf{f}_{.i}(t)$ and $\mathbf{g}_{j.}(t)$ are column i and row j of $\mathbf{F}_t$ and $\mathbf{G}_t$, respectively. In place of the infinite limit in Eq. 20, we used $T = 10\,000$.

As in the deterministic seasonal model, these stochastic elasticities sum to 1 within each season and can be interpreted as the proportional contributions of the matrix entries to stochastic population growth. The contributions have changed dramatically over the last
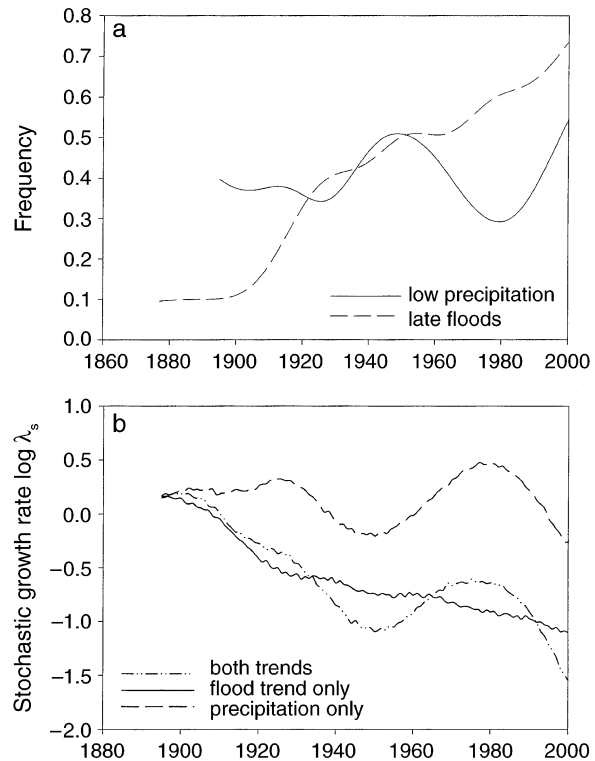

FIG. 9. (a) Frequencies of late floods and of low precipitation calculated from historical data on the Illinois River. Binary data were smoothed with a Gaussian kernel smoother with a standard deviation of 9 yr. (b) The stochastic growth rate $\log \lambda_s$ calculated from the observed historical frequencies of late floods and of low precipitation from 1895 to 2000. Curves show the result of the flood trend with the frequency of low precipitation fixed at its 1895 value, the result of the precipitation trend with the frequency of late floods fixed at its 1895 value, and the result of both trends.
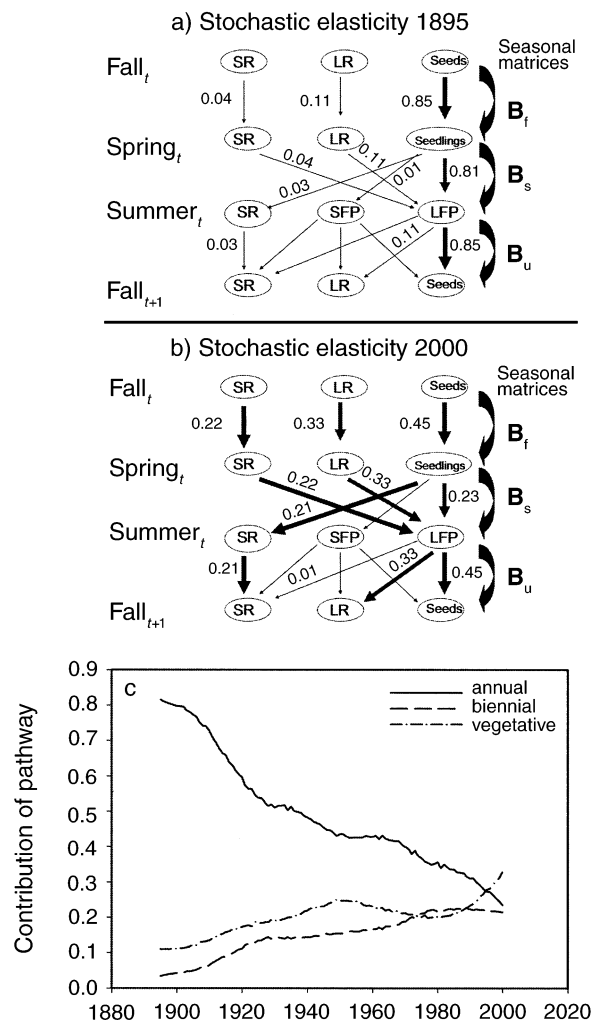
a) Stochastic elasticity 1895

b) Stochastic elasticity 2000

FIG. 10. (a, b) The elasticity of the stochastic growth rate, log λ_s, to the entries of the seasonal matrices for the frequencies of late floods and of low precipitation observed in 1895 and 2000. All elasticities ≥ 0.01 are shown; bold arrows indicate the major life history pathways (elasticity ≥ 0.1) responsible for stochastic population growth. (c) The proportional contribution of the annual, biennial, and clonal pathways to stochastic population growth, as determined by the historical trajectories in late flood and low precipitation frequencies.

century (Fig. 10). Unlike the changes in Fig. 5a–d, which reflect the effects of different fixed environmental conditions, the changes in Fig. 10 are caused by changes in the statistical properties of the floodplain environment. In 1895, when the frequency of early floods was high, the stochastic growth rate was almost completely determined by the annual life history pathway (Fig. 10a). By 2000, when late floods had become common, all three pathways contribute almost equally to λ_s (Fig. 10b). Summing the contributions of each of the three pathways to λ_s (assuming that the biennial pathway displays the symmetry shown in Fig. 5c), gives the results in Fig. 10c. The contribution of the

annual pathway has declined, while the contributions of the biennial and clonal pathways have increased. The contribution of vegetative reproduction reflects the oscillations in precipitation conditions from 1940 to 2000.

DISCUSSION

Habitat destruction threatens more species in the United States than overharvesting, invasive species, or diseases (National Research Council 1995). Discussions of habitat loss often focus on land use (e.g., draining marshes or converting prairie to farmland), but habitat loss is also caused by interruption or modification of natural stochastic environmental fluctuations. The change in the flood regime over the last century may not have ''destroyed'' habitat in the usual sense of the word; Illinois River floodplain still exists, and still experiences both early and late floods, but for *B. decurrens* the habitat has deteriorated dramatically.

Because of the economic and societal value of river-floodplain ecosystems, their natural hydrologic regimes have been altered by human activities (Johnson et al. 1995). Before alteration, these ecosystems were characterized by seasonal floods that provided pulses so dependable that plants and animals evolved life histories adapted to the disturbance regime (Junk et al. 1989, Bayley 1995, Middleton 2002). A systemic change to the flood regime results in the loss of all suitable habitat throughout the system for any species adapted to the historic flood patterns. From this perspective, more damage has been done by the combination of changing hydrology and land use than by changing land use alone.

Some intact river–floodplain ecosystems remain in the developing world, but they are rapidly diminishing as land use intensifies and as countries follow the western model of economic development (Welcomme 1985, Sparks 1992). It is often impossible to restore such ecosystems (Cairns 1991, Brookes and Shields 1996), and it is far more expensive to rehabilitate or reconstruct them (e.g., the ongoing effort to reconstruct the Kissimmee River in Florida; Toth et al. 2002) than it is to plan for their preservation. Thus, it is critical to assess the long-term biological impact of proposed alterations in flood regimes. Stochastic demographic analysis can reveal the interactions by which environmental variation and life histories combine to determine population growth. This approach becomes even more powerful when the results are related to long-term historical data.

Elasticity patterns

The environmental conditions encountered in our study produce dramatic shifts in the elasticity patterns, interpretable in terms of annual, biennial, and clonal life cycles. Some of these patterns agree with other comparative studies of elasticity patterns, although those generalizations were not based on seasonal mod-

els and thus are not directly comparable. For example, species in variable habitats sometimes have higher elasticity values for the seed-to-seedling transition than do populations in more stable habitats (van Groenendael and Slim 1988). *Boltonia decurrens* lives in a highly variable habitat, and the seed-to-seedling transition has a high elasticity value. When flood recession is late and precipitation is low, however, this transition has virtually no effect on population growth. Silvertown et al. (1996) reported that the contribution of fecundity to λ is higher during early stages of colonization than later in the successional process. *Boltonia decurrens* is an early colonizer (Schwegman and Nyboer 1985, Smith et al. 1998), and the flood regime under which it evolved favored the development of an annual life cycle in which fecundity and growth contribute heavily to population growth (Fig. 10a).

Long-lived perennials sometimes have higher elasticity values associated with survival in the same class than do shorter-lived, faster growing species (Caswell 1986, Silva et al. 1991, Silvertown et al. 1993). While *B. decurrens* is classified as a perennial in the taxonomic (Torrey and Gray 1841, Gleason and Cronquist 1991) and conservation literature (Schwegman and Nyboer 1985, USFWS 1990), it is certainly not a long-lived one. The elasticity of λ to survival is low, especially under conditions favoring rapid growth.

These patterns refer to hypothetical projections of constant flood and precipitation regimes, so it is significant that the differences in elasticity patterns among the deterministic matrices are mirrored in the historical changes in the elasticity of the stochastic growth rate, documenting the shift from the importance of annual to biennial and clonal life history pathways. This is the first time that such shifts have been documented in variable environments using stochastic elasticities.

Uncertainty and population fluctuation

Environmental stochasticity affects not only the growth rate, but also the variability in population size. One consequence is the high probability of quasi-extinction (Fig. 8). Another is that projections of population size are very uncertain. The variance growth rate σ^2 measures the rate at which the uncertainty in log $N(t)$ increases in the long run (and the short-run behavior is often predicted by σ^2 with only small errors; see Runge and Moen 1998, Caswell 2001). Values of σ^2 for *B. decurrens* are large (~1.5–2.5). This creates extreme variability in short-term projections of population growth. Since log $N(t)$ is asymptotically normally distributed with a variance equal to $t\sigma^2$, the ratio of the upper to the lower 95% projection interval for $N(t)$ is $\exp(3.92\sqrt{t\sigma^2})$. During the 20th century, this interval of uncertainty surrounding a 10-yr population projection was between six and eight orders of magnitude. This means that it is essentially impossible to predict population size even over short time scales.

Such extreme population fluctuations have indeed been observed. For example, in Jersey County, Illinois, a population of fewer than 10 large flowering plants in September 1992 exploded into a population of 20 000 flowering individuals in the fall of 1994, a year with early flood recession and high precipitation (Smith 1995). Conversely, in 2001, a late flood and low precipitation resulted in the decline of a population in Fulton County, Illinois from 18 000 individuals to 125 flowering plants in 2002 (Smith and Mettler 2002). In 2002, a GIS database for the Illinois River Valley enabled us to identify 26 populations (the most ever), but because of late floods and low precipitation the total number of plants declined from more than 1 000 000 in 2001 to fewer than 300 000 in 2002 (Smith 2001, 2002).

Future model extensions

A basic principle of population modeling in conservation is to begin with simple models and gradually build up complexity (Caswell 2001, Section 18.4). Here we have focused on the crucial factor of environmental stochasticity. Our analysis could be extended in several directions. It would be possible, for example, to describe floods in more detail than a binary choice between early and late flood recession, and to describe precipitation as a continuous, rather than a discrete variable. To develop such models would require demographic parameter estimates under a wider array of environmental conditions. It is unlikely, however, that such refinements would significantly change the patterns reported here.

It would be interesting to explore the consequences of correlation between flood recession and precipitation, and the autocorrelation patterns in each. A positive correlation between late-receding floods and high precipitation during the growing season would ameliorate some of the negative effects of changes in the flood regime. There is no obvious sign of such a correlation (Fig. 9a), but we have not investigated the time series in detail.

Perhaps the most interesting extension will be to include spatial structure. In recent years, GIS technology has permitted a systematic survey of all potential *B. decurrens* habitat in the Illinois River Valley (Smith 2002). In the short term, populations continue to appear, disappear and shift annually, typical of a metapopulation. The *B. decurrens* metapopulation is largely confined to the narrow littoral zone along a 400-km stretch of the Illinois River, and extinction of large populations is common (Schwegman and Nyboer 1985, Smith et al. 1998, Smith and Mettler 2002). The genesis of new populations is facilitated by the ability of the seeds to float for extended periods (Smith and Keevin 1998), provided that suitable habitat exists in areas connected to the ebb and flow of the river. The Illinois River flows slowly and meets a hydrological barrier at its confluence with the Mississippi River. When both

rivers are in flood stage, this results in significant back and lateral flow (Cooley as cited in Kofoid 1903, Akanbi and Singh 1997), so dispersal was possible in any direction. In addition, seed dispersal was historically unimpeded by navigation structures. Today, however, the frequency of a favorable annual flood regime has fallen to 30%, and genetic evidence (DeWoody 2002) indicates that population establishment depends upon seeds from a small number of source populations.

In a metapopulation model, each location would experience its own flood timing and precipitation regime. An important parameter would be the degree of spatial autocorrelation between the flood and precipitation regimes among sites. Current evidence suggests that flood timing and precipitation can vary substantially over very small spatial scales. A metapopulation model incorporating dispersal and stochastic environmental variation would permit evaluation of the threat of extinction for *B. decurrens*, and the role of alterations to the floodplain system in its decline. Preliminary results (*unpublished data*) suggest that incorporating spatial structure modifies the details but does not change any of the conclusions of our study here.

Implications for management

Our study indicates that the threatened status of *B. decurrens* can be explained by historical changes in flooding. One strategy for species recovery would be to restore the river–floodplain system to pre-1900 conditions; economic and political considerations make this unlikely (Sparks et al. 2000). Conservation efforts will necessarily focus on mitigating the effects of levees and dams, whenever possible. The combination of technological advances in managing navigation pools (Busse 1998, Flowers et al. 1998) and a rising concern about the effects of navigation structures on floodplain species (Sparks et al. 1998, 2000) has resulted in experimentation with a pool drawdown strategy that would lengthen the summer growing season for many mudflat species. Our results indicate that the annual life cycle is responsible for *B. decurrens* population growth; therefore, any extension of the growing season that would facilitate this life-history pathway would reduce the probability of extinction. Management plans for *B. decurrens* should include controlled flooding during the winter and spring, with drawdown implemented by 1 June. This would result in an expanding population if rainfall in the latter part of the summer was favorable, and minimize population decline if it was not. During low precipitation years, irrigation of populations in the latter portion of the growing season would increase rosette survival and the production of seeds and increase population growth. The dominance of the annual life cycle during years of rapid growth suggests that preserving plants in the vegetative stage is unlikely to be an effective management option; therefore, when a well-timed flood regime is impossible to implement, other disturbances that provide bare ground suitable for seed germination and seedling establishment may offer viable alternatives. One thing is certain: to be successful, conservation strategies for this species must look beyond efforts to maintain static ''protected'' populations and make strategic use of the environmental variability to which *B. decurrens* is adapted.

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APPENDIX

Condition-specific seasonal projection matrices for *Boltonia decurrens* are presented in ESA's Electronic Data Archive: *Ecological Archives* A015-028-A1.