# LINKING SURFACE- AND GROUND-WATER LEVELS TO RIPARIAN GRASSLAND SPECIES ALONG THE PLATTE RIVER IN CENTRAL NEBRASKA, USA

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*Abstract:* Nearly all the techniques used to quantify how plants are linked to environmental gradients produce results in general terms, such as low to high elevation, xeric to mesic, and low to high concentration. While ecologists comprehend these imprecise scales, managers responsible for making decisions affecting these gradients need more precise information. For our study, we preserved the measurement scale and units of a dominant environmental gradient by using non-linear models to fit plant frequency to a water-level gradient ranging from shallow ground water to standing water along the Platte River in central Nebraska, USA. Non-linear models, unlike polynomials, have coefficients that can be interpreted with a biological meaning such as population peak, optimum gradient position, and ecological amplitude. Sixty-three riparian grassland species had sufficient information to link their plant frequency to the water-level gradient. From among 10 water-level summary statistics evaluated for a subset of 22 species, the best plant-frequency response curves were obtained by using the growing season 10% cumulative frequency water level, followed closely by the growing season 7-day moving average high water level and two other high water-level statistics. This suggests that for Platte River riparian grasslands, high water levels are more influential than mean, median, or low water levels. Land-management practices (i.e., grazing, haying, and extended rest) affected six species by a change in frequency or a shift in position along the water-level gradient. Four general plant communities composed of species responding individually to the water-level gradient and other factors were identified for Platte River riparian grasslands: emergent, sedge meadow, mesic prairie, and dry ridge. Plant response curves are the first step toward predicting how plants responding to riparian-grassland water levels might also respond to river management.

*Key Words:* riparian vegetation, wet meadow, direct gradient analysis, species response curve, non-linear models, surface- and ground-water level, water table, plant frequency, coenocline

## INTRODUCTION

Ecologists began quantifying ecological gradients in the first half of the 20th century by first describing species relationships to environmental gradients (e.g., Shreve 1922, Wells 1928) and later by fitting mathematical expressions (e.g., Gause 1930, 1931, 1932). By the mid-20th century, gradients were used by Whittaker (1951, 1956) in support of Gleason's individualistic hypothesis (Gleason 1926, 1939) to challenge Clements' community-unit theory (Clements 1916,

## Canonical Correspondence Analysis with Select Environmental Variables
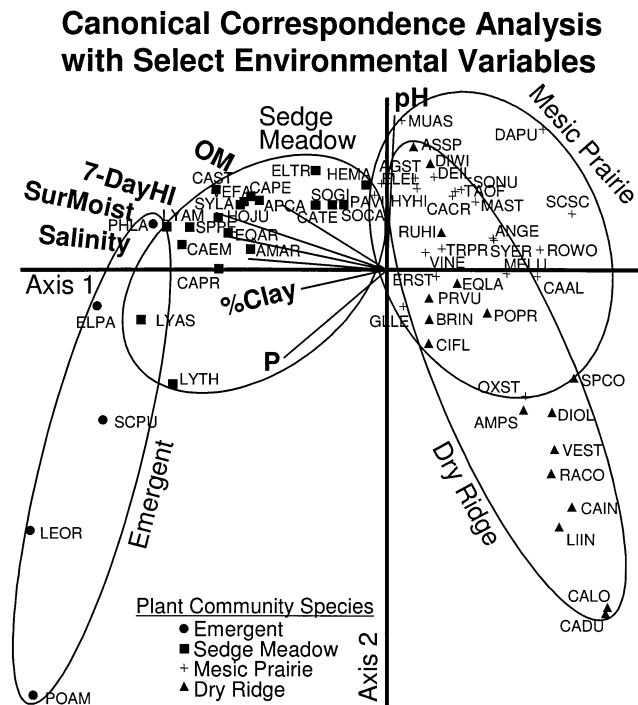


Figure 1. An example of a biplot from a canonical correspondence analysis of the data for our study. Note how the species can be ranked along an environmental gradient by extending a perpendicular line to the gradient axis (vector radiating from the origin with only the positive side shown), but there is no information on how each species is distributed along the gradient. The length and angle of the environmental vectors shows their importance and their relationship with other gradients. The eigenvalues representing the variance attributed to Axes 1 and 2 are 0.605 and 0.221. Parts per million phosphorus (P), percent clay content (%Clay), salinity, organic matter (OM), and pH are from a companion study by Simpson (2001), while the surface water content (SurMoist) and the growing season 7-day moving average high water level (7-DayHI) are from our study. Axis 1 is correlated with water availability (7-DayHI, SurMoist) and water-mediating gradients (Salinity, OM, %Clay) and can be considered a gradient from nearly hydric to almost xeric, while Axis 2 with less than half the explained variance can be considered a pH gradient. The ellipses represent approximate plant community boundaries.

1936). At about this same time, Whittaker was also refining direct gradient analysis techniques to describe plant species responses along predetermined environmental gradients such as pH, while Curtis and his associates were developing indirect gradient analysis techniques to arrange species along axes of variation based on the degrees of difference in plant species composition (Whittaker 1967). Both techniques can incorporate multiple gradients or axes, although higher dimensional analyses can be difficult to visualize without a graphical technique similar to biplots (e.g., Figure 1), which use vector lengths and angles radiating

from a centroid to represent gradients (ter Braak 1986). Toward the latter part of the 20th century, plant response curves from actual and simulated gradients were used in simulation modeling to gain valuable insights into plant community ecology (e.g., Gauch and Whittaker 1972, Palmer 1992, Seabloom et al. 2001).

Nearly all these techniques and analyses produce results that represent environmental gradients (which may be measured quantitatively) in general terms, such as low to high elevation, xeric to mesic, and low to high concentration (e.g., Figure 1). While ecologists understand the implications of these imprecise scales, managers responsible for making decisions affecting one or more of these gradients need information that is more precise. For example, specifying that mesic conditions are necessary to maintain a particular plant community is much less informative than specifying that the community requires a water table within 10 cm of the surface for seven consecutive days each year.

In this paper, we preserve the measurement scale and units of a dominant environmental gradient by using non-linear models to fit plant-species response curves to a water-level gradient ranging from shallow ground water to standing water. Non-linear models are more useful than linear models, like polynomials, because their coefficients can be interpreted with a biological meaning such as population peak, optimum gradient position, and ecological amplitude. Note that the term ''linear'' refers to the linear arrangement of the parameter coefficients in the model, not the shape of the curve (AISN Software Inc. 2000). A linear model can describe very complex curves, possibly fitting the data better than a non-linear model, but the linear coefficients have little biological meaning. One of the earliest and by far the most frequently used models to fit plant response to gradients is the Gaussian model (Gause 1931, 1932, Austin 1976). This non-linear model produces the familiar symmetrical bell-shaped curve and has been used by many investigators (e.g., Gause 1932, Whittaker 1956). Several investigators (e.g., Austin and Austin 1980, Werger et al. 1983, Austin 1987, Minchin 1987), however, have criticized the Gaussian model because there appears to be no biological basis for a symmetric response. Indeed, many species appear to show an asymmetric (skewed) or possibly platykurtic (plateau shaped) or even bimodal (more than one peak) response. One solution to this debate is to use a versatile non-linear model like the beta model, which can produce symmetric, asymmetric, and platykurtic curves (Austin 1976, Minchin 1987). Since there is still some debate over the ''best'' model(s) to fit plant responses to an environmental gradient, we tested the Gaussian and beta models along
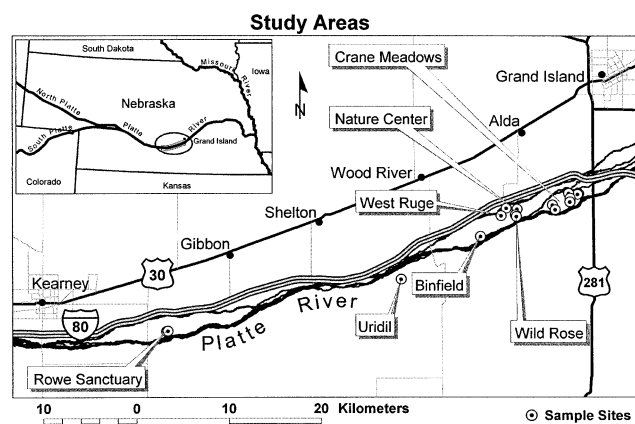
Figure 2. Map of the study areas and sampling sites along the Platte River in south central Nebraska, USA.

with 52 other non-linear models to obtain a best-fit plant response curve.

Our study was conducted in the riparian grasslands along the Platte River in central Nebraska, USA (Figure 2). These grasslands support a multitude of migratory birds and are being considered as part of a three-state, basin-wide, riverflow re-regulation plan to enhance migratory habitat for the endangered whooping crane (Cooperative Agreement 1997). This area offers low undulating topography with approximately 2 m of relief, which provides repeating water-level gradients ranging from standing water to approximately 3 m below the surface as the topography varies from sloughs to ridge tops. A study by Simpson (2001) used canonical correspondence to identify surface- and ground-water levels as the primary gradient in these grasslands, followed by salinity and phosphorus from among 12 parameters for hydrology, nutrients, organic matter, and soil texture. Our goal was to refine the plant response to surface- and ground-water levels further as a first step toward determining what influence river stage might have on these water levels and, in turn, on the plant species and communities.

## METHODS

### Study Area

The Platte River in central Nebraska, USA (40°49′N, 98°23′W) lies within the Central Great Plains ecoregion at 575–635 m elevation and is a wide, braided, shallow, low-gradient sand-bed river that drains approximately 137,000 km$^2$ from the states of Colorado, Wyoming, and Nebraska (Omernik 1987, Hitch et al. 2002). Mean annual precipitation within the study area is about 630 mm (National Climatic Data Center 2000). Mean monthly riverflows range from nearly bank full in June (72 m$^3$s$^{-1}$) to substantial areas of exposed riverbed in August (18 m$^3$s$^{-1}$, Hitch

et al. 2002). Much of the area formerly occupied by riparian grasslands within the Platte River valley, referred locally as wet meadows, has been converted to cropland (Sidle et al. 1989). The majority of remaining riparian grasslands now exist primarily as remnants within a matrix of agricultural land located within 3 km of the channel. These riparian grasslands are characterized by high water tables, slow runoff, nutrient-rich soils, and an undulating topography reminiscent of the braided channels from which they were formed. The principal aquifer within the Platte River valley is composed of unconfined Pleistocene sands and gravels (Schreurs and Rainwater 1956) and is recharged by the river and by precipitation (Hurr 1983, Wesche et al. 1994). Moderate to highly permeable soils (K = 5 to >50 cm·hr$^{-1}$), from 13–43 cm deep, formed in the loamy or sandy alluvium deposited over this highly permeable aquifer (Advanced copy, Hall County soil survey update, USDA Natural Resources Conservation Service, Grand Island, NE). Above the water table, saturated conditions are probably insignificant, since the coarse sands and gravels minimize the capillary fringe, and the highly permeable soil allows infiltrated precipitation to quickly pass through to the water table (USDA, NRCS, Soil Survey Division 2003).

Sample sites were located along a 50-km reach of the Platte River between Kearney and Grand Island, Nebraska (Figure 2). All sites were managed by the Platte River Whooping Crane Maintenance Trust, except that the Rowe Sanctuary sites were managed by the National Audubon Society and the Binfield site was managed by a private landowner. Land-management practices included livestock grazing rotations, hay rotations, and extended rest (4 to 8 years). Stocking rate varied by management unit but was typically about 0.3 animal unit months per hectare. All three practices also included periodic prescribed burns as part of their management. Since it was impractical to sample all combinations of these management practices (e.g., early or late grazing, and burned or unburned), we chose to limit our analysis to three broad-based management practices: grazed, hayed, or extended rested.

### Study Design and Analyses

A three-step process was used to link surface- and ground-water levels to plant response: describe the seasonal water-level pattern, describe the plant species frequency, and finally fit a curve through the data to quantify the linkage between water levels and plant frequency. The general procedure included sampling plant species frequency along a water-level gradient from the bottom of a swale to the top of an adjacent ridge (~200 cm change in relative elevation, Figure
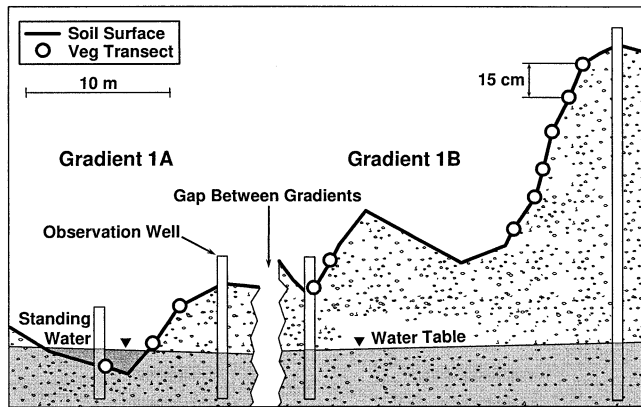
Figure 3. Cross-section profiles for one of the multiple-swale sites showing how an additional swale-ridge profile (Gradient 1B) was used to extend the surface- and ground-water-level gradient up slope. Four of the 12 replicates (three hayed and one rested) required an additional swale-ridge profile located from 0.2 to 18 km away to complete their water-level gradient. The two wells for each profile were used to determine the water-level slope between wells. Vegetation sampling transects were located at 15-cm intervals in relative elevation starting from near the bottom of each swale.

3). Several distinct plant communities occur along this gradient as individual species express their response to optimum water levels. Sample sites (individual swale-ridge profiles) were selected during the summer of 1998 to represent four replicates of the three broad-based land-management practices (grazed, hayed, or rested) and to represent the full water-level gradient typical for native Platte River riparian grasslands (about $+50$ to $-200$ cm relative to the land surface, where positive values are surface water and negative values are ground water). Ideally, each replicate should only need one swale-ridge profile to cover the full water-level gradient, but in practice, four replicates (three hayed and one rested) required an additional ''higher'' swale located from 0.2 to 18 km away to extend the water-level gradient up slope (e.g., Figure 3). The completed study design, therefore, consisted of 16 sample sites: four grazed, seven hayed, and five rested.

*Water-Level Pattern.* Each study site had a pair of shallow observation wells, one located near the bottom of the swale and one located near the top of an adjacent ridge (Figure 3). These wells were used to determine the water-level slope between the wells and to estimate the water-level gradient (i.e., surface or ground-water depth) from the bottom of the swale to the top of an adjacent ridge. Most wells were installed to Nebraska state standards (Nebraska Health and Human Services 1999) using 5.1-cm-diameter schedule 40 polyvinyl chloride casings with the lower 150 cm screened and open to the aquifer, and a 60-cm-thick

bentonite seal placed above the water table. The remaining wells were previously installed by Wesche et al. (1994) with less stringent standards (e.g., no bentonite seal, hand-made screens) but were considered suitable for monitoring the shallow water table. All water levels were measured biweekly to the nearest 0.3 cm (0.01 ft) using a fiberglass tape equipped with an electronic sensor (Henszey 1991), except during the winter when they were measured monthly. At least one well at each site was also equipped with a continuous water-level recorder. Continuous water levels for the non-recording wells were estimated by regression with these adjacent recording wells. Linear interpolation between each pair of wells was then used to estimate continuous water levels for the vegetation transects located between the bottom of the swale and the top of an adjacent ridge. If the interpolation predicted surface water in the swale, then the surface-water level was further adjusted to account for excess runoff or run-on by regression with the surface-water levels observed for that swale during the periodic biweekly and monthly measurements. Precipitation and evapotranspiration were continuously monitored onsite by four weather stations and five recording rain gages. These gages were located so that all sample sites were within 4.4 km of a weather station and 0.8 km of a rain gage.

Since no single water-level summary statistic can adequately describe the complex pattern of seasonal water levels, we chose to evaluate three types of summary statistics (cumulative frequencies, moving averages, and arithmetic mean) as appropriate statistics for linking surface- and ground-water levels to plant frequency. Before calculating these summary statistics, the continuous water levels were first summarized as mean daily water levels for each 24-hour period. This minimized transient diurnal fluctuations caused by daily cycles of evapotranspiration and other factors, which are probably much less important to plants than the mean daily water level. Mean daily water levels were then summarized for each vegetation transect using the summary statistics for the 1999 and 2000 growing seasons (15 March to 15 October; e.g., Figure 4).

Cumulative frequency distributions (e.g., Zarr 1974) show the number of days (i.e., the percent of time) during the growing season that the water was at or above a particular level, similar to the streamflow-duration curves (Searcy 1959) used by hydrologists. Water levels at the 10%, 50% (median), and 90% cumulative frequency for mean daily water level were chosen to test for plant-response linkages ($L_{10\%}$, $L_{50\%}$, $L_{90\%}$), since these levels represent what might be called the typical high, median, and low water levels for the growing season. The actual highest and lowest mean-daily water levels for the growing season would be the
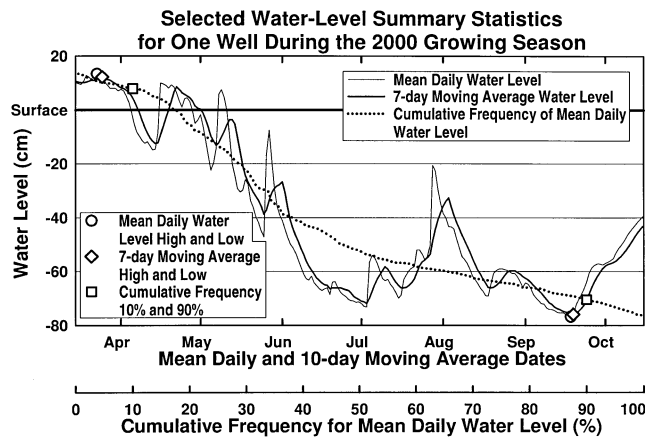
Figure 4. Water-level pattern and summary statistics for one well during the 2000 growing season (15 March to 15 October). The mean daily water level is the average water level for each 24-hour period and is already a summary of the instantaneous water level, which is too transitory for summarizing seasonal water levels. The 7-day moving average removes some of this variability and takes into account preceding water levels by averaging the mean daily water level for the current and previous six days. The cumulative frequency of mean daily water levels eliminates the time sequence altogether by showing the percent of days during the growing season that the water was at or above a particular level.

0% and 100% cumulative frequency values respectively. For example, in Figure 4, the 10% cumulative frequency for mean daily water levels was 8 cm, showing that for 10% of the growing season (22 of 215 days), the water was at or above 8 cm above the surface. Likewise, the 90% cumulative frequency for mean daily water levels was −70 cm, showing that the water was at or above 70 cm below the surface for 90% of the growing season (194 of 215 days). Although this 90% value might not seem to be too useful since it covers a considerable portion of the growing season, the cumulative frequency scale can be easily reversed so that the 90% value also represents the value for 10% of the growing season when the mean daily water level was *below* a particular level (e.g., −70 cm). Cumulative frequencies are useful for describing how often the water was at or above a specific level, but they do not represent the actual sequence of observed events. For example, in Figure 4, the mean daily water level was at or above the land surface for 17% of the growing season (37 of 215 days), but that percentage was distributed across three periods of widely different duration and for at least some portion of March, April, and May.

Moving-average water levels for 7, 10, and 14 days ($\bar{L}_7$, $\bar{L}_{10}$, $\bar{L}_{14}$) were also tested to determine if an average of the immediately preceding mean daily water levels might be more important to plants than simply how

often the water was at or above a particular level during the growing season. Moving averages can be calculated in a variety of ways (e.g., Shumway and Stoffer 2000), but we chose to calculate a simple moving average ($\bar{L}_n$) by averaging the mean daily water level for the current ($\bar{L}_t$) and previous number ($n − 1$) of days:

$$\bar{L}_n = \frac{1}{n}[L_t + L_{t-1} + \cdots + L_{t-(n-1)}],$$

where $\bar{L}_n$ is the current moving-average water level at time $t$ and $n$ is the number of days used to calculate the moving average. For testing plant response linkages, the $n$-day high and low moving-average water levels for the growing season ($\bar{L}_{nH}$ and $\bar{L}_{nL}$) were chosen, like the 10% and 90% cumulative frequencies, because they may represent periods of high or low water-level stress for plants. Unlike the cumulative frequencies, however, the $n$-day moving averages can be associated with a date (or dates). For example, in Figure 4, the growing season 7-day moving average high water level ($\bar{L}_{7H}$) was 12 cm above the surface for 25 March, while the growing season 7-day moving average low water level ($\bar{L}_{7L}$) was 76 cm below the surface on 19 September. While not specifically intended to meet any particular standard for wetland hydrology (National Research Council 1995), the $\bar{L}_{10H}$ closely approximates the 5% criterion of the 1987 Corps manual (Environmental Laboratory 1987), the $\bar{L}_{7H}$ meets the 1989 interagency manual criterion (Federal Interagency Committee for Wetland Delineation 1989), and the $\bar{L}_{14H}$ approximates the 15-day criterion for the 1991 proposed revisions (U.S. Environmental Protection Agency et al. 1991).

The arithmetic mean is simply the mean water level for the growing season ($\bar{L}_S$) and, together with the $L_{50\%}$, is a measure of the central tendency or "average" growing season water level. Growing season high water levels are represented by $L_{10\%}$, $\bar{L}_{7H}$, $\bar{L}_{10H}$, $\bar{L}_{14H}$, while the growing season low water levels are represented by $L_{90\%}$, $\bar{L}_{7L}$, $\bar{L}_{10L}$, $\bar{L}_{14L}$ None of these statistics, however, consider the root zone. The standard normal deviate (Hunt et al. 1999) is one high water-level statistic that considers the root zone but was not tested here because our water levels never entered the root zone on the upslope end of the water-level gradient. The standard normal deviate measures the root zone residence time by using a cumulative frequency to summarize the number and duration of contiguous periods when the water level was at or above the root zone (typically within 30 cm below the land surface). This statistic combines aspects of the cumulative frequency and the moving average, and it should be considered for studies where the water level consistently enters the root

zone (i.e., wetlands and possibly shallow subirrigated plant communities).

*Plant Response.* Vegetation transects aligned along topographic contours were established at 15-cm increments in relative elevation from the bottom of each swale to the top of an adjacent ridge (Figure 3) using a rotating laser level. Transects were marked with a thin polypropylene line interwoven with stainless steel threads so the transects could be relocated in subsequent years, even after a prescribed burn. Two hundred points per transect, spaced 10 cm apart, were used to calculate plant frequency by species based on the nearest plant to each point. This technique for botanical composition is similar to Evans and Love (1957) and Owensby (1973), except that a 10-pin point frame was placed sequentially along a relatively short transect (i.e., 20 m) to stay within a reasonable distance ($\pm10$ m) of the water-level gradient between the wells, rather than single points along a longer transect (e.g., 100 m). Starting points were randomly selected from within the first meter of the transect's downstream end. Although frequency has some limitations (Mueller-Dombois and Ellenberg 1974), we chose this metric instead of canopy cover or biomass because frequency is less affected by plant phenology or by herbage removal from grazing or haying. To minimize phenological effects on plant frequency, sampling was conducted in the early summer of 1999 and 2000 while the early-flowering sedges (*Carex* spp.) were still identifiable to species and the warm season species had emerged sufficiently to be identified. Frequency for perennials, like the vast majority of Platte River species evaluated, is slower to respond to environmental fluctuations about a seasonal norm than canopy cover or biomass, so the two years cannot be considered independent samples. Thus, the mean frequency for 1999 and 2000 by transect, and the associated mean water-level statistic, was considered the experimental unit. Nomenclature follows the PLANTS database (USDA, NRCS 2001), based on the taxonomy by Great Plains Flora Association (1986), Rolfsmeier (1995), and Rolfsmeier and Wilson (1997).

*Linking Water Levels to Plant Response.* Direct gradient analysis (e.g., Whittaker 1967) by fitting a non-linear curve through the data was used to evaluate potential links between water levels and plant species frequency. Non-linear models were used because their coefficients can be interpreted with a biological meaning (e.g., amplitude of the peak plant response, water level at the peak, and an indication of the range of favorable water levels; Figure 5). Complex polynomials (e.g., $y = a + b_1x + b_2x^2 + b_3x^3 + \ldots + b_nx^n$), on the other hand, may provide a better fit to the data, but their coefficients typically have little or no biolog-
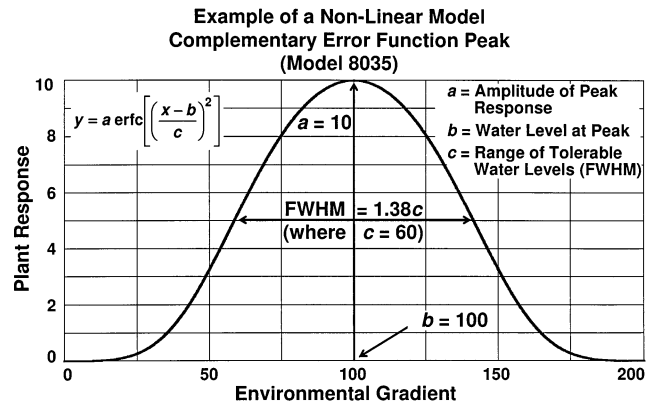


Figure 5.   An example of a non-linear model used to fit a theoretical plant response to an environmental gradient with arbitrary units. Note how the coefficients can be interpreted with a biological meaning (e.g., $a$ = amplitude of the peak plant response, $b$ = water level at the peak, and FWHM = an indication of the range of favorable water levels at half the peak response). The full width at half-maximum (FWHM) is a function of $c$.

ical meaning. Models were fit to the data with an automated curve fitting software program (AISN Software Inc. 2000), which can simultaneously fit 12 symmetrical and 25 asymmetrical non-linear peak models, as well as four symmetrical and 11 asymmetrical non-linear transition (sigmoid shape) models. The ranking of these models, however, does not include a combined test for model fit and a penalty for over-specifying the model by using more parameters than necessary, so we used the corrected Akaike information criterion ($AIC_c$, Burnham and Anderson 1998) to rank the models. $AIC_c$ incorporates the residual sum of squares, the number of parameters, and the sample size, so that the model with the lowest $AIC_c$ indicates the best fit from within the set of models evaluated. Since $AIC_c$ values occur on a relative scale specific to the data, we computed corrected Akaike information criterion differences ($\Delta_i = AIC_{ci} - \text{minimum } AIC_c$) to facilitate interpretation and to allow quick comparison and ranking of the candidate models by rescaling the $AIC_c$ values (Burnham and Anderson 1998). Burnham and Anderson (1998) suggest that as a rough rule of thumb models are essentially the same with a $\Delta_i \leq 2$, models have considerably less support for $\Delta_i$ values between about 4 to 7, and models have essentially no support for $\Delta_i$ values greater than 10. The responsibility for selecting appropriate models to evaluate, however, is up to the investigator. Since we did not have an *a priori* knowledge of which non-linear models might be appropriate, we tested all 52 non-linear models, including the Gaussian and beta models used by previous investigators (e.g., Gause 1931, 1932, Austin 1976, Minchin 1987). This occasionally produced a

superior AIC$_c$-fit model that showed little resemblance to the biological response (e.g., a narrow, out of range spike caused by one or two data points when a broader distribution was suggested by the data). Anderson et al. (2000) considered this process of including all possible models ''data dredging,'' but we argue that including all possible models is a necessary step until it becomes clear which non-linear models best fit the water levels to plant response. When a superior AIC$_c$ fit with an obvious poor biological relationship occurred, rather than mechanically accepting the model, we judiciously considered that model inappropriate for the data and excluded the model in favor of the next best AIC$_c$-fit model with a more appropriate biological relationship.

The three broad-based land-management practices (grazed, hayed, rested) were tested in the same manor described above for any species that was found in at least three sample sites per management practice and 12 transects per management practice. This requirement was intended to minimize the effects of only one or two sites dominating the species response for a management practice. Effects were tested by first fitting the best non-linear model regardless of management practice for the species. Then, that model was fit to the data for each management practice. The coefficients were tested for significant differences among management practices with a one-way ANOVA using the coefficient's means, standard errors, and sample sizes (Jandel Scientific Software 1994). Species having at least one coefficient with a significant difference (p $\leq$ 0.05) were considered to have a management effect, and the management practices were grouped accordingly for that species based on a Bonferroni mean separation test (Jandel Scientific Software 1994).

*Plant Community Classification.* Cluster analysis with Ward's method of linkage and Euclidean distance (McCune and Mefford 1999) was used to group transects into similar plant communities. Six transects were excluded from this analysis and manually assigned to an emergent plant community because they were the only transects with a $\bar{L}_{7H}$ greater than 20 cm above the surface and their dominant species were not consistent among transects. After the plant community groups were determined, three characteristic species for each community were selected by using the Indicator Species Analysis available in PC-ORD (McCune and Mefford 1999). Characteristic species with a broad distribution across more than one community, or with a distribution affected by management, were excluded in favor of the next best characteristic species without these traits. Finally, approximate plant community boundaries along the $\bar{L}_{7H}$ gradient were selected manually by examining the distribution of these character-
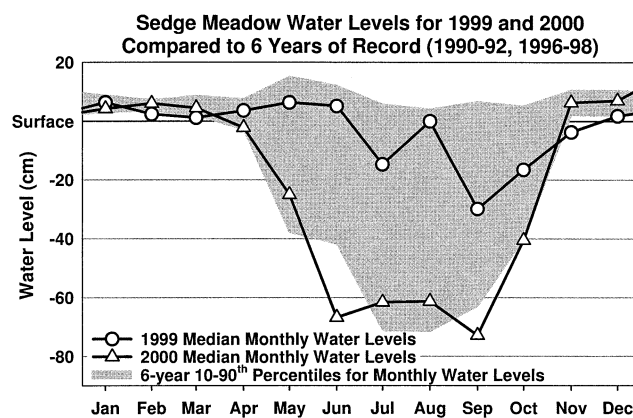


Figure 6. The water-level pattern from a well located in a sedge meadow along the Platte River, showing the range of water levels for a 6-year period before the study (1990–92, 1996–98) and for two years during the study (1999 and 2000). The 6-year range of water levels excludes 10% of the highest and lowest mean-daily water levels for each month to show the ''typical'' range for 80% of the monthly water levels.

istic species and the $\bar{L}_{7H}$ for the transects grouped in the cluster analysis.

## RESULTS

### Water-Level Pattern

Water levels during the study period, 1999–2000, ranged from near the highest observed to near the lowest observed for a six-year period before the study (Figure 6). By averaging the data from both a wet and a dry growing season, the plant-response curve coefficients may have more variation, but the curves may also more accurately represent the typical plant response. Vegetation transects covered a range of water levels from 40 cm of standing water to 172 cm below the surface, based on the two-year average for the growing season 7-day moving average high water level ($\bar{L}_{7H}$). The same transects were used for all species. For example, the frequency of *Agrostis stolonifera* for each transect is shown in Figure 7. Another species would have different frequencies, but the transect locations along the $\bar{L}_{7H}$ water-level gradient remain unchanged. The majority of transects (90%) had $\bar{L}_{7H}$ water levels between 18 cm of standing water and 130 cm below the surface, with 5% having more than 18 cm of standing water and 5% having deeper than 130 cm below the surface. Some predicted plant response curves presented below extend beyond this range of sampled transects to facilitate comparison with other species, but their predictions become increasingly less accurate beyond the majority of the data.

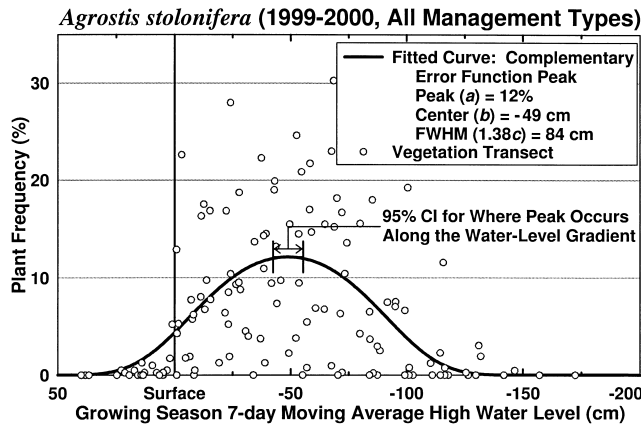To help choose the best water-level summary statis-

Figure 7. Fitting the frequency of *Agrostis stolonifera* to the growing season 7-day moving average high water level ($\bar{L}_{7H}$) with a Complementary Error Function Peak equation by using the mean of two years of data from 131 vegetation transects. Note how the coefficients can be interpreted with a biological meaning: $a$ = peak frequency, $b$ = location of peak along the water-level gradient $\bar{L}_{7H}$, and $1.38c$ = full width at half-maximum (FWHM—a measure of ecological amplitude at half the peak frequency). CI is the 95% confidence interval for $b$.

tic for linking water levels to plant frequency, all 10 water-level summary statistics were used to fit response curves to a subset of 22 species. Table 1 summarizes these results by averaging corrected Akaike information criterion differences ($\Delta_i$) for each water-level summary statistic. Based on Burnham and Anderson's (1998) rough rule of thumb that models are

essentially the same with a $\Delta_i \le 2$, the four growing season high water-level statistics ($L_{10\%}$, $\bar{L}_{7H}$, $\bar{L}_{10H}$, $\bar{L}_{14H}$) provide much better links to plant frequency than the other water-level statistics. The two growing season central tendency water-level statistics ($L_{50\%}$, $\bar{L}_S$), which are commonly used to summarize water levels, have considerably less support for linking plant frequency, since their $\Delta_i$ values are between about 4 to 7. The four growing season low water-level statistics ($L_{90\%}$, $\bar{L}_{7L}$, $\bar{L}_{10L}$, $\bar{L}_{14L}$) have essentially no support for linking plant frequency, since their $\Delta_i$ values are greater than 10. Although any of the four growing season high water-level statistics could be used to link water levels to plant frequency without much information loss, we chose to use the best statistic that has an equivalent in any current or proposed standard, the $\bar{L}_{7H}$, which meets the 1989 interagency manual criterion for wetland hydrology.

It might be helpful to put the 7-day moving average high water level ($\bar{L}_{7H}$) into terms of the currently used 1987 Corps manual for delineating jurisdictional wetlands. Based upon the $\bar{L}_{10H}$, which approximates the 1987 Corps criteria, the 1987 Corps 5% soil saturation criteria for the growing season (10.75 of 215 days for our sites) would be three days longer (10 instead of 7 consecutive days) and about 2.5 cm lower than the $\bar{L}_{7H}$ water levels presented below. Although the $\bar{L}_{7H}$ is not restricted to the 30-cm regulatory root zone depth, the 2.5 cm difference in water levels suggests that the regulatory depth for the $\bar{L}_{7H}$ would be about 27.5 cm. Thus, the $\bar{L}_{7H}$ used in this paper is a little less stringent

Table 1. Ranking water-level summary statistics, using the average corrected Akaike information criterion differences ($\Delta_i$) for a subset of 22 species.* The growing season 10% cumulative frequency water level ($L_{10\%}$) produced the best summary statistic for these 22 species, but any water-level statistic with a $\Delta_i \le 2$ (Burnham and Anderson 1998) could be considered equally suitable for linking water levels to plant frequency.

| Water-Level Statistic | Average AIC$_c$ $\Delta_i$ | Rank |
|---|---|---|
| Growing Season High Water-Level Statistics | | |
| 10% Cumulative Frequency ($L_{10\%}$) | 0 | 1 |
| 7-day Moving Average High ($\bar{L}_{7H}$) | 0.1 | 2 |
| 10-day Moving Average High ($\bar{L}_{10H}$) | 0.9 | 3 |
| 14-day Moving Average High ($\bar{L}_{14H}$) | 1.0 | 4 |
| Growing Season Central Tendency Water-Level Statistics | | |
| 50% Cumulative Frequency ($L_{50\%}$) | 3.9 | 5 |
| Arithmetic Mean ($\bar{L}_S$) | 6.5 | 6 |
| Growing Season Low Water-Level Statistics | | |
| 90% Cumulative Frequency ($L_{90\%}$) | 13.2 | 7 |
| 7-day Moving Average Low ($\bar{L}_{7L}$) | 15.2 | 10 |
| 10-day Moving Average Low ($\bar{L}_{10L}$) | 14.2 | 9 |
| 14-day Moving Average Low ($\bar{L}_{14L}$) | 13.5 | 8 |

* Subset of species tested: *Agrostis stolonifera, Andropogon gerardii, Apocynum cannabinum, Calamagrostis stricta, Calamovilfa longifolia, C. crawei, C. duriuscula, C. emoryi, C. pellita, C. praegracilis, C. tetanica, Eleocharis palustris, Leersia oryzoides, Lycopus asper, Panicum virgatum, Phyla lanceolata, Polygonum amphibium, Sorghastrum nutans, Spartina pectinata, Symphyotrichum lanceolatum, Verbena stricta, Viola nephrophylla.*

than the 1987 Manual for the number of consecutive days, and the regulatory depth for the root zone is a little more stringent than the 1987 Manual.

Plant Response

One hundred ninety-three species were observed along the vegetation transects out of approximately 300 Platte River riparian grassland species that occur in our area. Sixty-three of these species had sufficient information to link their frequencies to water levels, and 19 species had sufficient information to further test for management practice effects in addition to water-level linkages (Table 2). Table 2 also lists the U.S. Fish and Wildlife Service's wetland indicator category assigned to each species. In 1999, we had difficulty identifying sedges (*Carex* spp.), spikerushes (*Eleocharis* spp.), and yellow stargrass (*Hypoxis hirsuta*). In 2000, we paid particular attention to identifying these species, but the 1999 data were unusable, so these species have one year of data for plant frequency while still using the two-year average for water levels.

Linking Water Levels to Plant Response

Figure 7 shows an example of how the water level was linked to plant frequency for *Agrostis stolonifera* by fitting a Complementary Error Function Peak model through the data. Note how the coefficients can be interpreted with a biological meaning with *a* representing the peak plant frequency, *b* representing the location of the peak along the water-level gradient, and the full width at half-maximum (FWHM, a function of *c*) representing a measure of ecological amplitude at half the peak plant frequency (see also Figure 5). Some models also have a fourth or fifth parameter (e.g., *d, e* in Table 2) that affects the symmetry of the response curve, but these parameters do not appear to have a direct biological interpretation (i.e., water level or plant response). If confidence intervals were shown for plant frequency, most of the species presented below would have quite wide intervals due to the inherently wide range in plant frequency. These confidence intervals, however, are much less interesting than the confidence interval for where the peak frequency occurs along the water-level gradient (i.e., confidence interval for *b*). Table 2 details the values for these parameters by species and management practice (see the Appendix for model formulas and coefficient descriptions).

Figures 8–10 show the plant response arranged by species adapted to increasingly lower water levels, with Figure 8 showing the most frequent species (>10%), Figure 9 showing the common species (1–10%), and Figure 10 showing the least frequent species (<1%). The models and coefficients for these figures are presented in Table 2. Note that there are two basic plant-response curve shapes. The first shape describes those species that remain relatively unaffected by the water level until a critical level is reached, at which point the plant frequency rapidly decreases. Transition models typify this response, although the rising or the falling limb of a peak model centered off the water-level scale may have a similar pattern (e.g., *Poa pratensis*, Figure 8h). The emergent *Schoenoplectus pungens* (Figure 9i) shows this pattern when the $\bar{L}_{7H}$ drops below a critical level, while upland species such as *Bromus inermis* and *Ambrosia psilostachya* (Figures 9h and 9w) show this pattern when the $\bar{L}_{7H}$ rises above a critical level. The second basic shape for plant response curves describes those species that express a peak frequency at some point within the riparian-grassland portion of the water-level gradient. This peak response may be symmetrical like *Phyla lanceolata* and *Hypoxis hirsuta* (Figures 9f and 10s) or asymmetrical like *Carex emoryi* and *Muhlenbergia asperifolia* (Figures 8c and 10l). Most asymmetrical species tend to be truncated on the wetland side of the peak, rather than on the upland side, suggesting that these species have some difficulty adapting to high water levels. Some examples of strong truncation on the high-water side include *Panicum virgatum* and *Rudbeckia hirta* (Figures 8d and 10o), where their plant frequencies drop rapidly to zero as the $\bar{L}_{7H}$ approaches standing water. The opposite response is expressed by a few of the least abundant species like *Prunella vulgaris* and *Oxalis stricta* (Figures 10x and 10ac), where their plant responses are truncated on the upland side.

Upland species with transition or transition-like curves tend to have the broadest range of favorable water levels (e.g., *Bromus inermis* and *Symphyotrichum ericoides*, Figures 9h and 9s). These species remain unaffected by the water level until the $\bar{L}_{7H}$ rises above a critical level. Below this level, the water level has little or no effect, and species frequency is probably limited by other factors, such as soil moisture, chemistry, and texture. Of more interest than these upland species with transition models are the species that have peaks within the riparian-grassland portion of the water-level gradient. Most of these species have an $\bar{L}_{7H}$ ecological amplitude, as expressed by their full width at half-maximum (FWHM), of 25 to 97 cm. Species with the broadest FWHM range tend to be upland species like *Andropogon gerardii* (104–132 cm, Figure 8f), *Dichanthelium oligosanthes* (99 cm, Figure 9v), and *Verbena stricta* (99 cm, Figure 9u); while species with the narrowest range tend to be wetland species like *Carex praegracilis* (13 cm, Figure 10h), hayed and rested *Spartina pectinata* (17 cm, Figure 8a), and *Carex tetanica* (17 cm, Figure 9k). Sedge meadow

Table 2.   Model numbers and fitted coefficients used to link the plant frequency to the growing season 7-day moving average high water level ($\bar{L}_{7H}$) as shown in Figures 8–10, and the management practice or practices from which the coefficients were chosen.

| Species[1] | Mgt.[2] Practice | Model[3] Number |
|---|---|---|
| *Agrostis stolonifera* L. | GHR√ | 8035 |
| *Ambrosia artemisiifolia* L. | GHR | 8035 |
| *Ambrosia psilostachya* DC. | GHR√ | 8089 |
| *Andropogon gerardii* Vitman | G√ | 8035 |
|  | HR√ | 8035 |
| *Apocynum cannabinum* L. | GH | 8036 |
| *Asclepias speciosa* Torr. | GHR | 8031 |
| *Bromus inermis* Leyss. ssp. *inermis* | GHR | 8074 |
| *Calamagrostis stricta* (Timm) Koel. | GH√ | 8038 |
|  | R√ | 8038 |
| *Calamovilfa longifolia* (Hook.) Scribn. | GHR | 8089 |
| *Callirhoe alcaeoides* (Michx.) Gray | GHR | 8031 |
| *Callirhoe involucrata* (Torr. & Gray) Gary | GHR | 8033 |
| *Carex crawei* Dewey | GH√ | 8034 |
|  | R√ | 8035 |
| *Carex duriuscula* C.A. Mey. | GHR | 8032 |
| *Carex emoryi* Dewey | GHR√ | 8033 |
| *Carex pellita* Muhl ex Willd. | GHR√ | 8036 |
| *Carex praegracilis* W. Boott | GHR | 8035 |
| *Carex tetanica* Schkuhr | GHR | 8031 |
| *Cirsium flodmanii* (Rydb.) Arthur | GH | 8034 |
| *Dalea purpurea* Vent. | GHR | 8035 |
| *Desmanthus illinoensis* (Michx.) MacM. ex B.L. Robins. & Fern. | HR | 8036 |
| *Dichanthelium oligosanthes* (J.A. Schultes) Gould var. *scribnerianum* (Nash) Gould | GHR√ | 8030 |
| *Dichanthelium wilcoxianum* (Vasey) Freckmann | GHR | 8032 |
| *Eleocharis elliptica* Kunth | GHR√ | 8031 |
| *Eleocharis palustris* (L.) Roemer & J.A. Schultes | GHR | 8035 |
| *Elymus trachycaulus* (Link) Gould ex Shinners ssp. *trachycaulus* | GHR√ | 8033 |
| *Equisetum arvense* L. | GHR | 8052 |
| *Equisetum laevigatum* A. Braun | GHR√ | 8083 |
| *Erigeron strigosus* Muhl. ex Willd. | GHR | 8035 |
| *Glycyrrhiza lepidota* Pursh | GHR | 8030 |
| *Helianthus maximiliani* Schrad. | GHR | 8033 |
| *Hordeum jubatum* L. | GHR | 8035 |
| *Hypoxis hirsuta* (L.) Coville | GHR | 8035 |
| *Leersia oryzoides* (L.) Sw. | GR | 8035 |
| *Lithospermum incisum* Lehm. | GHR | 8083 |
| *Lycopus americanus* Muhl. ex W. Bart. | GHR | 8035 |
| *Lycopus asper* Greene | GHR | 8036 |
| *Lysimachia thyrsiflora* L. | GHR | 8035 |
| *Maianthemum stellatum* (L.) Link | GHR | 8031 |
| *Medicago lupulina* L. | GHR√ | 8032 |
| *Muhlenbergia asperifolia* (Nees & Meyen ex Trin.) Parodi | GHR | 8033 |
| *Oxalis stricta* L. | GHR | (8033) |
| *Panicum virgatum* L.[8] | GHR√ | 8186 |
| *Phyla lanceolata* (Michx.) Greene | GHR | 8030 |
| *Poa pratensis* L. | GHR√ | 8083 |
| *Polygonum amphibium* L. | GHR | 8030 |
| *Prunella vulgaris* L. | GH | (8033) |
| *Ratibida columnifera* (Nutt.) Woot. & Standl. | GR | 8030 |
| *Rosa woodsii* Lindl. | GHR | (8036) |
| *Rudbeckia hirta* L. | GH | 8036 |
| *Schizachyrium scoparium* (Michx.) Nash | GHR | 8034 |
| *Schoenoplectus pungens* (Vahl) Palla var. *pungens* | GHR | 8077 |

Table 2. Extended.

| Model Coefficients (±95% CI)[3,4,8] | | | | Non-Zero Transects[5] | Center (cm)[6] | FWHM (cm)[6] | Ind.[7] Category |
|---|---|---|---|---|---|---|---|
| *a* | *b* | *c* | *d* | | | | |
| 12.2 ± 1.9 | 48.9 ± 6.5 | 60.8 ± 10.9 | | 33G, 35H, 34R | 49 | 84 | FAC+ |
| 0.2 ± 0.1 | 23.0 ± 12.4 | 29.5 ± 20.8 | | 5G, 1H, 5R | 23 | 41 | FACU |
| 4.7 ± 1.4 | 113.4 ± 15.1 | 0.6 ± 36.0 | 0.0 ± 0.9 | 23G, 13H, 27R | — | — | FAC |
| 16.6 ± 4.8 | 89.8 ± 31.6 | 95.6 ± 47.0 | | 25G | 90 | 132 | FAC− |
| 33.1 ± 4.2 | 86.0 ± 8.4 | 75.1 ± 13.4 | | 40H, 33R | 86 | 104 | |
| 0.6 ± 0.2 | −17.4 ± 3.9 | 19.9 ± 8.2 | | 8G, 19H | −4 | 35 | FAC |
| 0.2 ± 0.1 | 36.5 ± 9.3 | 15.8 ± 13.4 | | 2G, 6H, 8R | 37 | 32 | FAC |
| 3.3 ± 1.2 | 10.2 ± 10.4 | 1.6 ± 8.0 | | 7G, 32H, 3R | — | — | upl |
| 4.0 ± 0.9 | −6.1 ± 3.4 | 11.1 ± 3.3 | 12.4 ± 46.1 | 12G, 12H | −6 | 22 | *FACW |
| 3.6 ± 0.8 | 9.8 ± 2.7 | 27.2 ± 6.5 | 22.8 ± 83.3 | 21R | 10 | 54 | |
| 10.8 ± 3.0 | 142.3 ± 8.9 | 0.3 ± 19.9 | 0.0 ± 0.9 | 5G, 3H, 5R | — | — | upl |
| 0.2 ± 0.1 | 74.7 ± 6.8 | 12.1 ± 10.0 | | 4G, 8H, 1R | 75 | 24 | *OBL |
| 2.9 ± 1.2 | 168.2 ± 50.8 | 62.6 ± 35.4 | | 12G, 15H, 11R | 168 | 153 | upl |
| 6.9 ± 2.3 | 62.8 ± 8.9 | 14.0 ± 6.2 | | 21G, 15H | 63 | 49 | FACW |
| 1.3 ± 0.4 | 65.1 ± 10.6 | 47.4 ± 17.5 | | 19R | 65 | 65 | |
| $10^{18} \pm 10^{21}$ | $10^{12} \pm 10^{15}$ | 2.5 ± 84.8 | | 6G, 4H, 5R | — | — | upl |
| 35.1 ± 3.8 | −10.8 ± 3.0 | 17.6 ± 2.7 | | 24G, 29H, 32R | −11 | 43 | OBL |
| 7.9 ± 1.6 | −20.0 ± 3.5 | 22.8 ± 5.4 | | 18G, 29H, 26R | −4 | 40 | OBL |
| 0.4 ± 0.2 | 2.1 ± 2.2 | 9.7 ± 3.8 | | 5G, 2H, 5R | 2 | 13 | FACW |
| 1.3 ± 0.6 | 22.9 ± 5.3 | 8.6 ± 6.2 | | 2G, 12H, 1R | 23 | 17 | FACW+ |
| 0.6 ± 0.3 | 59.0 ± 7.1 | 8.4 ± 4.9 | | 8G, 5H | 59 | 30 | NI |
| 0.2 ± 0.1 | 76.7 ± 21.8 | 52.4 ± 35.3 | | 1G, 2H, 8R | 77 | 72 | upl |
| 0.1 ± 0.1 | 10.5 ± 18.6 | 43.0 ± 40.0 | | 3H, 7R | 40 | 76 | FACU |
| 2.9 ± 0.7 | 122.9 ± 20.1 | 41.9 ± 15.7 | | 18G, 26H, 22R | 123 | 99 | *FACU |
| 0.3 ± 0.2 | 35.7 ± 12.6 | 0.5 ± 0.3 | | 1G, 8H, 3R | 36 | 40 | upl |
| 6.3 ± 1.9 | 38.6 ± 4.9 | 15.8 ± 6.8 | | 20G, 22H, 19R | 39 | 32 | upl |
| 12.4 ± 2.2 | −16.8 ± 3.8 | 25.3 ± 5.3 | | 11G, 11H, 13R | −17 | 35 | OBL |
| 0.9 ± 0.3 | 14.3 ± 7.8 | 20.4 ± 8.3 | | 19G, 14H, 14R | 14 | 50 | FACU |
| 0.5 ± 0.2 | −0.7 ± 18.6 | 39.5 ± 15.1 | 1.5 ± 0.6 | 12G, 7H, 7R | −1 | 50 | FAC |
| 2.2 ± 0.4 | 1.5 ± 8.4 | 8.8 ± 13.3 | | 31G, 40H, 39R | — | — | FACW |
| 0.2 ± 0.1 | 66.4 ± 22.1 | 64.8 ± 35.9 | | 9G, 11H, 5R | 66 | 90 | FAC |
| 0.4 ± 0.2 | 41.6 ± 16.5 | 27.7 ± 17.4 | | 15G, 9H, 2R | 42 | 65 | FACU |
| 1.3 ± 0.5 | 20.4 ± 9.4 | 20.3 ± 10.3 | | 10G, 18H, 3R | 20 | 50 | UPL |
| 0.3 ± 0.1 | −1.1 ± 9.5 | 26.7 ± 15.8 | | 4G, 8H, 6R | −1 | 37 | FACW |
| 0.5 ± 0.3 | 48.0 ± 16.4 | 48.1 ± 26.8 | | 8G, 8H, 3R | 48 | 66 | FACW |
| 4.1 ± 1.0 | −18.8 ± 4.6 | 26.3 ± 7.0 | | 8G, 10R | −19 | 36 | OBL |
| 0.2 ± 0.1 | 99.6 ± 3.4 | 2.0 ± 7.7 | | 9G, 3H, 1R | — | — | upl |
| 0.2 ± 0.1 | 1.7 ± 12.4 | 37.6 ± 20.6 | | 5G, 4H, 7R | 2 | 52 | OBL |
| 0.4 ± 0.2 | −25.00 ± 4.9 | 16.1 ± 7.8 | | 5G, 1H, 12R | −14 | 28 | OBL |
| 0.6 ± 0.3 | −7.6 ± 5.7 | 18.2 ± 9.5 | | 4G, 5H, 5R | −8 | 25 | OBL |
| 1.1 ± 0.7 | 58.9 ± 12.5 | 20.1 ± 18.5 | | 5G, 15H, 2R | 59 | 40 | FAC |
| 3.1 ± 0.9 | 81.7 ± 24.9 | 0.6 ± 0.4 | | 20G, 34H, 27R | 82 | 135 | FAC |
| 0.4 ± 0.2 | 35.7 ± 23.8 | 39.5 ± 28.8 | | 6G, 8H, 24R | 36 | 97 | FACW |
| 0.4 ± 0.1 | −117.4 ± 9.3 | 19.6 ± 8.2 | | 9G, 10H, 5R | 117 | 48 | FACU |
| 11.1 ± 2.7 | 16.7 ± 3.6 | 7.6 ± 6.4 | 0.6 ± 0.4 | 24G, 39H, 37R | 17 | 33 | FAC |
| 1.9 ± 0.9 | 0.5 ± 11.1 | 16.9 ± 11.6 | | 10G, 4H, 10R | 0 | 40 | OBL |
| 36.1 ± 13.4 | 46.1 ± 35.3 | 61.0 ± 45.7 | | 32G, 43H, 38R | — | — | FACU |
| 6.2 ± 3.2 | −24.9 ± 7.1 | 11.7 ± 6.3 | | 8G, 3H, 6R | −25 | 28 | OBL |
| 0.4 ± 0.3 | −75.8 ± 17.3 | 22.4 ± 17.2 | | 8G, 5H | 76 | 55 | FAC |
| 0.2 ± 0.1 | 107.1 ± 26.1 | 31.3 ± 24.4 | | 7G, 3R | 107 | 74 | upl |
| 0.3 ± 0.1 | −132.1 ± 5.5 | 21.1 ± 10.8 | | 3G, 4H, 7R | 117 | 37 | FACU |
| 0.6 ± 0.3 | 23.8 ± 6.9 | 24.4 ± 15.9 | | 6G, 8H | 41 | 43 | FACU |
| 5.3 ± 1.8 | 101.8 ± 10.8 | 16.6 ± 7.6 | | 8G, 18H, 23R | 102 | 59 | FACU |
| 6.1 ± 2.2 | 27.8 ± 14.3 | −8.8 ± 15.6 | | 29G, 11H, 25R | — | — | OBL |

Table 2.   Continued.

| Species[1] | Mgt.[2] Practice | Model[3] Number |
|---|---|---|
| *Solidago canadensis* L. | GHR | 8033 |
| *Solidago gigantea* Ait. | GR | 8032 |
| *Sorghastrum nutans* (L.) Nash | GR√ | 8035 |
|  | H√ | 8033 |
| *Spartina pectinata* Bosc ex Link | G√ | 8036 |
|  | HR√ | 8064 |
| Sporobolus *compositus* (Poir.) Merr. var. *compositus* | GHR | 8077 |
| *Symphyotrichum ericoides* (L.) Nesom var. *ericoides* | GHR√ | 8036 |
| *Symphyotrichum lanceolatum* (Willd.) Nesom ssp. *lanceolatum* var. *lanceolatum* | GH√ | 8036 |
|  | R√ | 8033 |
| *Taraxacum officinale* G.H. Weber ex Wiggers | GHR | 8033 |
| *Trifolium pratense* L. | GHR | 8036 |
| *Verbena stricta* Vent. | GR | 8033 |
| *Vernonia fasciculata* Michx. | GHR | 8036 |
| *Viola nephrophylla* Greene | GHR√ | 8035 |

[1] Nomenclature follows the PLANTS database (USDA, NRCS 2001), based on the taxonomy by Great Plains Flora Association (1986), Rolfsmeier (1995), and Rolfsmeier and Wilson (1997).

[2] Management practices (G = Grazed, H = Hayed, R = Rested) with a check (√) indicate that there were sufficient data to test for differences among management practices. Species with a significant management effect ($p \leq 0.05$) have additional models to reflect their management responses. Species without a testable management effect, but were absent from a management practice are shown with the appropriate managements, but without a check.

[3] Models and their coefficients are described by AISN Software Inc. (2000) and are presented in the Appendix.

[4] For the purposes of coefficient selection, standing water was assigned negative values and ground water was assigned positive values. This facilitated fitting the majority of species, which were positively skewed, to models that are only positively skewed. Thus, for the majority of species (those without parentheses around their model number), a positive value for $b$ signifies that the peak frequency occurs when the water level is below the surface. In contrast, the models with parentheses were fit with positive standing water and negative ground-water values (as presented in the Figures and text) to facilitate fitting some negatively skewed species.

[5] Non-zero transects is the number of transects with a frequency greater than zero for each management practice.

[6] The center of the peak and the Full Width at Half-Maximum (FWHM) are functions of parameters $b$ and $c$, respectively. Transition models do not have a peak, so a center and the FWHM are not presented for these models.

[7] Wetland indicator categories were taken from the PLANTS database, Region 5 (USDA, NRCS 2001). Listed in order from occurring almost always in wetlands to occurring almost always in uplands, these categories are: obligate wetland (OBL), facultative wetland (FACW), facultative (FAC), facultative upland (FACU), and obligate upland (UPL). Species without a wetland designation and assumed to be upland are listed in lowercase letters (upl), and species with insufficient information are designated ''NI.'' A plus (+) indicates an affinity toward wetland, a minus (−) indicates an affinity toward upland, and an asterisk (*) indicates the designation was taken from a related subspecies or another region. Since wetland indicators do not consider management, the designation is listed only once at the first instance for each species.

[8] *Panicum virgatum* has a fifth parameter (*e*) equal to $-1.0 \pm 1.1$.

plant community species (described below) typically have about half the range of favorable water levels as the mesic prairie plant community species (median FWHM of 38 cm vs. 72 cm, Kruskal-Wallis ANOVA on Ranks: H = 15.5, df = 1, p < 0.0001).

Of 19 species that had sufficient data to test for land-management-practice effects, six species showed a significant response ($p \leq 0.05$) to management (Figures 8–10, Table 2) by a change in frequency or a shift in position along the water-level gradient. An additional nine species had insufficient data to test for management effects but were absent in one of the three land-management practices. Three more species had insufficient data to test for management effects but appeared to have a management preference by having at least four times the number of sites for the preferred management practice than for any other management practice (Table 2—Non-zero transects). Grazing decreased the frequency of *Spartina pectinata* and *An-*

*dropogon gerardii* (model coefficient *a*: F = 6.29, df = 130, p = 0.0025 and F = 11.6, df = 130, p < 0.0001; Figure 8a and 8f), while grazing and haying decreased the frequency of *Symphyotrichum lanceolatum* (model coefficient *a*: F = 8.83, df = 130, p = 0.0003; Figure 9e) and grazing and rest decreased the frequency of *Sorghastrum nutans* (model coefficient *a*: F = 3.51, df = 130, p = 0.0327; Figure 9o). In contrast, grazing and haying increased the frequency of *Carex crawei* (model coefficient *a*: F = 6.46, df = 130, p = 0.0021; Figure 9q). The only shift in position along the water-level gradient or change in ecological amplitude was by *Calamagrostis stricta* in the grazed and hayed sites (model coefficients *b* and *c*: F = 14.9, df = 130, p < 0.0001 and F = 5.94, df = 130, p < 0.0034; Figure 9c), where the peak shifted toward a higher $\bar{L}_{7H}$ and the ecological amplitude decreased. Management avoidance was observed for *Desmanthus illinoensis*, which was absent on grazed sites (Figure

Table 2. Continued extended.

| Model Coefficients (±95% CI)[3,4,8] | | | | Non-Zero Transects[5] | Center (cm)[6] | FWHM (cm)[6] | Ind.[7] Category |
|---|---|---|---|---|---|---|---|
| *a* | *b* | *c* | *d* | | | | |
| 1.6 ± 0.6 | 25.3 ± 8.6 | 20.1 ± 9.2 | | 20G, 3H, 12R | 25 | 49 | FACU |
| 1.4 ± 0.8 | 28.2 ± 10.0 | 0.5 ± 0.3 | | 6G, 6R | 28 | 32 | FACW |
| 3.8 ± 0.8 | 70.2 ± 9.4 | 61.8 ± 15.3 | | 24G, 29R | 70 | 85 | FACU |
| 7.1 ± 3.1 | 52.4 ± 17.7 | 31.8 ± 19.3 | | 35H | 52 | 78 | |
| 10.6 ± 3.6 | −38.3 ± 3.1 | 20.6 ± 6.5 | | 24G | −24 | 37 | FACW |
| 23.2 ± 6.5 | −15.7 ± 15.7 | 14.4 ± 6.7 | 0.2 ± 1.2 | 32H, 27R | −13 | 17 | |
| 2.7 ± 1.5 | 116.3 ± 27.8 | 21.6 ± 15.4 | | 8G, 5H, 23R | — | — | FACU |
| 2.3 ± 0.5 | 0.1 ± 15.3 | 131.5 ± 85.5 | | 28G, 26H, 38R | 91 | 232 | FACU |
| 2.3 ± 0.7 | −17.2 ± 4.4 | 24.1 ± 9.5 | | 20G, 18H | −1 | 43 | FACW |
| 8.1 ± 1.8 | 6.2 ± 4.2 | 15.6 ± 4.5 | | 25R | 6 | 38 | |
| 0.2 ± 0.1 | 47.2 ± 10.4 | 15.0 ± 10.9 | | 6G, 2H, 9R | 47 | 37 | FACU |
| 0.1 ± 0.1 | 7.9 ± 20.8 | 54.3 ± 52.0 | | 5G, 7H, 2R | 46 | 96 | FACU |
| 1.1 ± 0.4 | 117.2 ± 27.7 | 40.5 ± 26.7 | | 15G, 10R | 117 | 99 | upl |
| 0.3 ± 0.1 | −6.3 ± 4.4 | 12.4 ± 6.7 | | 7G, 3H, 5R | 2 | 22 | FAC |
| 0.6 ± 0.2 | 65.1 ± 16.4 | 69.8 ± 27.0 | | 19G, 21H, 13R | 65 | 96 | FACW |
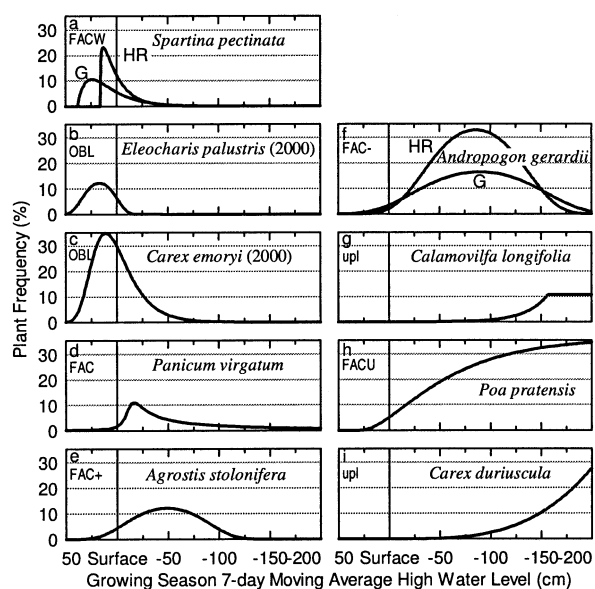


Figure 8. The most frequent species (>10%) response to the growing season 7-day moving average high water level ($\bar{L}_{7H}$). Species are arranged in columns by adaptation from the highest to the lowest $\bar{L}_{7H}$, and the effects of land management are indicated with capital letters (G = Grazed, H = Hayed, R = Rested). The wetland indicator category (e.g., OBL, FAC) is listed in the upper left-hand corner for each species adjacent to the Figure letter (see Table 2, Note 7 for indicator category descriptions). Species with a significant management effect ($p \leq 0.05$) include additional curves to reflect their management responses. Species without management labels were either unaffected by management or have insufficient data to test for management effects. See Table 2 for the management effects, equations, and coefficients used to fit these curves.

10n) for *Leersia oryzoides*, *Solidago gigantea*, *Verbena stricta*, and *Ratibida columnifera*, which were absent on hayed sites (Figures 9b, 9m, 9u, and 10aa) and for *Apocynum cannabinum*, *Rudbeckia hirta*, *Cirsium flodmanii*, and *Prunella vulgaris*, which were absent on rested sites (Figures 10c, 10o, 10t and 10x). Two species had a management preference for hayed sites: *Bromus inermis* and *Carex tetanica* (Figures 9h and 9k, Table 2), while one species preferred rested sites: *Dalea purpurea* (Figure 10y, Table 2).

Plant Community Classification

Four general plant communities were identified and arranged along the water-level gradient to show the range of growing season 7-day moving average high water levels ($\bar{L}_{7H}$) that can be expected for each community (Figure 11). The emergent community occurs where the $\bar{L}_{7H}$ exceeds 20 cm above the surface and was manually assigned because this portion of the gradient is characterized by three to five species that tend to dominate the community while excluding the other potential dominant species. Only one of these emergent species (*Polygonum amphibium*) had sufficient observations to fit a plant-response curve, but other species were also observed within this zone including: *Sparganium eurycarpum* Engelm. ex Gray, *Schoenoplectus fluviatilis* (Torr.) M.T. Strong, *Typha* spp., and *Schoenoplectus tabernaemontani* (K.C. Gmel.) Palla. The remaining three plant communities were identified with cluster analysis, and the characteristic species for each community were identified with an indicator species analysis. *Carex emoryi*, *Carex pellita*, and *Symphyotrichum lanceolatum* characterize the sedge meadow community, which occurs over a 50-cm range of
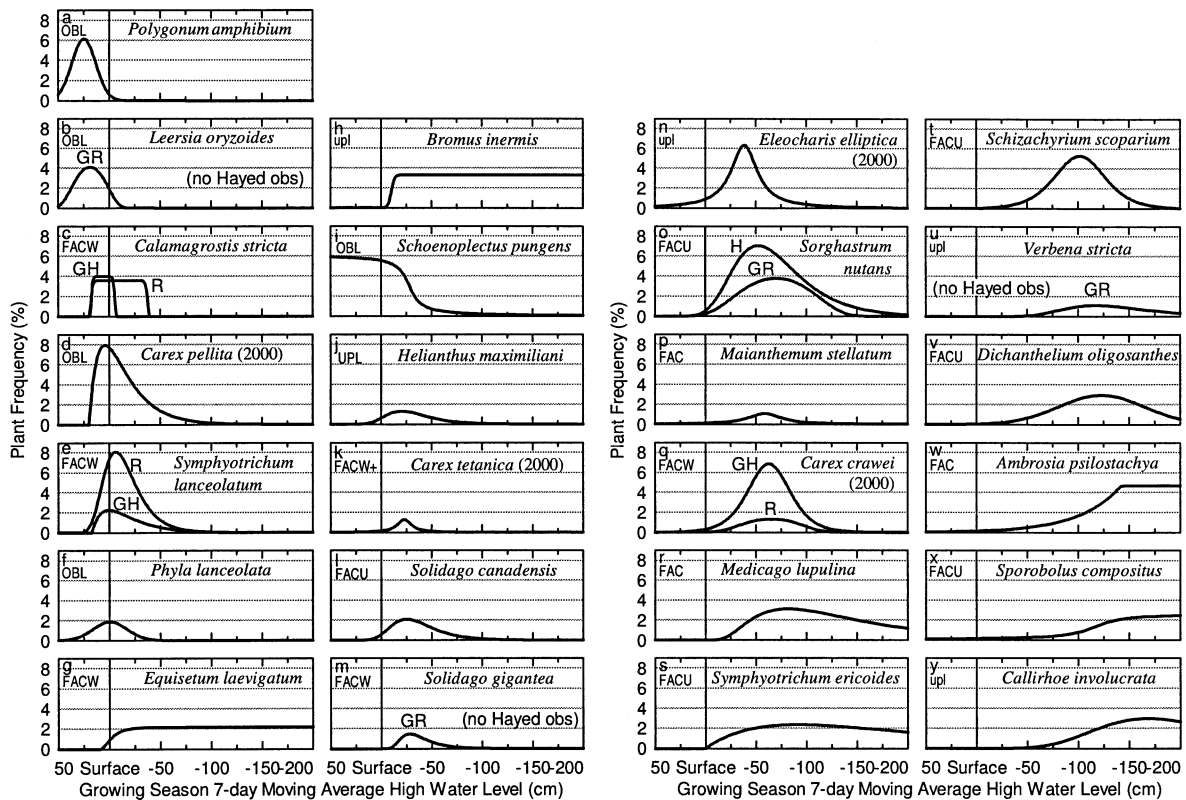
Figure 9.  Common species (1–10%) response to the growing season 7-day moving average high water level ($\bar{L}_{7H}$). Species are arranged in columns by adaptation from the highest to the lowest $\bar{L}_{7H}$, and the effects of land management are indicated with capital letters (G = Grazed, H = Hayed, R = Rested). The wetland indicator category (e.g., OBL, FAC) is listed in the upper left-hand corner for each species adjacent to the Figure letter (see Table 2, Note 7 for indicator category descriptions). Species with a significant management effect (p ≤ 0.05) include additional curves to reflect their management responses, while species absent from a management practice are labeled but have only one curve. Species without management labels were either unaffected by management or have insufficient data to test for management effects. See Table 2 for the management effects, equations, and coefficients used to fit these curves.

$\bar{L}_{7H}$ water levels (20 cm above to 30 cm below the surface). Other notable sedge-meadow species include *Apocynum cannabinum*, *Elymus trachycaulus*, and *Hordeum jubatum*. The plant community with the broadest range of $\bar{L}_{7H}$ water levels (105 cm) occurs in the mesic prairie, which is characterized by *Andropogon gerardii*, *Schizachyrium scoparium*, and *Sorghastrum nutans*. Other notable mesic prairie species include *Medicago lupulina*, *Agrostis stolonifera*, and *Carex crawei*. The dry ridge community occurs where the $\bar{L}_{7H}$ is deeper than 135 cm below the surface and tends to include upland species that are unaffected by deeper water levels. Characteristic dry-ridge species include *Carex duriuscula*, *Ambrosia psilostachya*, and *Callirhoe involucrata*, as well as these other notable species: *Poa pratensis*, *Dichanthelium oligosanthes*, and *Calamovilfa longifolia*.

The rankings of key species along the $\bar{L}_{7H}$ gradient are similar for both non-linear regression models (Figure 11) and for canonical correspondence analysis (Figure 1). Only the ranking of two very closely ranked species was interchanged (*Carex pellita* and *Symphyotrichum lanceolatum*). The non-linear models, however, show the distribution and frequency of each species along a single gradient (e.g., $\bar{L}_{7H}$), while the canonical correspondence analysis shows only the ranking of species but in a multi-gradient space.

## DISCUSSION

For this study, we examined only one gradient, the water level from shallow ground water to standing water, but obviously, these species may also respond to a host of other gradients and factors, including physical (e.g., soil properties, water-flow velocity, aspect), biological (e.g., life cycle, regional variation, competition), and management (e.g., grazing, fire, introduced species). Indeed, the effect of many of these additional gradients and factors has been observed in Platte River riparian grasslands (personal observation, Simpson 2001, Figure 1), as well as at numerous other mesic and wetland locations (e.g., Wells 1928, Walter 1985,

**Figure 10.** The least frequent species (<1%) response to the growing season 7-day moving average high water level ($\bar{L}_{7H}$). Species are arranged in columns by adaptation from the highest to the lowest $\bar{L}_{7H}$, and the effects of land management are indicated with capital letters (G = Grazed, H = Hayed, R = Rested). The wetland indicator category (e.g., OBL, FAC) is listed in the upper left-hand corner for each species adjacent to the Figure letter (see Table 2, Note 7 for indicator category descriptions). No species in this figure have a significant management effect (p ≤ 0.05), but species absent from a management practice are labeled and have only one curve. Species without management labels were either unaffected by management or have insufficient data to test for management effects. See Table 2 for the management effects, equations, and coefficients used to fit these curves.

Scott et al. 1989, Rood and Mahoney 1990, Weiher and Keddy 1995, Stromberg et al. 1996, Ukpong 1998). These additional gradients can be modeled simultaneously with direct gradient ordination (e.g., ter Braak 1986, Palmer 1993) to help determine the dominant gradients, but the axes produced usually represent more than one gradient and the units are difficult to relate to the original gradients (e.g., Figure 1). From a management or regulatory standpoint, these composite units make it difficult to quantify the amount of change required to produce a desirable or undesirable effect. In contrast, fitting a non-linear model to the data maintains the original axes and yields a plant response curve with coefficients that have biological meaning and variation (e.g., amplitude of the peak plant frequency, water level at the peak, and an indication of the range of favorable water levels).

To a limited extent, additional gradients can also be examined with two-dimensional (i.e., *x* and *y*) non-linear models by stratifying the data and fitting additional curves, similar to the technique used here for testing management effects and by other investigators for additional gradients (e.g., Whittaker 1956, 1960, 1967). For most riparian and wetland ecosystems, however, water levels are considered to be the driving gradient, as well as the gradient most easily and commonly managed (Walter 1985, Hall and Harcombe 1998). In addition, many soil-property gradients are directly modified by water levels, suggesting that their influence may be reasonably well-represented by the water level alone (Walker and Wehrhahn 1971, Grootjans and ten Klooster 1980, Hultgren 1988, Chambers et al. 1999, Mitsch and Gosselink 2000). If a second highly influential gradient is identified, it may be

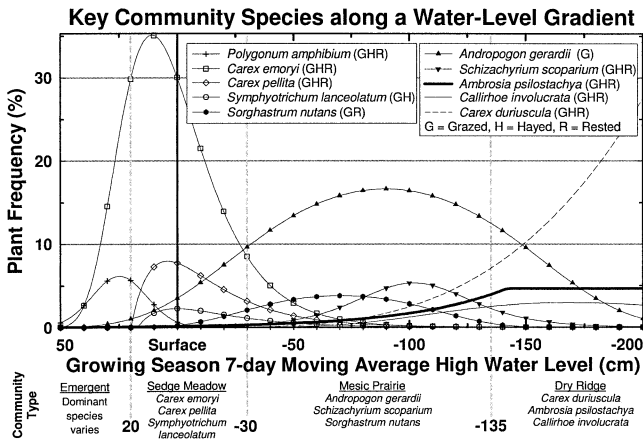## Key Community Species along a Water-Level Gradient



Figure 11. Four general plant communities arranged along the water-level gradient to show the range of growing season 7-day moving average high water levels ($\bar{L}_{7H}$) that can be expected for each species and community. Vertical dashed lines indicate the approximate plant community boundaries, and the key species for each community are listed below the graph.

possible to use a three-dimensional (i.e., *x, y,* and *z*) non-linear model-fitting program. Ordination could still be used to identify the two most influential gradients, followed by modeling these gradients with a three-dimensional curve fitting routine to quantify the axes. When the number of species is large, however, separate analyses for each species can be time-consuming, and the results still do not provide an integrated overview of how plant community composition varies with the environment (ter Braak 1986). So, when the number of environmental gradients exceeds two or three, and a common community response is desired, ordination is still the best method (ter Braak 1986).

Model shape reflects how a species responds to its physical and biological environment along a gradient, with a symmetrical, bell-shaped curve representing a normal distribution and an asymmetrical curve suggesting that an external factor or factors may be skewing the distribution. The selection of model shape is discussed presently, followed by examples of external shaping factors later in the discussion. Although we tested two frequently used models for describing plant response (the symmetrical Gaussian (Gause 1932) and the ''versatile'' beta (Austin 1976, Minchin 1987)), only seven Gaussian or modified Gaussian, and no beta models, were the best fit for the 69 plant frequencies in Table 2 (see also the Appendix). The Gaussian models met the corrected Akaike information criterion (AIC$_c$) for 32 potential model selections, while the beta model did not meet the criterion for any model selection. So, technically, the Gaussian models could be used with equal confidence as the top choice,

but the beta model might best be used for solely theoretical modeling. A better choice for empirical plant-frequency responses, however, would be to use the Complementary Error Function Peak (Model 8035) for symmetrical responses or the Extreme Value (Model 8033 or (8033)) or Pulse Peak (Model 8036 or (8036)) models for asymmetrical responses. The Complementary Error Function Peak was the best model for 16 of 31 symmetrical plant frequency fits in Table 2, with an additional 22 that met the AIC$_c$ for model consideration for all response types in Table 2. The Complementary Error Function Peak model is derived by integrating the ''bell-shaped'' Gaussian distribution, and it produces somewhat smaller peaks, broader FWHMs and shorter tails, which appear to fit symmetrical plant distributions better than the Gaussian model. Of the 30 asymmetrical plant frequencies in Table 2, 12 were best fit with the Extreme Value, and 11 were fit with the Pulse Peak. In addition, the Extreme Value model could potentially be used with equal confidence to fit an additional 26 of the frequencies in Table 2, while the Pulse Peak could be used for an additional 15 fits based on their AIC$_c$ values. The Pulse Peak fits species with an abrupt response over a very small gradient change (e.g., *Carex pellita* Figure 9d), while the Extreme Value model fits species with a more gradual asymmetrical response (e.g, *Muhlenbergia asperifolia* Figure 10l). Although the beta model can duplicate the shape of these symmetrical and asymmetrical responses very closely once the shape is known, the model was not used because it could not be fit to the data, or it had a lower AIC$_c$ rank, possibly because the model uses four parameters instead of three.

Besides the peak models, eight plant frequencies in Table 2 were fit with transition (sigmoid shaped) models. Previously (e.g., Whittaker 1956), and for some species in this study (e.g., *Poa pratensis* and *Carex duriuscula*, Figures 8h and 8i), plant responses that went beyond the sampled range for the gradient were modeled with peak models, but with the peaks occurring beyond the sampled range. In some cases, however, a transition model might be more appropriate, especially for species that might remain unaffected by the $\bar{L}_{7H}$ until the water level becomes too high or too low and begins to cause the plant some physiological stress. For example, *Callirhoe involucrata* (Figure 9y) is an upland species that remains unaffected by the water table until the $\bar{L}_{7H}$ rises to about 150 cm below the land surface and begins to affect its frequency adversely. When it becomes necessary to fit a model with the peak beyond the sampled range for the gradient, great care must be taken in the interpretation. For example, the rising limb of a peak model provides the best fit for *Carex duriuscula* within the range sampled

(Figure 8i), but the predicted peak frequency is $10^{18} \pm 10^{21}$ percent (Table 2). Perhaps, a transition model would be more appropriate for this species, but the gradient was not sampled far enough into the upland to provide a good transitional fit.

From among 10 water-level summary statistics evaluated for a subset of 22 species (Table 1), we found the growing season 10% cumulative frequency ($L_{10\%}$), followed closely by the growing season 7-day moving average ($\bar{L}_{7H}$) and the other two high water-level statistics ($\bar{L}_{10H}$, $\bar{L}_{14H}$), to be the most useful for linking water levels to plant frequency. The standard normal deviate (Hunt et al. 1999) should also fall within this category of useful statistics for sites where the water level enters the root zone (e.g., within 30 cm of the land surface), since it is another high water-level statistic that describes the root zone residence time by using a cumulative frequency for moving average water levels within the root zone. The superiority of the high water-level statistics suggests that for Platte River riparian grasslands, high water levels are more influential than mean, median, or low water levels. This conclusion agrees with a large body of literature for wetlands, which shows that plants respond to periods of physiological stress caused by saturated or flooded soils (e.g., Lambers et al. 1998, Cronk and Fennessy 2001). Wetland plants are able to grow in anaerobic saturated and flooded soils because they have special morphological and physiological adaptations to mitigate this stressful period, while upland species lack these adaptations (Lambers et al. 1998, Cronk and Fennessy 2001). Thus, upland species thrive across the landscape responding to other gradients until their topographic position results in saturated and flooded soils for a sufficient duration that they are either killed or unable to compete with wetland species. Although Platte River riparian grasslands do not extend very far up the water-level gradient into the upland, Figure 11 clearly shows that the frequency of upland dry ridge species quickly decreases as the $\bar{L}_{7H}$ approaches the land surface. *Calamovilfa longifolia*, for example (Figure 8g), has roots to about $-150$ cm (Weaver 1968), which suggests that this species would be unaffected by the $\bar{L}_{7H}$ until its topographic position allowed the $\bar{L}_{7H}$ to approach its roots (about $-155$ cm in Figure 8g) and expose increasingly more of its roots to anaerobic stress.

Within the mesic prairie and sedge meadow communities, plant species express their individual optima as the $\bar{L}_{7H}$ gradient progresses from soil conditions that are too dry to too wet for each species' individual adaptations and competitive advantages (i.e., niche). Many of these species have truncated distributions on the wet end of this gradient, which is probably a function of stress induced by anaerobic soil conditions

(e.g., *Panicum virgatum* and *Medicago lupulina*, Figures 8d and 9r). On the dry end, however, water availability may not be as much of a limitation as might be expected. Weaver's classic *in situ* work on rooting depth and patterns (e.g., Weaver 1968) suggests that at least some Platte River sedge-meadow and mesic-prairie species should have little difficulty tapping the water table with their roots throughout the growing season. Platte River sedge-meadow water levels seldom drop below $-100$ cm (e.g., Figure 6), and Weaver (1968) observed roots to at least $-150$ cm for the following species: *Spartina pectinata*, *Panicum virgatum*, *Sorghastrum nutans*, *Andropogon gerardii*, and *Schizachyrium scoparium*. This suggests that some mechanism besides lack of water, such as seedling establishment or competition with other species, might be limiting or helping to limit the distribution of these species up slope from their optima. For example, Rahman (1976) and Rahman and Rutter (1980) concluded that *Deschampsia cespitosa* (L.) Beauv. is restricted to wet soils because this species is unable to compete with other species in drier soils.

Similar to the upland dry ridges, which do not extend very far into the upland, Platte River riparian grasslands do not extend very far into the emergent community, so the $\bar{L}_{7H}$ gradient does not show water levels too high for the single emergent species evaluated (*Polygonum amphibium*, Figures 9a and 11). There is a point on the $\bar{L}_{7H}$ gradient, however, where the water level becomes too low for this species, and its frequency decreases as the level of standing water for the $\bar{L}_{7H}$ diminishes. This lower $\bar{L}_{7H}$ limit may be due at least in part to competition with other species (e.g., Rahman 1976, Rahman and Rutter 1980) and not simply a lack of available water, since this species can have roots to $-240$ cm (Weaver 1958).

From the preceding discussion on plant response and root depth, it is apparent that water levels much lower than those within the "major portion of the root zone (usually within 30 cm of the surface)" (Environmental Laboratory 1987) have an influence on Platte River riparian grasslands. Although the major portion of the root zone may extend to whatever depth that more than half the roots occur (Environmental Laboratory 1987), limited root biomass data collected to 300 cm below the land surface for Platte River riparian grasslands suggest that the 1987 criterion for the 30 cm root zone would be met, since more than 60% of the belowground biomass for Platte River riparian grasslands occurs within the top 15 cm of the soil profile (Henszey, unpublished data). Our plant frequency response curves that use the $\bar{L}_{7H}$ to describe the water level (Figures 8–10) do not take into account the root zone, but it is apparent from Figures 8–10 and Table 2 that most Platte River wetland species (OBL and

FACW) have peak frequencies with an $\bar{L}_{7H}$ above 30 cm below the land surface and that most Platte River upland species (FACU and UPL) have peak frequencies with an $\bar{L}_{7H}$ below 30 cm below the land surface. So, our data are consistent with the 30 cm root zone criterion for wetlands (Environmental Laboratory 1987), but water levels below 30 cm should not be ignored, since they are still very important for the sub-irrigated Platte River mesic prairie (e.g., Figure 11).

Several investigators caution that plant species distributions observed in nature represent the species' *ecological optimum* and not their *physiological optimum* (Ellenberg 1953 in Mueller-Dombois and Ellenberg 1974, Whittaker 1956, Austin and Austin 1980, Walter 1985). Therefore, the ecological optima presented here may not match precisely the ecological optima observed from other locations or the full range of their physiological response. The physiological optimum occurs without competition from other plant species and always has a distribution along the gradient at least as broad as the ecological optimum. Competition may force the distribution of a species toward one side or the other of its physiological optimum, limit the tails of its distribution, or may even divide its distribution so that it has two ecological optima. While we did not test for differences between the physiological and ecological optimum, examples of these responses are given by Mueller-Dombois and Ellenberg (1974), Rahman (1976), Austin and Austin (1980), Rahman and Rutter (1980), and Walter (1985). We did observe, however, distribution shifts and peak frequency shifts caused by management (e.g., rest, grazed, hayed). For example, grazing diminished the peak frequency of *Spartina pectinata* (Figure 8a), while grazing and haying shifted *Calamagrostis stricta* toward wetter sites (Figure 9c).

As shown in Figure 11, plant community boundaries were assigned to approximate locations along the $\bar{L}_{7H}$ gradient, but in reality, the individual species that compose these communities occur over a continuum, or coenocline (Whittaker 1960, Gauch and Whittaker 1972), that may span two or more communities. From a management standpoint, we tend to think of communities, but management actually influences individual species as they express their unique combination of physiology, life history, and response to random events (viz., Gleason 1926, 1939). These species occur across the riparian landscape where the topographic elevation provides suitable water levels. If a particular site has a wide range of topographic diversity, then permanently raising or lowering the $\bar{L}_{7H}$ should cause the positioning of species to move up or down slope, and at most, the aerial extent of their distribution may increase or decrease in proportion to the availability of suitable topographic elevations (e.g., Austin and

Smith 1989). If, on the other hand, the topographic diversity is limited, it is possible that several species, if not entire communities, may be eliminated from that site (Whittaker 1956). For example, within Platte River riparian grasslands, there are very few deep sloughs that can support emergent communities, and a permanent drop of 20 cm for the $\bar{L}_{7H}$ might eliminate this community entirely from the landscape. Likewise, a 20-cm change would have little effect on species with a broad water-level distribution, such as *Andropogon gerardii* (FWHM = 104–132 cm, Figure 8f), but that same change might completely displace a species with a narrow distribution, such as *Carex praegracilis* (FWHM = 13 cm, Figure 10h).

How long it might take a permanent shift in the $\bar{L}_{7H}$ to affect plant species and community distributions along the Platte River is unknown. Currier (1989) documented both positive and negative responses to exceptionally high water levels within a single year for hydrophyte and upland canopy cover respectively along the Platte River. He still felt, however, that migration up- or down-slope is a much slower process (personal communication). Squires and van der Valk (1992) suggested that a minimum of three years is necessary to document a shift in wetland vegetation. Well-established perennial species, such as the vast majority of riparian grassland species along the Platte River, might persist for many years, if not as reproducing individuals, at least in some reduced vegetative state. For example, permanently elevated standing water levels have been shown to ''eliminate'' certain species, only to have them reappear decades later from vegetative propagules lying dormant during unfavorable conditions (Squires and van der Valk 1992). Similarly, Weaver (1968) found that several grass species, which also occur in Platte River riparian-grassland sedge meadow and mesic prairie communities, reemerged from dormant rhizomes following seven years of severe drought. In any event, perennial species with their emphasis on vegetative reproduction will probably be much less able to move across the slope in response to a water-level shift than annual species with their seed dispersal strategy for reproduction. Since nearly all the Platte River riparian grassland species are perennial, we expect any shift across the slope in response to a permanent water-level change to be slow.

Finally, linking the plant response to the growing season 7-day moving average high water level ($\bar{L}_{7H}$) is just the first step in a two-step process to manage the $\bar{L}_{7H}$ for Platte River riparian grasslands. Platte River riparian-grassland surface- and ground-water levels are affected by a complex interaction of river stage, precipitation, and evapotranspiration (Wesche et al. 1994). Precipitation and evapotranspiration are difficult to manage, but rivers with storage reservoirs like

the Platte can potentially be managed for riparian-grassland water levels in conjunction with other river-management actions. Others have used soil type, streamflow volume, relative ground surface elevation, and distance from channel edge to link river stage to riparian water levels and plant response indirectly (e.g., Scott et al. 1989, Stromberg 1993, Stromberg et al. 1996), but a direct link for plants responding to an aquifer influenced by the river requires a ground-water model linking riparian-grassland water levels to river stage. These models are widely available (Anderson 1995, van der Heijde 1996, Barlow and Moench 1998), but most require considerable information and skill to construct and calibrate. Once this second step is completed, however, it should be possible to predict if plants will respond to river management by knowing the $\bar{L}_{7H}$ plant response and how the $\bar{L}_{7H}$ at the location of interest is affected by river management.

## ACKNOWLEDGMENTS

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## APPENDIX

### Non-Linear Models and Their Coefficients
(After AISN Software Inc. 2000)

For the following models, $f$ = plant frequency, $\bar{L}_{7H}$ = the growing season 7-day moving average high water level, and FWHM = full width at half maximum.

Symmetric Peak Models:

Model 8030: Gaussian (5 species fit)

$$f = a \exp\left[-\frac{1}{2}\left(\frac{\bar{L}_{7H} - b}{c}\right)^2\right]$$

Amplitude: $a$
Center: $b$
Area: $\sqrt{2\pi}ac$
FWHM: $2.354820044c$
Constraints: $c > 0$

Model 8031: Lorentzian (5 species fit)

$$f = \frac{a}{1 + \left(\frac{\bar{L}_{7H} - b}{c}\right)^2}$$

Amplitude: $a$
Center: $b$
Area: $\pi ac$
FWHM: $2c$
Constraints: $c > 0$

Model 8034: Logistic Peak (3 species fit)

$$f = 4a\frac{\exp\left[-\left(\frac{\bar{L}_{7H} - b}{c}\right)\right]}{\left\{1 + \exp\left[-\left(\frac{\bar{L}_{7H} - b}{c}\right)\right]\right\}^2}$$

Amplitude: $a$

Center: $b$
Area: $4ac$
FWHM: $3.525494348c$
Constraints: $c > 0$

Model 8035: Complementary Error Function Peak (16 species fit)

$$f = a \operatorname{erfc}\left[\left(\frac{\bar{L}_{7H} - b}{c}\right)^2\right]$$

Amplitude: $a$
Center: $b$
Area: Analytic Solution Unknown
FWHM: $1.381211406c$
Constraints: $c > 0$

Model 8038: Modified Gaussian (2 species fit)

$$f = a \exp\left[-\frac{1}{2}\left(\frac{|\bar{L}_{7H} - b|}{c}\right)^d\right]$$

Amplitude: $a$
Center: $b$
Area: Analytic Solution Unknown
FWHM: $2c(2 \ln 2)^{1/d}$
Constraints: $c > 0$, $d \geq 1$

Asymmetric Peak Models:

Model 8032: Log Normal (4 species fit)

$$f = a \exp\left\{-\frac{1}{2}\left[\frac{\ln(\bar{L}_{7H}/b)}{c}\right]^2\right\}$$

Amplitude: $a$
$\bar{L}_{7H}$ at Maximum: $b$
Area: $abc\sqrt{2\pi} \exp(c^2)$
FWHM: $b \exp(c\sqrt{2 \ln 2}) - b \exp(-c\sqrt{2 \ln 2})$
Constraints: $b \neq 0$, $c > 0$, $\bar{L}_{7H} \neq 0$, $\bar{L}_{7H}/b > 0$

Model 8033: Extreme Value (10 species fit)

$$f = a \exp\left[-\exp\left(-\frac{\bar{L}_{7H} - b}{c}\right) - \frac{\bar{L}_{7H} - b}{c} + 1\right]$$

Amplitude: $a$
$\bar{L}_{7H}$ at Maximum: $b$
Area: $2.718281828ac$
FWHM: $2.446386037c$
Constraints: $c > 0$

Model (8033): $-\bar{L}_{7H}$ Extreme Value (2 species fit)

$$f = a \exp\left[-\exp\left(-\frac{b - \bar{L}_{7H}}{c}\right) - \frac{b - \bar{L}_{7H}}{c} + 1\right]$$

Amplitude: $a$
$\bar{L}_{7H}$ at Maximum: $-b$
Area: $2.718281828ac$
FWHM: $2.446386037c$
Constraints: $c > 0$

Model 8036: Pulse Peak (10 species fit)

$$f = 4a \exp\left(-\frac{\bar{L}_{7H} - b}{c}\right)\left[1 - \exp\left(-\frac{\bar{L}_{7H} - b}{c}\right)\right]$$

Amplitude: $a$
Pulse Initiation: $b$
$\bar{L}_{7H}$ at Maximum: $b + c \ln 2$
Area: $2ac$
FWHM: $1.762747173c$
Constraints: $\bar{L}_{7H} \geq b, \ c > 0$

Model (8036): $-\bar{L}_{7H}$ Pulse Peak (1 species fit)

$$f = 4a \exp\left(-\frac{b - \bar{L}_{7H}}{c}\right)\left[1 - \exp\left(-\frac{b - \bar{L}_{7H}}{c}\right)\right]$$

Amplitude: $a$
Pulse Initiation: $-b$
$\bar{L}_{7H}$ at Maximum: $-b + c \ln 2$
Area: $2ac$
FWHM: $1.762747173c$
Constraints: $b \geq \bar{L}_{7H}, \ c > 0$

Model 8052: Weibull (1 species fit)

$$f = a\left(\frac{d-1}{d}\right)^{(1-d)/d}\left[\frac{\bar{L}_{7H} - b}{c} + \left(\frac{d-1}{d}\right)^{1/d}\right]^{d-1}$$
$$\times \exp\left\{-\left[\frac{\bar{L}_{7H} - b}{c} + \left(\frac{d-1}{d}\right)^{1/d}\right]^{d} + \frac{d-1}{d}\right\}$$

Amplitude: $a$
$\bar{L}_{7H}$ at Maximum: $b$

Area: $\dfrac{ac^d}{d}\left[c\left(\dfrac{d-1}{d}\right)^{1/d}\right]^{1-d}\exp\left(\dfrac{d-1}{d}\right)$

FWHM: Analytic Solution Unknown
Constraints: $\bar{L}_{7H} > b - c[(d-1)/d]^{1/d}, \ c \geq 0, \ d > 1$

Model 8064: Pulse Peak Modified with Power Term (1 species fit)

$$f = \frac{a\left[1 - \exp\left(-\dfrac{\bar{L}_{7H} - b}{c}\right)\right]^{d}\exp\left(-\dfrac{\bar{L}_{7H} - b}{c}\right)}{d^d(d+1)^{-d-1}}$$

Amplitude: $a$
Pulse Initiation: $b$
$\bar{L}_{7H}$ at Maximum: $b + c \ln(1 + d)$
Area: $ac/[(d+1)d^d(d+1)^{-d-1}]$
FWHM: Analytic Solution Unknown
Constraints: $\bar{L}_{7H} \geq b, \ c > 0, \ d > 0$

Model 8186: Pearson IV (1 species fit)

$$f = a\left(\left\{1 + \frac{[\bar{L}_{7H} - (ce/2d) - b]^2}{c^2}\right\}^{-d}\right.$$
$$\times \exp\left[-e\left\{\tan^{-1}\left[\frac{\bar{L}_{7H} - (ce/2d) - b}{c}\right]\right.\right.$$
$$\left.\left.\left.+ \tan^{-1}\left(\frac{e}{2d}\right)\right\}\right]\right)\Big/\left(1 + \frac{e^2}{4d^2}\right)^{-d}$$

Amplitude: $a$
$\bar{L}_{7H}$ at Maximum: $b$
Area: Analytic Solution Unknown
FWHM: Analytic Solution Unknown
Constraints: $c > 0, \ d > 0$

Symmetric Transition Models:
Model 8074: Sigmoid (1 species fit)

$$f = \frac{a}{1 + \exp\left(-\dfrac{\bar{L}_{7H} - b}{c}\right)}$$

Transition Height: $a$
Transition Center: $b$
Transition Width: $2.197224578c$
Constraints: $c \neq 0$

Model 8077: Lorentzian Cumulative (2 species fit)

$$f = \frac{a}{\pi}\left[\arctan\left(\frac{\bar{L}_{7H} - b}{c}\right) + \frac{\pi}{2}\right]$$

Transition Height: $a$
Transition Center: $b$
Transition Width: $2c$
Constraints: $c \neq 0$

Asymmetric Transition Models:
Model 8083: Pulse Cumulative (3 species fit)

$$f = a\left[1 - \exp\left\{-\frac{\bar{L}_{7H} - c\ln[1 - (\sqrt{2}/2) - b]}{c}\right\}\right]^2$$

Transition Height: $a$
Transition Center: $b$
Transition Width: $1.3169578969c$

Constraints: $\quad \bar{L}_{7H} \geq b + c\ln\left(1 - \dfrac{\sqrt{2}}{2}\right) \quad$ if $c > 0$

$$\bar{L}_{7H} \leq b + c\ln\left(1 - \frac{\sqrt{2}}{2}\right) \quad \text{if } c < 0$$

$$c \neq 0$$

Model 8089: Asymmetric Sigmoid (2 species fit)

$$f = \frac{a}{\left\{1 + \exp\left[-\dfrac{\bar{L}_{7H} - c \ln(2^{1/d} - 1) - b}{c}\right]\right\}^d}$$

Transition Height: $a$

Transition Center: $b$

Transition Width: $c \ln(4^{-1/d} - 1) - c \ln(4^{1/d}3^{-1/d} - 1)$

Constraints: $c \neq 0$, $d \neq 0$