

**RIPARIAN VEGETATION OF THE BLACK CANYON OF THE
GUNNISON RIVER, COLORADO: COMPOSITION AND RESPONSE
TO SELECTED HYDROLOGIC REGIMES BASED ON A DIRECT
GRADIENT ASSESSMENT MODEL**

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Background

The Black Canyon of the Gunnison National Monument is located along the Gunnison River on the western slope of the Rocky Mountains in Montrose County, Colorado. The canyon is narrow because it is cut into resistant pre-Cambrian gneiss: it has a maximum depth of 900 m and a minimum width of 300 m from rim to rim (Hansen 1987). The watershed is 10,000 square km.

A 450-m study reach was selected by the National Park Service (Fig. 1). The width of the canyon bottom within the study reach varies from 40 to 90 m, the gradient is 0.0128, and the elevation is approximately 1707 m. Average annual precipitation is 370 mm (Colorado Climate Center 1984). Because of the steep canyon walls the study reach is inaccessible to livestock and has probably never been grazed.

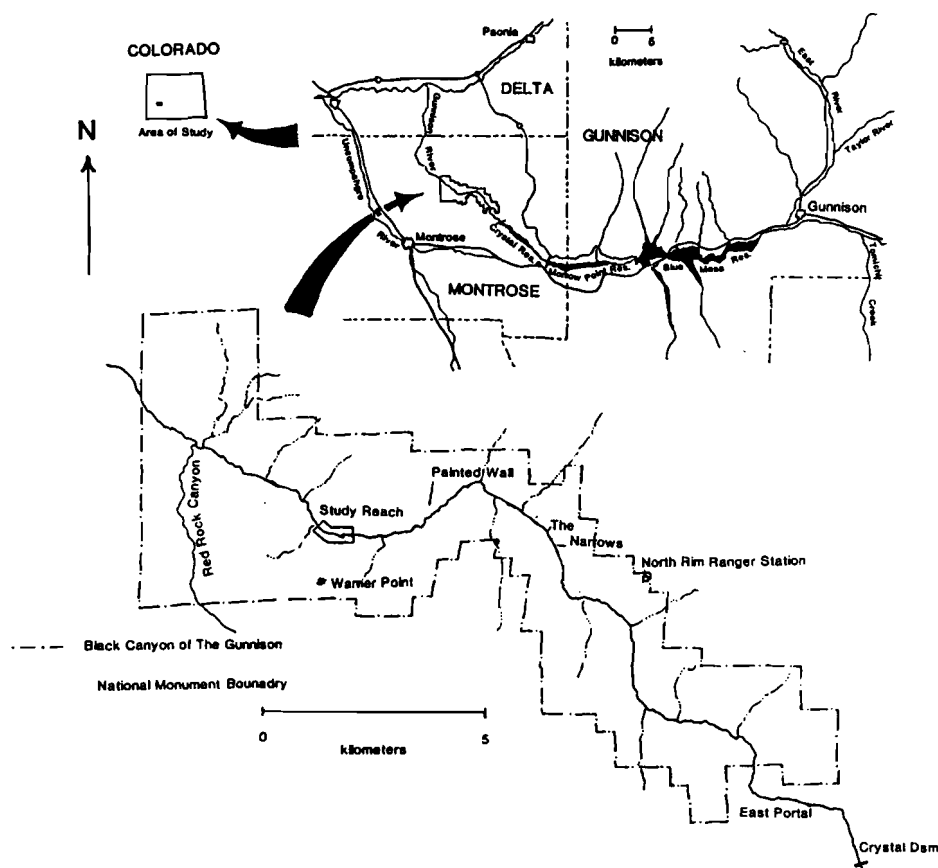


Fig. 1. Location of study reach.

The U.S. Geological Survey (USGS) has measured discharge of the Gunnison River below Gunnison Tunnel, near the upstream boundary of the monument, since 1903 (USGS gage 09128000). However, some of the early records consist only of monthly discharge estimates (Ugland et al. 1989). Tributary input between the USGS gage and the study reach is minimal. Withdrawals via the Gunnison Tunnel at East Portal just upstream of the gage began in 1912 (Fig. 2).

Four dams modify flow in the Gunnison River upstream from the Black Canyon: Taylor Park Dam, completed in 1936; Blue Mesa Dam, 1966; Morrow Point Dam, 1970; and Crystal Dam, 1976 (U.S. Department of the Interior 1990). Blue Mesa, Morrow Point, and Crystal Dam together comprise the Aspinall Unit.

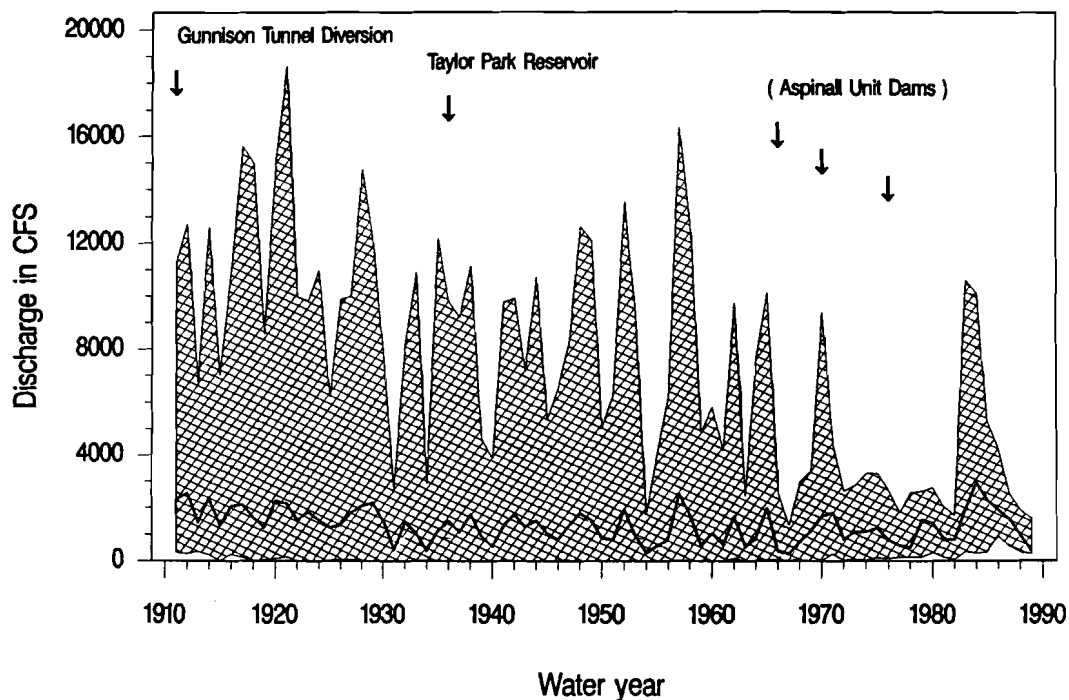


Fig. 2. Annual maximum, average, and minimum mean daily discharge for the Gunnison River below Gunnison Tunnel, water years 1911-1989.

Before construction of the dams, riparian vegetation was sparse (Figs. 3-6) presumably due to a combination of scouring floods in the spring and low flows in late summer and fall. Flow regulation has decreased the magnitude and frequency of spring floods. Since completion of Crystal Dam, minimum flows have been gradually increased to the current 300 cfs in order to protect trout (U.S. Department of the Interior 1990). Discharge was near 300 cfs from April 1988 up through the vegetation sampling in June and July of 1990 because of drought (Fig. 7).

The Black Canyon of the Gunnison National Monument was established in 1933 as a unit of the National Park system. In 1934, the first survey crew traveled down the canyon. Fifty photographs from that expedition (Walker 1967) have been reproduced in Warner and Walker (1972). The geology of the canyon has been described by Hansen (1987). U.S. Department of the Interior (1990) summarized the history of water development in the Gunnison River basin. Stanford and Ward (1983, 1985) discussed the limnology and physicochemistry of the river. There has been little detailed study of the vegetation of the canyon bottom. Rominger (1963) identified five grasses that



Fig. 3. Warner crossing sandbar, first day of trip through the Black Canyon, 1934. Reproduced from negatives of Walker (1967).

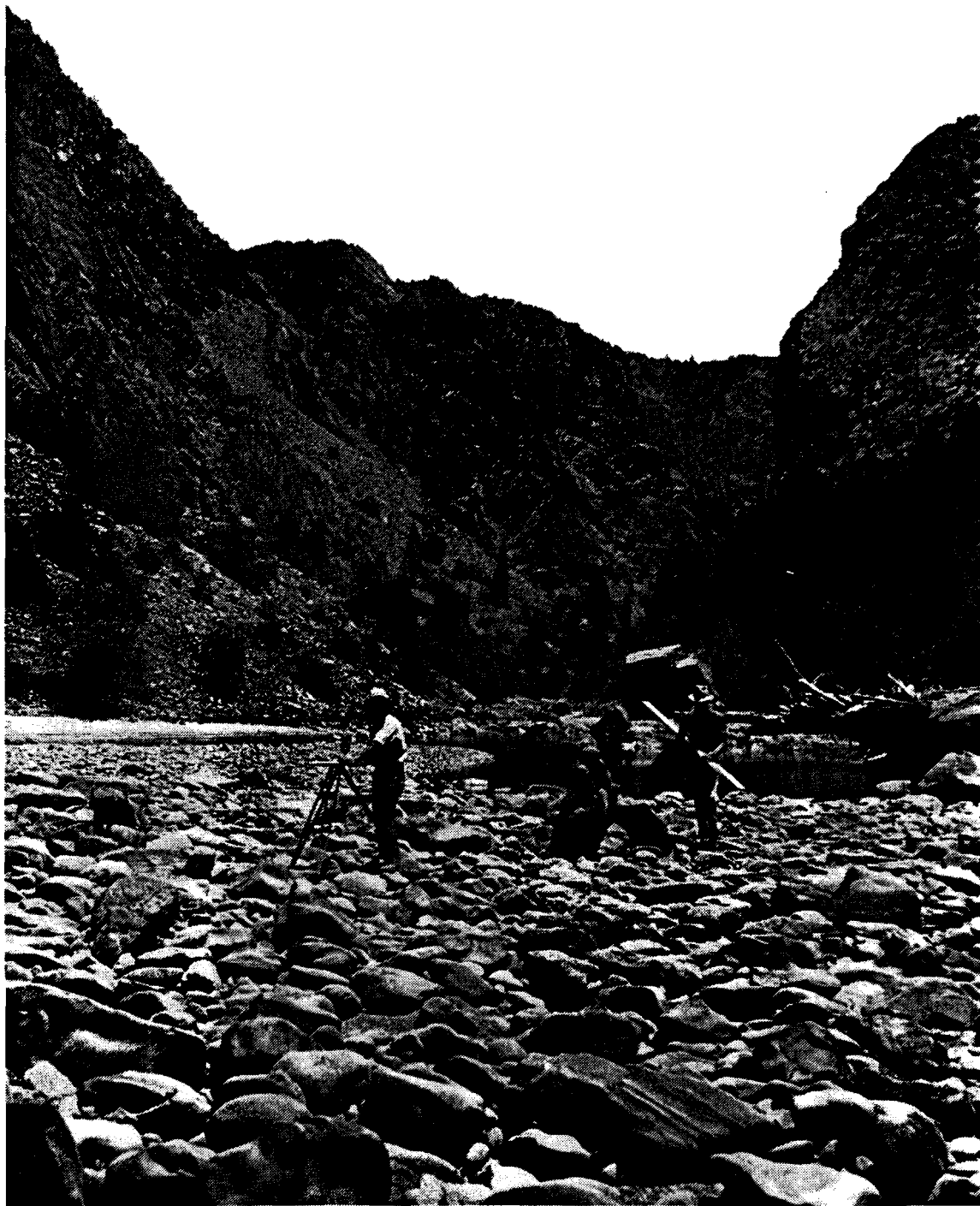


Fig. 4. Upper canyon, first day of trip through the Black Canyon, 1934.
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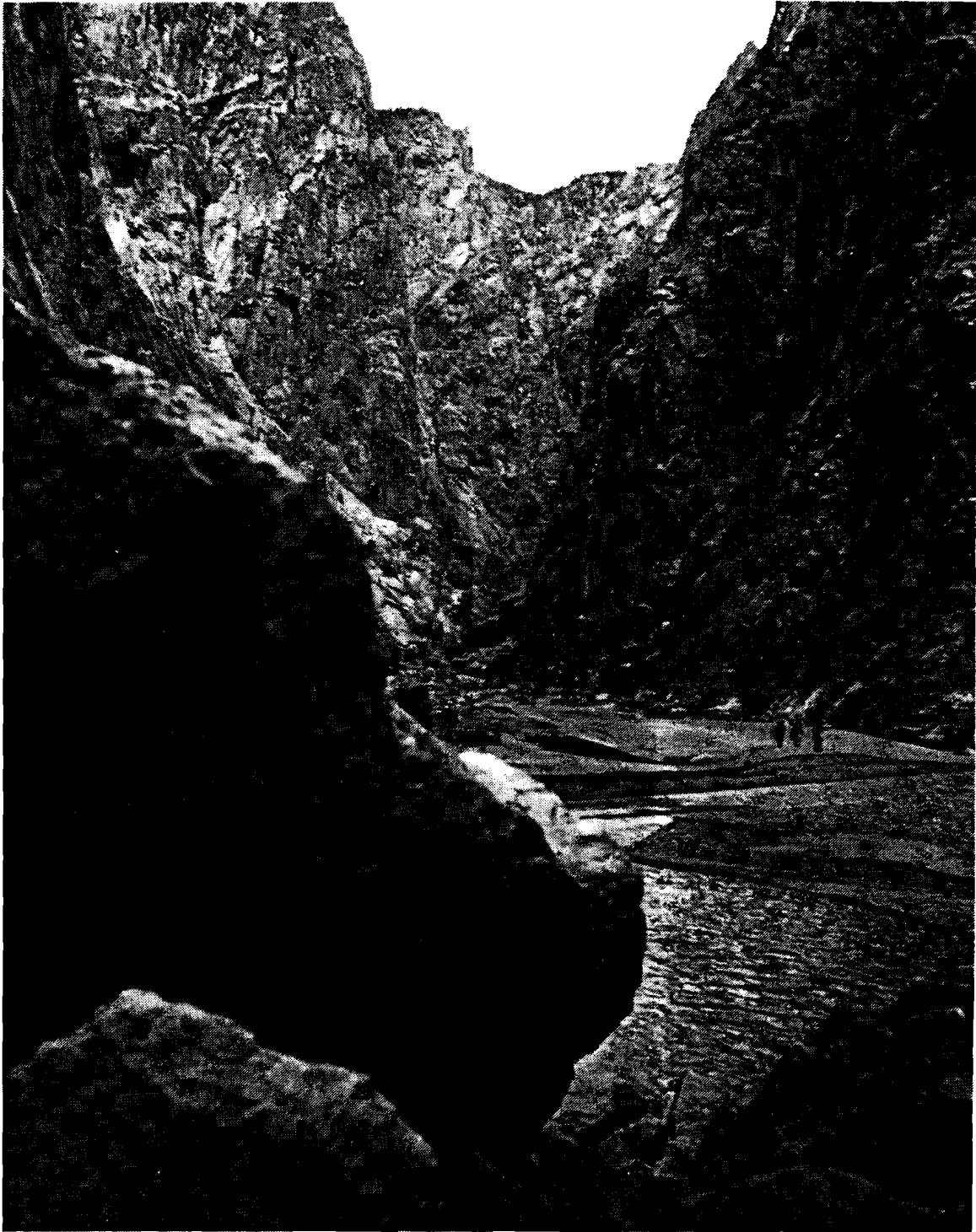


Fig. 5. "Unusual" sandbar, fourth day of trip through the Black Canyon, 1934. Reproduced from negatives of Walker (1967).

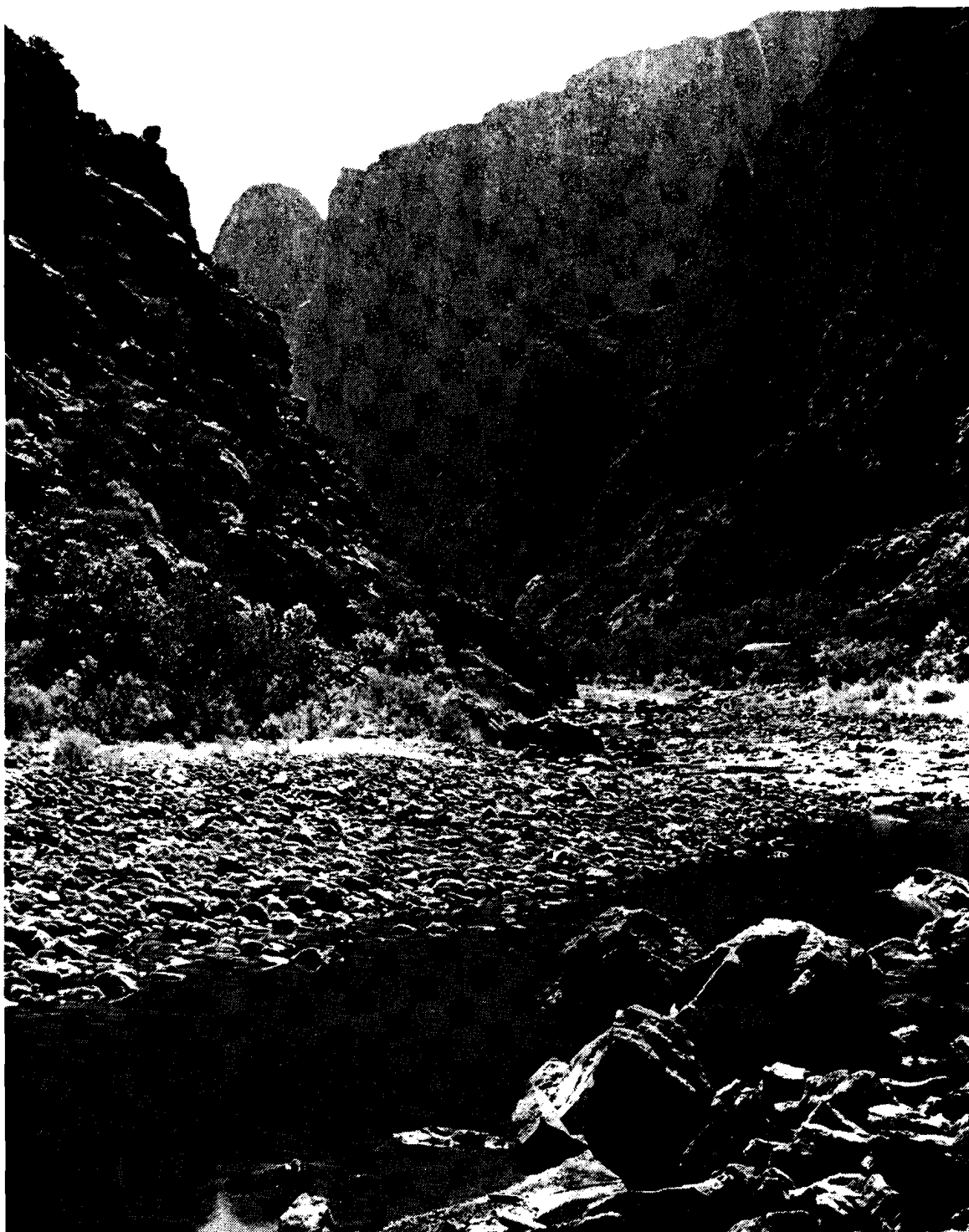


Fig. 6. Upstream from Red Rock Canyon at discharge of 73 cfs, fifth day of trip through the Black Canyon, 1934. Reproduced from negatives of Walker (1967).

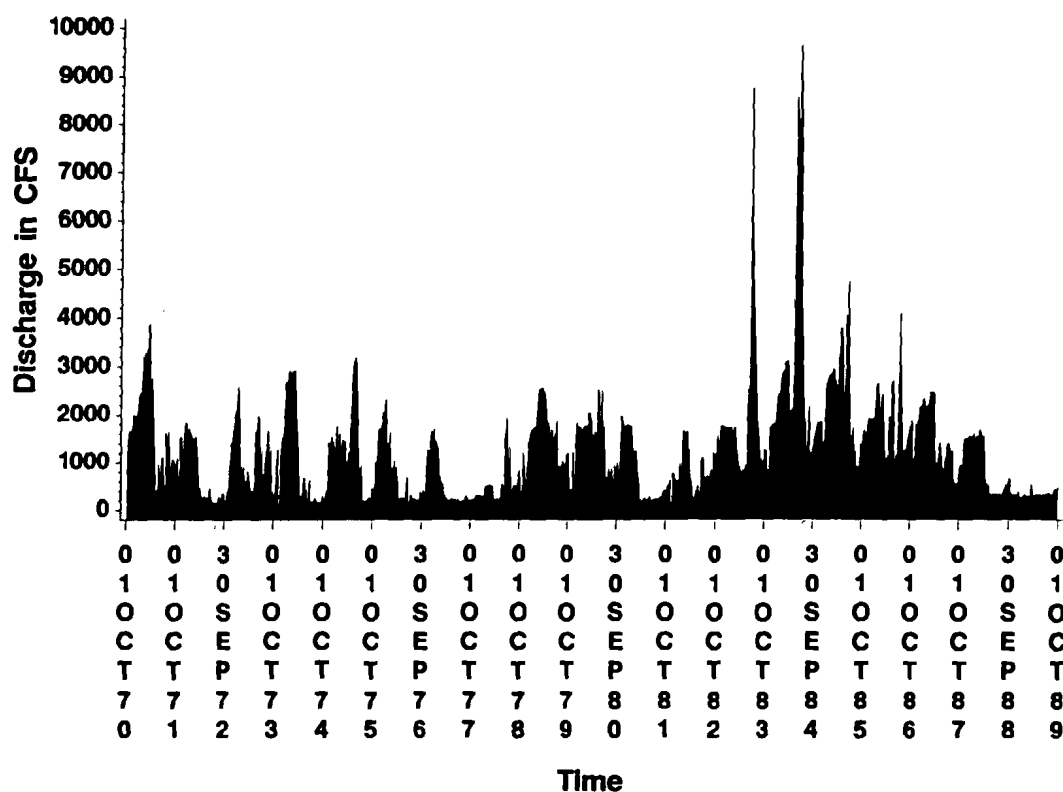


Fig. 7. Weekly average discharge of Gunnison River below Gunnison Tunnel, water years 1971-1989.

occur there. Reed and Norton (1963) prepared a comprehensive list of the algae as well as a list of 16 plant species that occur on the canyon bottom. Lichvar (1987) carried out a reconnaissance of the vegetation of the canyon bottom downstream of the monument. Weber (1983) prepared a checklist of all vascular plants that had been collected in the monument.

Overview of Assessment Approach

Comparison of the impacts of alternative water management options on riparian vegetation is a multi-step process integrating several disciplines. A general framework for riparian vegetation assessment is presented in Fig. 8. The following material provides a brief outline of the direct gradient assessment method as we applied it to the riparian vegetation of the Gunnison River. We then critically discuss various characteristics of the direct gradient assessment method in order to provide a better understanding of the strengths and weaknesses of this approach. This entire section is intended to provide an overview of the particular assessment model we used and an evaluation of its general strengths and weaknesses. The Methods section describes our specific field and analytical procedures in more detail.

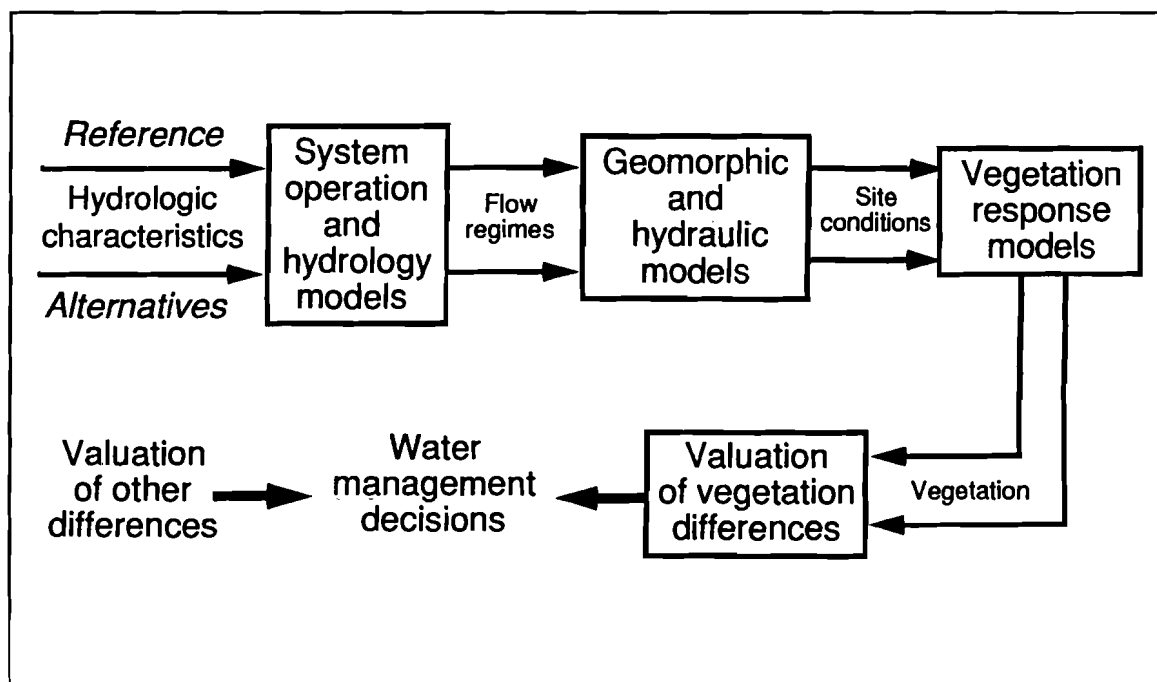


Fig. 8. Riparian vegetation assessment in water management decision making.

Outline of Direct Gradient Assessment Method

The vegetation assessment starts with application of models of system operation and hydrology to determine the hydrologic regime or flows associated with each water management alternative. The resultant set of hydrologic regimes includes a reference or baseline flow regime generally representing historical or current conditions.

Geomorphic and hydraulic models are used to translate flow regimes to environmental parameters relevant to the establishment, growth, or survival of vegetation. In this assessment, the environmental parameter is hydroperiod, which we define as fraction of time inundated. A hydraulic model is used to predict water surface elevations associated with different flows. The hydraulic position, or discharge required to inundate a point on the bank, is estimated by assuming the point is inundated when the water surface elevation predicted by the hydraulic model exceeds the surveyed ground elevation at the point.

The fraction of time a point is inundated can be determined from a flow exceedance curve by reading the fraction of time that discharge exceeds the value required to inundate the point. If channel geometry is assumed to be static, then the discharge necessary to inundate a point remains constant across different hydrologic regimes. However, each hydrologic regime has a different flow exceedance curve and thus produces a different fraction of time inundated for a given point.

The vegetation response model employed in this assessment is based on direct gradient analysis, a common approach in plant ecology (e.g., Whittaker 1967; Jongman et al. 1987). Most simply, direct gradient analysis consists of portraying the distribution of vegetation (dependent variables) along a measured environmental gradient (independent variable). Changes in vegetation distribution are estimated by determining how a particular flow regime would alter the environmental gradient (Fig. 9). In this assessment, hydroperiod is the environmental gradient. Franz and Bazzaz (1977) used a similar approach to assess impoundment impacts on trees.

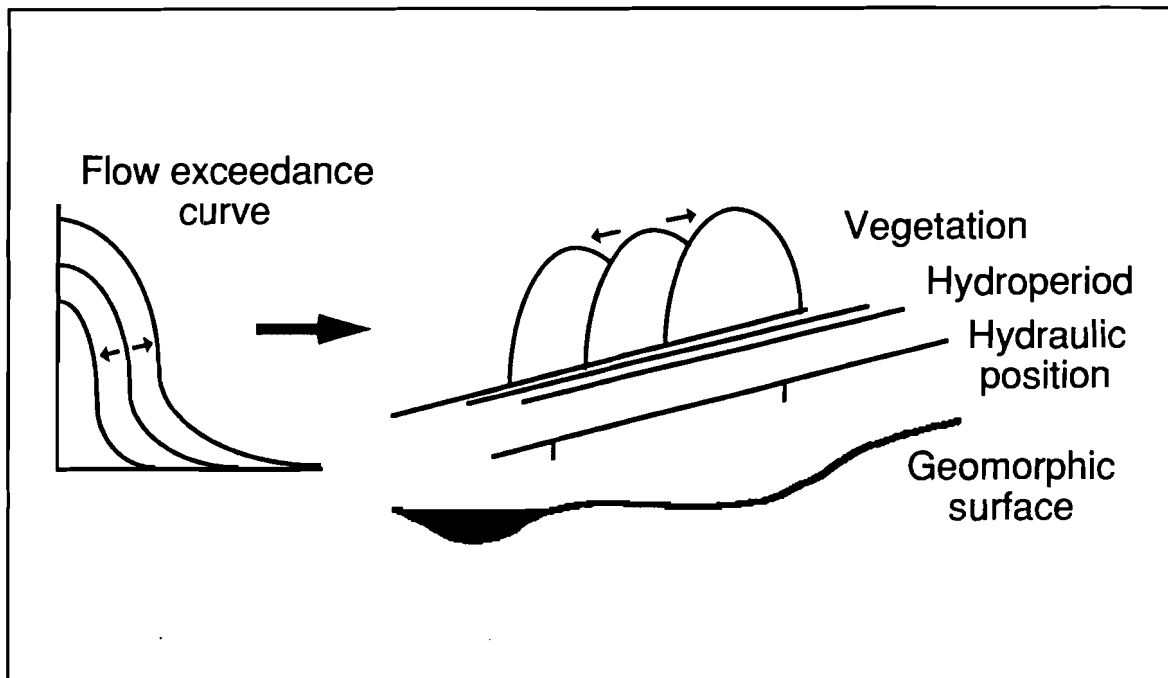


Fig. 9. Application of direct gradient assessment to simple flow alterations.

In this assessment, vegetation is represented as a set of cover types. We used TWINSpan (Hill 1979), a clustering program based on correspondence analysis, to help identify vegetatively distinct cover types that become the basic units of vegetation change and description.

The model of vegetation response is calibrated by measuring the existing distribution of vegetation along a hydroperiod gradient. This is accomplished by census of a number of discrete plots, assignment of each plot to one of the cover types, and determination of fraction of time inundated for each plot based on the discharge required to inundate the plot and the historical flow exceedance curve. The hydroperiod gradient is broken into a set of classes. Each class is then analyzed to determine the proportion of plots in that class that are in each cover type. These proportions are assumed to estimate the probabilities that a plot in a given inundation class is, or would be, in a given cover type.

After calibrating the relationship between hydroperiod class and cover type probabilities, future vegetation is estimated by applying a new flow exceedance curve to the plots. Each alternative flow exceedance curve can

result in different hydroperiods for the plots. The different hydroperiods can result in different cover type probabilities for individual plots and shifts in total cover type composition aggregated across plots. Our plots were randomly selected. Thus, we interpret changes in the proportion of plots as changes in the cover type composition of the study area.

The basic output from the vegetation response model is the expected number of plots in each cover type for each alternative hydrologic regime. Ancillary output includes fractions of time inundated and cover type probabilities for each plot and associated transition matrices depicting aggregate and plot-by-plot change in hydroperiods and cover type probabilities. This output from the vegetation response model is the endpoint of the work described here.

Characteristics of Direct Gradient Assessment Method

Water management framework. The purpose of the direct gradient assessment method is to incorporate a consideration of impacts on riparian vegetation into water management decisions. The closer the method fits with the current conceptual, dimensional, and computational framework for making these decisions, the more likely the method will be used. Representing the river through a series of hydraulic cross-sections and modeling water surface elevations using Manning's equation or a step-backwater model are standard practices in water management. Likewise, summarizing hydrologic time series in flow exceedance curves is a common analysis technique. Such curves would either be available as part of project engineering design or could be reasonably requested from hydrologic engineers.

Finally, the basic output of the direct gradient model is a statement about the new, quasi-equilibrium vegetation associated with a new flow regime. This is a simplification of complex spatial and temporal response potentials. However, it has the strong advantage of being a single result, rather than a whole family of response curves. The alternative of a dynamic simulation model naturally produces a family of output sequences in response to sequences of hydrologic input (e.g., Pearlstine et al. 1985; Johnson 1988). While these models are potentially more accurate and precise, their use dictates another complicated step of properly representing or synthesizing a family of possible vegetation responses. Vegetation response has to be represented simply enough

to allow it to become one of a number of variables (e.g., fish habitat, water supply, hydropower) considered in a larger water management decision. Furthermore, dynamic simulation models may require more detailed autecological data than is available for many riparian species.

Extension of Instream Flow Incremental Methodology. The Instream Flow Incremental Methodology (Bovee 1982) has been widely used to relate instream flow to fish habitat and to incorporate impacts on fish in making water management decisions. Harris et al. (1985) used the hydraulic components of this methodology to sample and describe the distribution of riparian vegetation along headwater streams. As described in the Methods section, the direct gradient assessment approach employs many of the same conceptual elements, computational procedures, and field methods as the Instream Flow Incremental Methodology.

Cover type units. An assessment model of vegetation change using a direct gradient relationship to hydroperiod can be formulated at either the species or cover type level. Species tend to respond individualistically to environmental change, and this is the most appropriate level for understanding details of a temporally and spatially complex response. However, valuation of vegetation differences is often formulated in terms of cover types. Rather than attempting to compose cover type response from the individualistic responses of a large number of species, we have formulated the model directly with cover types by using the distribution of cover types along the environmental gradient. This greatly simplifies formulation of the model and interpretation of output.

Quasi-equilibrium vegetation. The direct gradient assessment model describes vegetation as a quasi-equilibrium set of species or cover types determined by the hydrologic regime. In fact, vegetation is constantly varying in response to new hydrologic and other inputs. Therefore, the model's prediction of vegetation is more appropriately viewed as one point within a range of compositions. The exact composition varies as a function of the exact nature of the recent hydrologic history. For example, the exact composition of an infrequently flooded plot will obviously differ before and after a major flooding event. The direct gradient approach using long-term hydroperiod is successful to the extent that the cluster of compositions on an

infrequently flooded plot is different from the cluster of compositions on a frequently flooded plot.

Vegetation sampling. The field vegetation sampling required to calibrate the direct gradient assessment model for a particular site is essentially the same as would commonly be conducted to provide a basic site description of the vegetation. Species composition is determined for a number of plots spanning an elevational gradient. We are using species presence on plots, but the model could be refined to use density, cover, or basal area. Some sort of direct gradient analysis is often employed to summarize this type of vegetation data.

Use of the data to calibrate a change model based on hydroperiod introduces some additional considerations. Estimates of present and alternative future hydroperiods are required for each vegetation plot. Thus, geomorphic and hydraulic models must be able to estimate the hydraulic position, or inundating discharge, for each plot. The basic tradeoff in vegetation sampling design concerns random placement in the riparian zone versus close association of plots with the hydraulic cross-sections used to relate discharge to water surface elevation. Random placement simplifies extrapolation to the whole riparian area, but complicates estimation of environmental conditions at each plot from hydraulic cross-sections. Locating plots along hydraulic cross-sections simplifies data collection and integration with the hydraulic models, but complicates extrapolation to the whole riparian area.

Hydroperiod. Hydroperiod, as determined by a flow exceedance curve, is the single environmental variable determining vegetation response in the direct gradient assessment model. The simplicity of this approach has both advantages and disadvantages. A large number of studies (e.g., Wells 1928; Teskey and Hinckley 1977; Klimas et al. 1981; Harris et al. 1985; Hupp and Osterkamp 1985) have demonstrated that plant species and communities can be distinctly arrayed along the gradient of hydroperiod. In many cases, tolerance of inundation translates simply to tolerance of the anoxic rooting conditions that are often associated with extended inundation.

However, in our direct gradient assessment, hydroperiod is used as more than just an index of anoxia. Fraction of time inundated serves as a

surrogate measure for flow-related variation in a suite of environmental conditions in the riparian zone. These include shear stress, sediment deposition and erosion, soil moisture, and depth to groundwater, in addition to soil oxygen and oxidation-reduction potentials. These factors are all related to the fraction of time inundated. For example, frequently inundated sites are likely to be closer to groundwater when not flooded, are likely to be inundated to greater depths when flooded, and are likely to be subject to greater and more frequent shear stress than infrequently inundated sites. Nonetheless, the relation of these other variables to hydroperiod will be imperfect. While the error involved in using a single surrogate measure may be acceptable for comparisons within a site, it does limit the transferability of information between sites. For example, the position of a species on a hydroperiod gradient determined at a strongly losing reach may be different from the position of the same species determined at a strongly gaining reach because of a different relationship between fraction of time inundated and depth to groundwater.

Many studies of plant response to hydroperiod have considered inundation only in the growing season because physiological stress from soil anoxia is reasonably restricted to the growing season. However, in western riparian systems much of the influence of flow on plant communities is associated with physical processes, such as mechanical damage to plants and sediment dynamics, which may operate throughout the year depending on flow. For this reason, we use a flow exceedance curve based on the whole year rather than just the growing season.

A flow exceedance curve is a highly synthetic description of a hydrologic time series. The advantage of this description is that the analysis avoids considering a large number of specific hydrologic sequences each with a specific sequence of vegetation response. The disadvantage is that the analysis is relatively insensitive to timing issues because the flow exceedance curve does not specify when or in what sequence the flows occur.

Channel change. The direct gradient assessment model does not explicitly represent processes of channel change. This is not a problem if channel morphology is constant. Problems arise, however, if the hydraulic position of plots changes over time. The inundating discharge of a plot estimated by the hydraulic model, and the calibration of the hydraulic model

itself, will likely be in error if the channel geometry changes. The difficulty stems from changes in channel geometry or net changes in the elevation of points in hydraulic cross-sections, not necessarily gross sediment disturbance or flux at a plot.

It is possible that errors propagated from channel change through the hydraulic calculations and subsequent vegetation response model could cancel out at a larger scale. In this case, the overall proportions of plots in different hydraulic positions would not change and predicted vegetation responses would be accurate. However, the primary justification for assuming a constant channel geometry is expediency. Channel change is clearly a very important aspect of the environment of riparian plants, but accurate and precise prediction of future channel geometry is dauntingly difficult.

Methods

Field Sampling

Vegetation

We visited the study reach June 19-20 and July 18-31, 1990. All plot surveys were carried out during the second visit. Vegetation sampling was restricted to the five bars, or relatively flat areas of alluvial sediment, within the study reach. The location of these bars in relation to the cross sections used to estimate water surface elevations is depicted in Fig. 10. Adjacent to the stream, bars were delimited by the water's edge. This line also marked the streamward limit of emergent vegetation. Away from the stream, bars were bounded by the base of a cliff or the toe of a talus slope. The narrow, uneven areas of alluvial sediment between bars were not sampled.

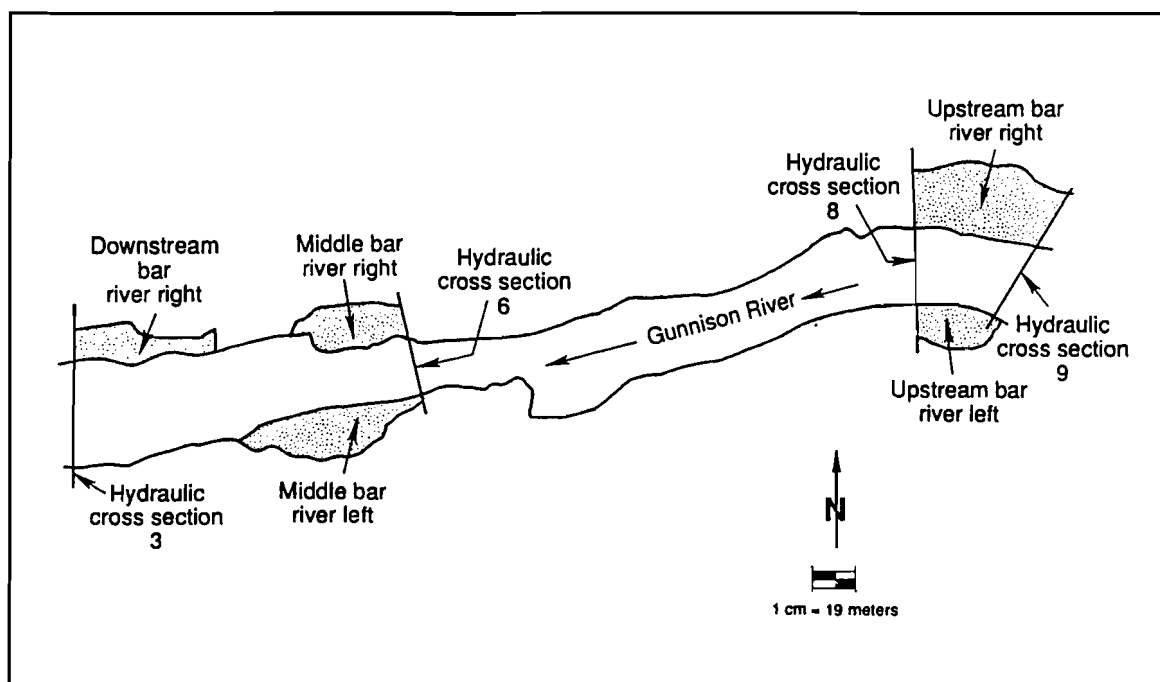


Fig. 10. Location of sampled bars within study reach.

Initially, 134 1x2-m plots were randomly located on the bars. One plot was discarded because an extreme slope made it impossible to describe the plot adequately with a single elevation. Table 1 shows the area and distribution of the remaining 133 plots across bars. For each plot we recorded all species present, total vegetative cover, and substrate particle size. For woody species we recorded the height of each stem in the plot. Total vegetative cover was recorded as one of four classes: 1 = 0-25%, 2 = 25-50%, 3 = 50-75%, and 4 = 75-100%. Substrate particle size was recorded as two variables. SOIL1 represented the dominant particle size and SOIL2 represented the subdominant, if present. SOIL1 and SOIL2 were coded as follows: 0 = organic, 1 = silt, 2 = sand, 3 = gravel, 4 = cobble, and 5 = boulder.

Table 1. *Description of sampled gravel and cobble bars.*

Bar	Area (m ²)	Number of plots
Upstream, River Right	2,206	39
Upstream, River Left	708	24
Middle, River Right	910	25
Middle, River Left	1,326	20
Downstream, River	880	25
Total	6,030	133

We prepared a map of each bar showing the location of all woody stems over 0.6 m tall, including stems that were not in any of the plots. Three individual trees were cored using an increment borer. Two orthogonal cores were extracted as close to the bottom of the tree as possible. Cores were placed in plastic straws and returned to the laboratory for analysis. The following is a brief description of the cored trees:

A1--*Acer negundo* (*Ace_neg*). This tree was approximately 8.2 m (27 feet) tall and was located in the center of the Upstream, River Right bar (Fig. 23). Cores were extracted at approximately 30 cm above the ground.

A2--*Acer negundo* (*Ace_neg*). This tree was approximately 1.3 m (4.3 feet) tall and was the most upstream individual in a line of *Ace_neg* and *Tamarix ramosissima* (*Tam_ram*) on the Upstream, River Right bar. This was the only one of the *Ace_neg* on this bar whose original, central stem had not been removed by beaver. The cores were both taken approximately 5 cm above the ground.

T1--*Tamarix ramosissima* (*Tam_ram*). This tree was 8.4 m (27.5 feet) tall, the largest individual tamarisk observed in the study reach. It was located on the upland edge of the Upstream, River Right bar. Cores were taken approximately 30 and 60 cm above the ground.

Hydraulics

The National Park Service established a series of nine hydraulic cross-sections along the Gunnison River. The locations of the cross sections within our study reach are indicated in Fig. 10. The Park Service surveyed the geometry of each cross section using a total station surveying instrument. In the summer and fall of 1990, the Park Service measured water surface elevations at all cross sections for a set of known discharges from the USGS gage (336, 614, 766, 1024, and 1584 cfs). In addition, the Park Service provided locations and elevations for all the randomly selected vegetation sample plots on the bars and for some individual trees.

Analysis

Vegetation Characterization

The purpose of vegetation characterization was to aggregate plant species information into units that were physically and biologically distinct at the scale of individual alluvial bars or several bars within a reach of river. More specific objectives included the following: (1) to identify and characterize patterns in the distribution of riparian plant species; (2) to relate the distribution of plant groupings or cover types to key environmental variables; and (3) to succinctly characterize cover types in terms of floristics, physiognomy, vegetative cover, soil characteristics, geomorphic position, and hydrology.

Cover type definition. Cover types of riparian plant species were defined using a method of Two-Way INDicator SPecies ANALysis or TWINSpan (Hill 1979). This program arranges sites (or plots) and species and constructs an ordered, two-way site-by-species table. These features make TWINSpan one of the most commonly used programs in plant community ecology (Jongman et al. 1987).

TWINSpan divides plots into groups by establishing repeated, hierarchical dichotomies. The method first identifies any pattern or direction in the data by ordering or ordinating the plots. This ordination is referred to as the primary ordination and is made using the method of correspondence analysis (CA) by iterative application of the algorithm of reciprocal averaging or two-way weighted averaging (Hill 1979). This algorithm is outlined mathematically in Appendix 1.

Starting with arbitrary but unequal values for plots (or species), application of correspondence analysis results mathematically in plot and species values, or scores, that have maximum dispersion along the CA axis. Subsequent arrangement of species and plots in a two-way table, in rank order of their scores, typically results in a diagonal structure. Such a structure can, and typically does, result from the distribution of species across underlying environmental gradients.

Once the primary ordination is made, it is divided at the middle and the process is repeated on each subset, resulting in successive subsets of two, four, eight, etc.; through a specified number of levels of division (the default value = 6). A second or refined ordination is then made from the primary ordination on the basis of differential species. Differential species are defined as those species with clear ecological preferences. In TWINSpan, good differential species would show a preference for a particular group of plots. The presence of such a species, in theory, could be used to identify a particular suite of environmental conditions (Hill 1979). The refined ordination is the one that is used to determine the actual divisions.

A third ordination called the indicator ordination is made using a few of the most "preferential" species, that is, species that show a marked preference for the left (-) or right (+) side of a particular division. Hill (1979) indicates that this final ordination was added to TWINSpan simply to

provide a streamlined summary of each division and does not actually determine the division.

The TWINSpan program allows up to 15 levels of division; however, there is often little interpretative value in dividing subgroups (plots and species) beyond a certain level. Often, final divisions are made on the presence or absence of individual species (Hill 1979) and, therefore, offer little ecological insight. In interpreting TWINSpan output in this analysis, we required that each division result in visually, floristically, and spatially distinct cover types. Subsequent divisions that did not resolve distinct cover types were not considered.

We used presence-absence of species in our sample plots to run the TWINSpan analysis. All of the default settings specified in Hill (1979) were used with the added restriction that a species must have occurred in three or more plots in order to be included in the analysis.

Additional cover type characterization. The relation between plant cover types and physical environmental variables was examined using Wilcoxon Scores (Rank Sums) for each variable. A Kruskal-Wallis Test (Chi-Square Approximation) was used to test for significant differences in the distribution of a variable across cover types. The variables examined were (1) cover index, (2) soil indices, and (3) hydroperiod, or fraction of time inundated.

Using the TWINSpan output, field notes, and measurements, we summarized the cover types in terms of biological attributes including (1) indicator species (identified by TWINSpan), (2) dominant species (>60% occurrence in plots), and (3) physiognomic description of the dominant species. Cover types were further described by measured physical environmental variables as well as by their geomorphic position across the sample gravel bars.

In addition to the cover types defined from the TWINSpan analysis, an Open Water cover type was introduced to describe the streamward environment below the edge of the sampled area. This cover type is represented by a single artificial plot with an inundating discharge assigned so that it is slightly less than the streamward boundary of the vegetated bar area.

Woody Vegetation

Tree cores. All tree cores were mounted on wooden blocks and sanded smooth with increasingly fine sand paper. A binocular scope was then used to identify and enumerate rings. *Acer negundo* displayed a number of false rings, and criteria were established to distinguish between true and false rings following Brown (1981). Ring widths were measured to the nearest 0.01 mm with a digital micrometer. For each core, ring widths were standardized to the mean ring width for graphical purposes (Stokes and Smiley 1968). Finally, Pearson correlations were run on ring widths between cores from the same tree.

Hydrology

The basic steps in the systems operation and hydrology analysis are depicted in Fig. 11. The historical record of mean daily discharges for water years 1971 through 1989 was defined as the reference hydrologic regime.

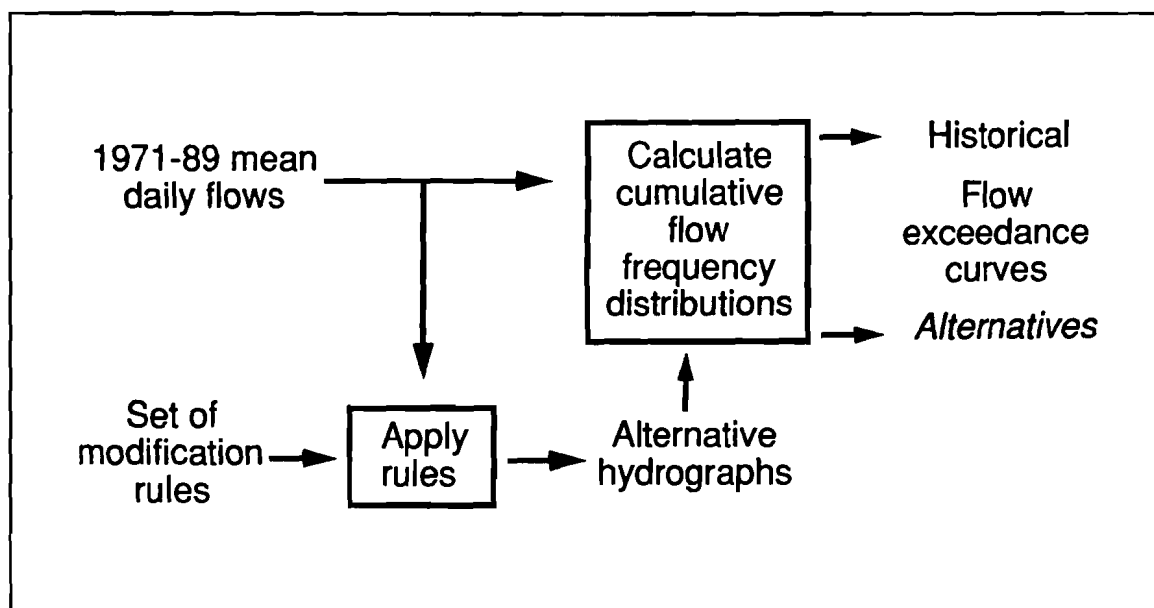


Fig. 11. Diagram of basic steps in systems operation and hydrology analysis.

Flow records of mean daily discharge were obtained from a CD-ROM compilation (EarthInfo 1991) of U.S. Geological Survey data for Station 0912800, Gunnison River below Gunnison Tunnel, CO. Hydrologic alternatives were formulated as simple modification rules applied to the historical record (Table 2). Each

Table 2. *Hydrologic alternatives.*

Title	Description	Modifying rule	n
71-89 Mean Daily Flow	1971-89 mean daily flows	None: Flows = 1971-89 daily flows (71-89DF)	6,940
50% 71-89	50% of 1971-89 flows	Flows = 71-89DF * 0.5	6,940
80% 71-89	80% of 1971-89 flows	Flows = 71-89DF * 0.8	6,940
50% 71-89 >1,500	1971-89 flows with 50% reduction in flow greater than 1,500 cfs	If 71-89DF $\leq$ 1,500, then Flows = 71-89DF If 71-89DF > 1,500, then Flows = 1,500 + [(71-89DF - 1,500) * 0.5]	6,940
50% 71-89 >2,000	1971-89 flows with 50% reduction in flow greater than 2,000 cfs	If 71-89DF $\leq$ 2,000, then Flows = 71-89DF If 71-89DF > 2,000, then Flows = 2,000 + [(71-89DF - 2,000) * 0.5]	6,940
50% 71-89, 300 min	1971-89 flows with 300 cfs minimum and 50% reduction in flow greater than 300 cfs	If 71-89DF $\leq$ 300, then Flows = 300 If 71-89DF > 300, then Flows = 300 + [(71-89DF - 300) * 0.5]	6,940
80% 71-89, 300 min	1971-89 flows with 300 cfs minimum and 80% reduction in flow greater than 300 cfs	If 71-89DF $\leq$ 300, then Flows = 300 If 71-89DF > 300, then Flows = 300 + [(71-89DF - 300) * 0.8]	6,940
50% 71-89, 600 min	1971-89 flows with 600 cfs minimum and 50% reduction in flow greater than 600 cfs	If 71-89DF $\leq$ 600, then Flows = 600 If 71-89DF > 600, then Flows = 600 + [(71-89DF - 600) * 0.5]	6,940

Table 2. *Continued.*

Title	Description	Modifying rule	n
80% 71-89, 600 min	1971-89 flows with 600 cfs minimum and 80% reduction in flow greater than 600 cfs	If 71-89DF ≥ 600 , then Flows = 600 If 71-89DF > 600 , then Flows = $600 + [(71-89DF - 600) * 0.8]$	6,940
91-day Moving Average	Moving average of 1971-89 flows using 91-day window	Flows = (Sum of 91 days of 71-89DF) / 91	6,850
1-year Moving Average	Moving average of 1971-89 flows using 365-day window	Flows = (Sum of 365 days of 71-89DF) / 365	6,576
24 Winter 300	1971-89 flows with phased reduction to 300 cfs in winter and 300 cfs minimum throughout year	If Time ≥ 15 April and ≤ 15 Oct, then Flows = maximum of 300 and 71-89DF If Time > 26 Oct and < 5 April, then Flows = 300 If Time > 15 Oct and ≤ 26 Oct, then Flows = maximum of 300 and (71-89DF of previous day - 200) If Time ≥ 5 April and < 15 April, then Flows = minimum of 71-89DF and Flow of previous day + 500)	6,940

Table 2. *Concluded.*

Title	Description	Modifying rule	n
Winter, 50% >300	1971-89 flows with phased reduction to 50% reduction in winter flow greater than 300, and 300 cfs minimum throughout year	If Time ≥ 15 April and ≤ 15 Oct, then Flows = maximum of 300 and 71-89DF If Time >26 Oct and <5 April, then Flows = maximum of 300 and [300 + (71-89DF - 300) * 0.5] If Time >15 Oct and ≤ 26 Oct, then Flows = maximum of 300 and [minimum of (71-89DF of previous day - 200) and (300 + {(71-89DF - 300) * 0.5})] If Time ≥ 5 April and <15 April, then Flows = maximum of 300 and [minimum of (71-89DF of previous day + 500)]	6,940
Power Generation	Fixed flows of 2,000; 1,000; and 300 cfs	158 days of 2,000; 165 days of 1,000; and 42 days of 300	365

hydrologic alternative was thus represented by an alternative set of daily discharges. Flow exceedance curves were constructed for the reference and each alternative hydrologic regime by calculating the cumulative flow frequency distribution for the respective sets of daily discharge values. These flow exceedance curves, sometimes referred to as flow duration curves, were based on discharge values throughout the year rather than just in the growing season.

Hydraulics

The basic steps in the geomorphic and hydraulic analysis are depicted in Fig. 12. The National Park Service provided water surface elevations for five measured discharges (336, 614, 766, 1024, and 1584 cfs) at the four cross sections within the study reach (Fig. 10). In addition, the Park Service provided output from a calibrated water surface profile model, HEC-2 (Hydrologic Engineering Center 1982; Hoggan 1989), corresponding to additional discharges ranging from 50 to 10,000 cfs at intervals of 50 to 1,000 cfs.

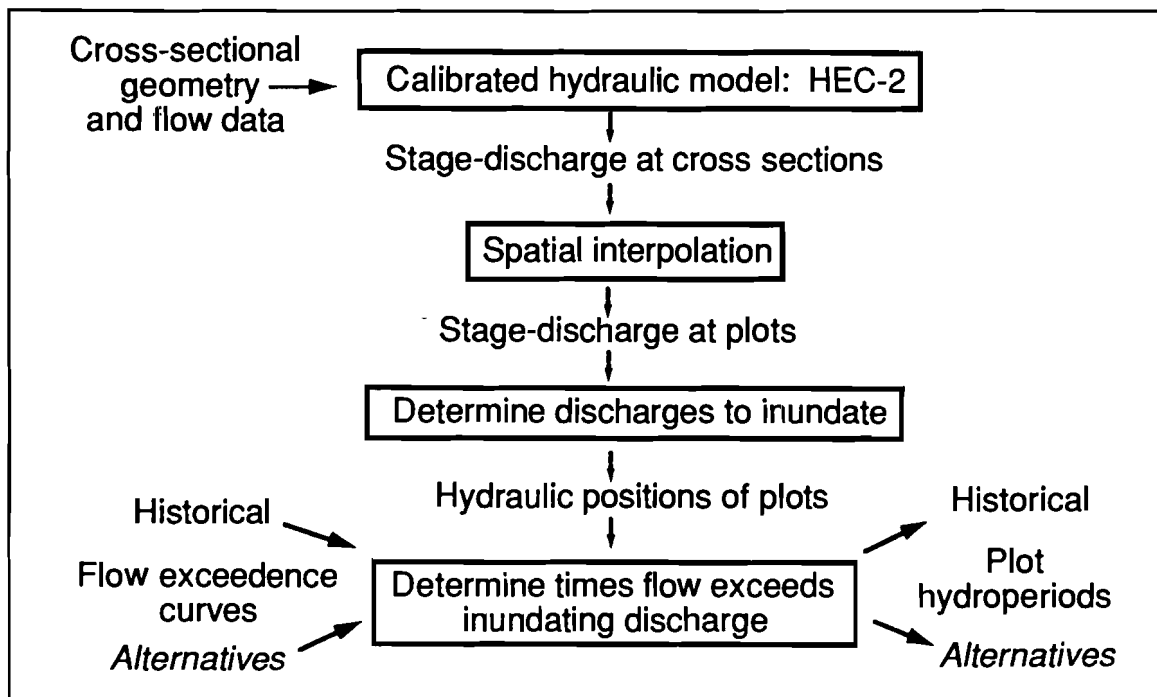


Fig. 12. Diagram of basic steps in geomorphic and hydraulic analysis.

A detailed stage-discharge rating table at 20-cfs increments was constructed for each of the four relevant cross sections by linear interpolation using the HEC-2 output from 50 to 200 cfs, the observed water surface elevations from 336 to 1,584 cfs, and HEC-2 output from 2,000 to 10,000 cfs. The rating table was extended downward by linear interpolation between the estimated stage at zero flow and the HEC-2 stage at 50 cfs. The rating table was extended upward to 12,000 cfs by linear extrapolation of the slope between the HEC-2 stages at 9,000 and 10,000 cfs.

The discharge required to inundate each vegetation plot was estimated by constructing a stage-discharge rating curve for each plot at 20-cfs increments (Fig. 13). For each discharge, the water surface elevations at cross sections upstream and downstream of the plot were read from the detailed rating curves for these cross sections. The plot water surface elevation for that discharge was then estimated by a simple linear interpolation based on the proportional location of the plot along an idealized channel edge connecting the two cross sections (Fig. 13).

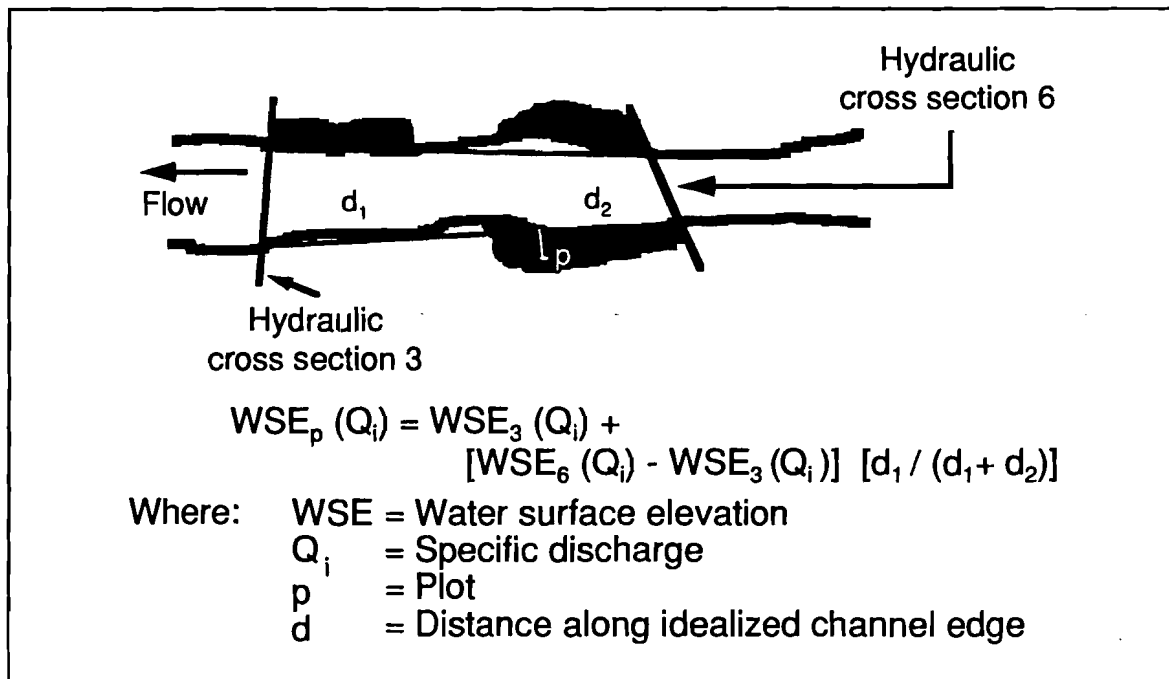


Fig. 13. Spatial interpolation of water surface elevations between hydraulic cross sections.

The discharge to inundate a plot was then determined from the stage-discharge rating curve by finding the discharge required to produce a water surface elevation equal to the surveyed ground elevation of the plot. Linear interpolation was used to estimate stage-discharge combinations between the 20-cfs increments used to define the detailed plot rating curve.

Hydroperiod was determined as the fraction of time the inundating discharge for a plot was equaled or exceeded in the flow exceedance curve for a particular hydrologic alternative. The inundating discharges, or hydraulic positions, are thus assumed to remain constant across hydrologic alternatives. Hydroperiods, however, vary across hydrologic alternatives that have different flow exceedance curves.

Alternatives Analysis

The basic steps in the procedure for estimating vegetation change are depicted in Fig. 14 with the associated algorithm summarized in Fig. 15. The model was calibrated using the TWINSpan-based cover types and the historical hydroperiod associated with the flow exceedance curve for 1971-1989 hydrologic data (Table 2). The hydroperiod gradient was divided into 12 classes and the fractions of plots in each cover type were calculated for each hydroperiod class. This representation of the current vegetation distribution was assumed to represent the probabilities that a plot in a given hydroperiod class would have a given cover type (Fig. 15).

For each hydrologic alternative, the flow exceedance curve was used to determine the hydrologic classes of all the plots. The cover type probabilities for each hydroperiod class were then multiplied by the number of plots in each hydroperiod class and summed across hydroperiod classes to determine the total number of plots in each cover type. The plots are assumed to represent an adequate random sample of the bar area. Thus, fractions of the total plots are presented and interpreted as fractions of the total bar area.

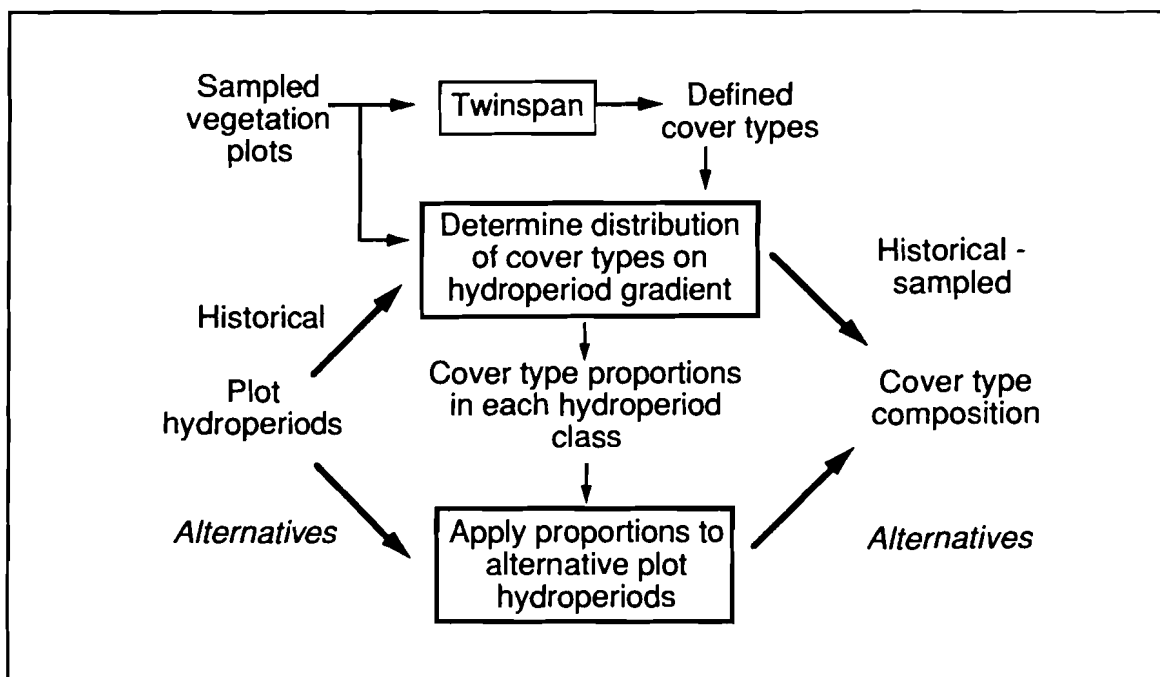


Fig. 14. Diagram of basic steps in vegetation analysis.

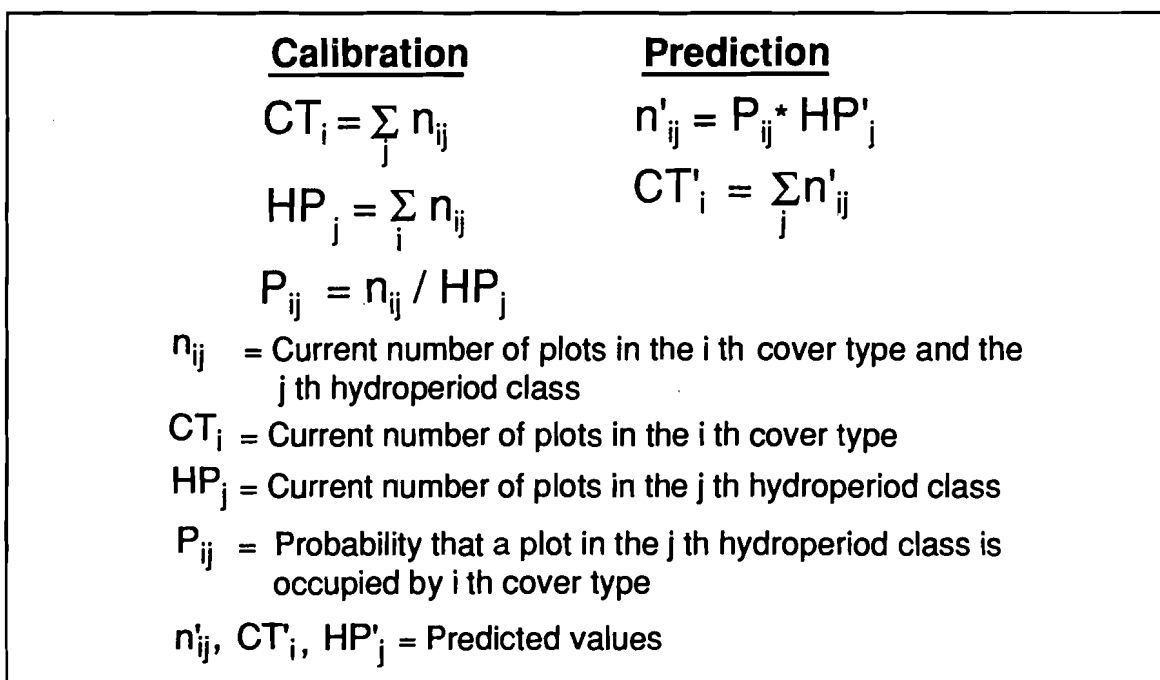


Fig. 15. Vegetation response algorithm.

Results and Discussion

Riparian Plant Species

The plants observed on the alluvial bars of the canyon bottom are listed in Table 3. Taxonomy follows U.S. Department of Agriculture (1982). Where these names differ from those of Weber (1987), Weber's names are included in parentheses. We observed 103 species, 41 of which were new to the monument (Weber 1983). One species, *Dicanthelium oligosanthes*, had not been previously reported in Colorado west of the continental divide (Weber 1987). Our list includes all common species and many of the rare species on the study reach at the time of survey. Future surveys at different times of the year and along different reaches would probably yield additional species.

Most of the plants recorded in the study reach are widely distributed species typical of low elevation riparian zones in Colorado. The dominant woody species were box elder (*Acer negundo*), sandbar willow (*Salix exigua*), and saltcedar (*Tamarix ramosissima*). The most abundant forbs were scouring rush (*Equisetum hyemale* and *E. laevigatum*), Louisiana sage (*Artemisia ludoviciana*), western goldenrod (*Euthamia occidentalis*), and sweet clover (*Melilotus alba* and *M. officinalis*). The principal sedges were woolly sedge (*Carex lanuginosa*) and common spikerush (*Eleocharis palustris*). The most abundant grasses were redtop (*Agrostis stolonifera*), satinegrass (*Muhlenbergia racemosa*), reed canarygrass (*Phalaris arundinacea*), Canada bluegrass (*Poa compressa*), and fowl bluegrass (*Poa palustris*).

A total of 83 plant species were observed in the 133 plots. The distributions of these species along the hydroperiod gradient (fraction of time inundated) are summarized in Appendix 2. The TWINSpan analysis was restricted to those 60 species that occurred in three or more plots. We used somewhat broader hydroperiod class intervals for individual species than for cover types (8 as opposed to 12 classes) to compensate for the higher variability of individual species locations. These distributions are normalized to account for the different areal extent of various hydroperiod classes and thus represent a measure of species location along the environmental gradient.

The basic focus of our assessment is on cover types. However, the distributions of the 10 most abundant grasses illustrate several points at the individual species level (Figs. 16 and 17). First, the species are individualistically distributed along the gradient, differing in both optimum hydroperiod and range of tolerance. Second, there is a good correspondence between the position of a species along a hydroperiod gradient and its wetland indicator status used in delineating vegetated wetlands (Reed 1988). *Aristida purpurea* and *Bromus tectorum* are listed as upland species (almost never occur in wetlands) and are restricted to the driest end of the hydroperiod gradient. *Sporobolus cryptandrus*, *Poa compressa*, and *Muhlenbergia racemosa* are listed as facultative upland species (occurring in uplands 67-99% of the time) and are generally located at dry to intermediate positions on the gradient, although the optimum position of the broadly distributed *M. racemosa* appears somewhat wetter than might be expected from its listing.

The facultative wetland species (occurring in wetlands 67-99% of the time) *Agrostis stolonifera* and *Poa palustris*, and the obligate species (almost always occurring in wetlands) *Phalaris arundinacea* and *Alopecurus aequalis* are located at relatively wet positions on the gradient (Fig. 16 and 17). *Hordeum jubatum* is the only real anomaly in this set of species with a relatively wet gradient position for a facultative listing (occurring in wetlands 34-66% of the time). However, the national range of indicator values for *H. jubatum* includes facultative wetland, and the assignment of facultative is provisional in the region containing the Black Canyon site (Reed 1988).

Finally, the distribution of individual species highlights the relative nature of the hydroperiod gradient. The gradient is constructed by applying a hydrologic regime to the different hydraulic positions of individual plots. Thus, absolute positions along the gradient may vary with the specific hydrologic record used and its length. In fact, the positions of species on the hydroperiod gradient constructed with the 1971-1989 historical record appear somewhat wetter than might be expected from general field observation of these species. This is easily explained by the relatively dry conditions in the several years immediately preceding the sampling (Fig. 7). However, the relative nature of the hydroperiod gradient does limit the generality of conclusions about species positions based on a single hydrologic record and sampling date.

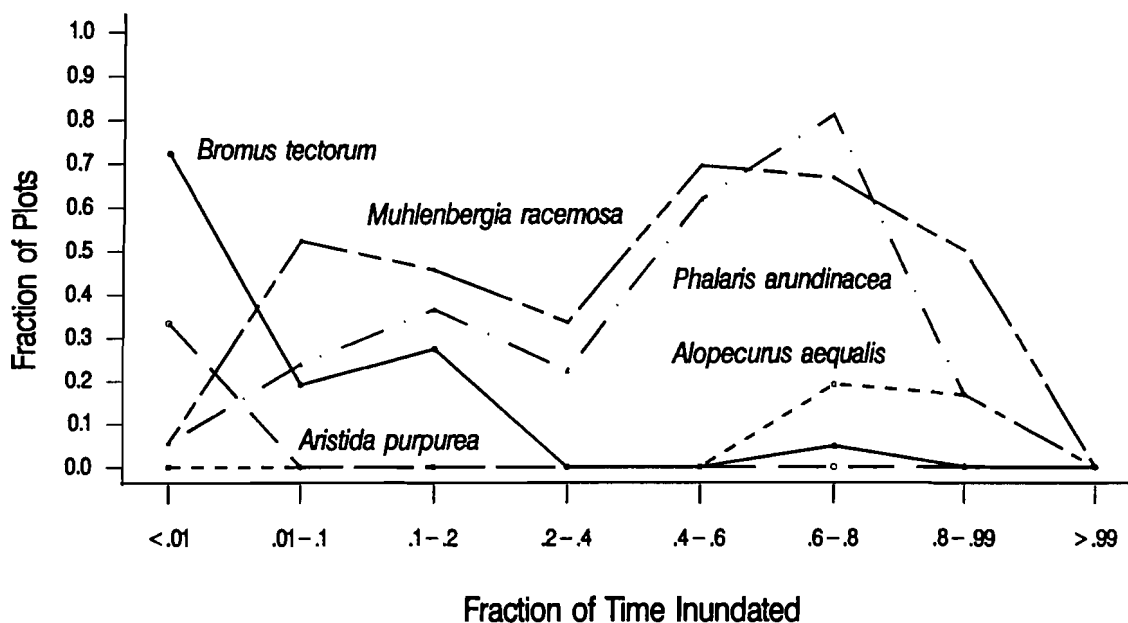


Fig. 16. Distribution of selected grasses on hydroperiod gradient (1).

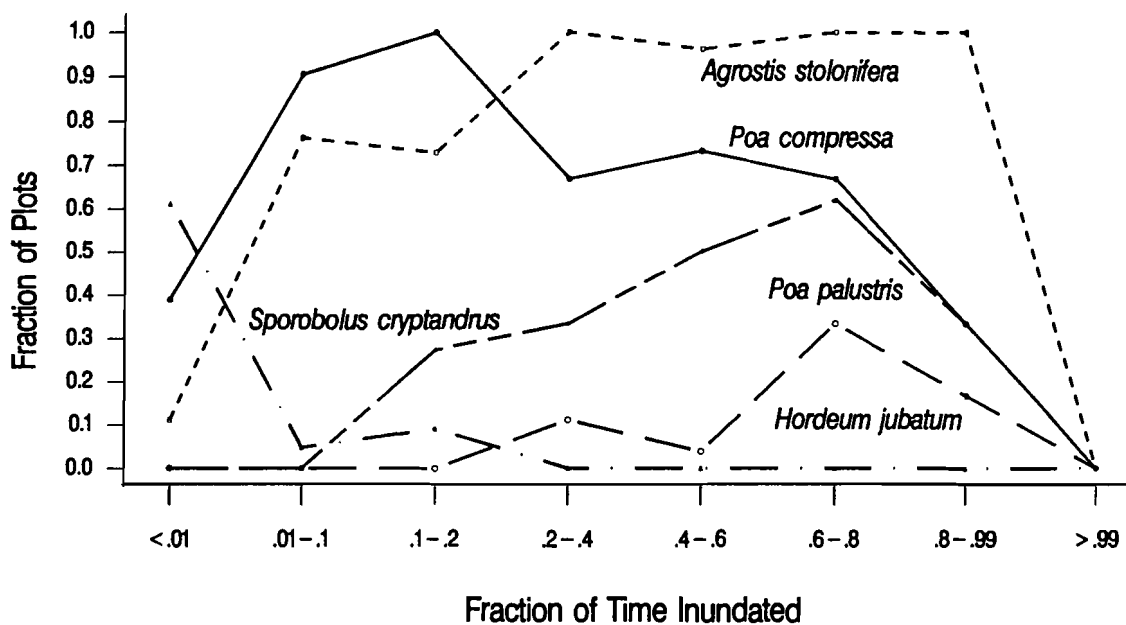


Fig. 17. Distribution of selected grasses on hydroperiod gradient (2).

Table 3. *Riparian plant species list for Black Canyon of the Gunnison National Monument. Species are listed by family with nomenclature following U.S. Department of Agriculture (1982). Where these names differ from those of Weber (1987), Weber's names are added in parentheses. A # indicates species previously unrecorded in the Black Canyon of the Gunnison National Monument (Weber 1983). Species acronyms used in data analyses follow the species names.*

CHARACEAE

Chara sp.: Cha_spe

EQUISETACEAE

Equisetum arvense: Equ_arv

Equisetum hyemale (*Hippochaete hyemalis*): Equ_hye

Equisetum laevigatum (*Hippochaete laevigata*): Equ_lae

ACERACEAE

Acer negundo (*Negundo aceroides*): Ace_neg

ANACARDIACEAE

Rhus trilobata (*Rhus aromatica* ssp. *trilobata*): Rhu_tri

Toxicodendron rydbergii: Tox_ryd

APOCYNACEAE

Apocynum sp.: Apo_spe

ASCLEPIADACEAE

Asclepias speciosa: Asc_spe

Asclepias subverticillata: Asc_sub

ASTERACEAE

Ambrosia sp.: Abm_spe

Artemisia ludoviciana: Art_lud

Aster hesperius: Ast_hes

Brickellia californica: Bri_cal

Chrysothamnus linifolius: Chr_lin

Cirsium arvense: Cir_arv

Cirsium vulgare: Cir_vul

Conyza canadensis: Con_can

Table 3. Continued.

-
- # *Euthamia occidentalis*: Eut_occ
Gutierrezia sarothrae: Gut_sar
Heterotheca villosa: Het_vil
Lactuca serriola: Lac_ser
Solidago sparsiflora (*Solidago velutina*): Sol_spa
Taraxacum sp.: Tar_spe
Tragopogon sp.: Tra_spe

BRASSICACEAE

- # *Rorippa teres*: Ror_ter

CHENOPODIACEAE

- Chenopodium fremontii*: Che_fre

CONVOLVULACEAE

- Convolvulus arvensis*: Con_arv

CYPERACEAE

- # *Carex atherodes*: Car_ath
Carex lanuginosa: Car_lan
Carex microptera: Car_mic
Carex nebrascensis: Car_neb
Carex praegracilis: Car_pra
Carex rostrata (*Carex utriculata*): Car_ros
Carex vesicaria: Car-ves
Eleocharis palustris: Ele_pal
Scirpus maritimus (*Bulboschoenus maritimus*): Sci_mar
Scirpus microcarpus: Sci_mic
Scirpus pallidus: Sci_pal
Scirpus sp.: Sci_spe

EUPHORBIACEAE

- # *Euphorbia serpyllifolia* (*Chamaesyce serpyllifolia*): Eup_ser
-

Table 3. Continued.

FABACEAE

Medicago lupulina: Med_lup
Melilotus alba: Mel_alb
Melilotus officinalis: Mel_off
Melilotus sp.: Mel_spe
Trifolium pratense: Tri_pra
Trifolium repens: Tri_rep
Trifolium sp.: Tri_spe

GROSSULARIACEAE

Ribes sp.: Rib_spe

HYPERICACEAE

Hypericum sp.: Hyp_spe

JUNCACEAE

Juncus balticus (*Juncus arcticus* ssp. *ater*): Jun_bal
Juncus bufonius: Jun_buf
Juncus ensifolius (*Juncus tracyi*): Jun_ens
Juncus nodosus: Jun_nod
Juncus tenuis (*Juncus dudleyi*): Jun_ten

LAMIACEAE

Mentha arvensis: Men_arv
Stachys palustris ssp. *pilosus*: Sta_pal

OLEACEAE

Fraxinus anomala: Fra_ano

ONAGRACEAE

Epilobium ciliatum: Epi_cil

PLANTAGINACEAE

Plantago major: Pla_maj

Table 3. Continued.

POACEAE

- Agropyron repens* (*Elytrigia repens*): Agr_rep
- Agropyron* sp.: Agr_spe
- Agropyron trachycaulum* (*Elymus trachycaulus*): Agr_tra
- Agrostis stolonifera* (*Agrostis gigantea*): Agr_sto
- Alopecurus aequalis*: Alo_aeq
- Aristida purpurea*: Ari_pur
- Bromus inermis* (*Bromopsis inermis*): Bro_ine
- # *Bromus japonicus*: Bro_jap
- Bromus tectorum* (*Anisantha tectorum*): Bro_tec
- Calamagrostis neglecta* (*Calamagrostis stricta*): Cal_neg
- # *Catabrosa aquatica*: Cat_aqu
- # *Dichanthelium oligosanthos* [first observation, west slope of CO Rockies]: Dic_oli
- # *Echinochloa crus-galli*: Ech_cru
- Elymus canadensis*: Ely_can
- Festuca arundinacea*: Fes_aru
- # *Glyceria grandis*: Gly_gra
- Hordeum jubatum* (*Critesion jubatum*): Hor_jub
- Muhlenbergia asperifolia*: Mul_asp
- Muhlenbergia racemosa*: Muh_rac
- # *Panicum capillare* var. *occidentale*: Pan_cap
- # *Phalaris arundinacea* (*Phalaroides arundinacea*): Pha_aru
- Phleum pratense*: Phl_pra
- Poa compressa*: Poa_com
- # *Poa palustris*: Poa_pal
- Poa pratensis*: Poa_pra
- # *Setaria viridis*: Set_vir
- Sporobolus cryptandrus*: Spo_cry

POLYGONACEAE

- # *Polygonum pensylvanicum* (*Persicaria pensylvanicum*): Pol_pen
- Rumex* sp.: Rum_spe

POTAMOGETONACEAE

- # *Potamogeton pectinatus*: Pot_pec
-

Table 3. *Concluded.*

RANUNCULACEAE

- # *Ranunculus circinatum* (*Batrachium circinatum* ssp. *subrigidum*): Ran_cir
Ranunculus cymbalaria (*Halerpestes cymbalaria*): Ran_cym

ROSACEAE

- # *Geum* sp.: Geu_spe
Holodiscus dumosus: Hol_dum
Potentilla sp.: Pot_spe

SALICACEAE

- # *Populus deltoides* ssp. *Wislizenii*: Pop_del
Salix exigua ssp. *interior*: Sal_exi

SCROPHULARIACEAE

- Mimulus* sp.: Mim_spe
Verbascum thapsus: Ver_tha
Veronica anagallis-aquatica (*Veronica catenata*): Ver_ana
Veronica peregrina var. *xalapensis* (*V. peregrina* ssp. *xalapensis*): Ver_per

TAMARICACEAE

- # *Tamarix ramosissima*: Tam_ram

TYPHACEAE

- # *Typha latifolia*: Typ_lat
Typha sp.: Typ_spe

ULMACEAE

- # *Celtis reticulata*: Cel_ret

URTICACEAE

- Urtica dioica*: Urt_dio

VERBENACEAE

- Verbena bracteata*: Ver_bra
-

Cover Type Definition

We identified three major cover types from the TWINSpan classification: xeric *Bro_tec/Het_vil*, mesic-xeric *Equ_hye/Poa_com*, and mesic-hydric *Agr_sto/Eut_occ* (Fig. 18). The cover type identification process, using TWINSpan output, is summarized in Table 4. Detailed plot-by-species output from TWINSpan is presented in Table 5. In addition to the cover types derived from the sampled area, we defined an Open Water type to represent the unvegetated area beyond the streamward, lower boundary of the study bars. Several of the individual vegetation plots on the Downstream, River Right bar are shown in Fig. 19, along with their respective cover type designations. The general areas occupied by the various cover types are shown on Figs. 20-24 for each of the bars.

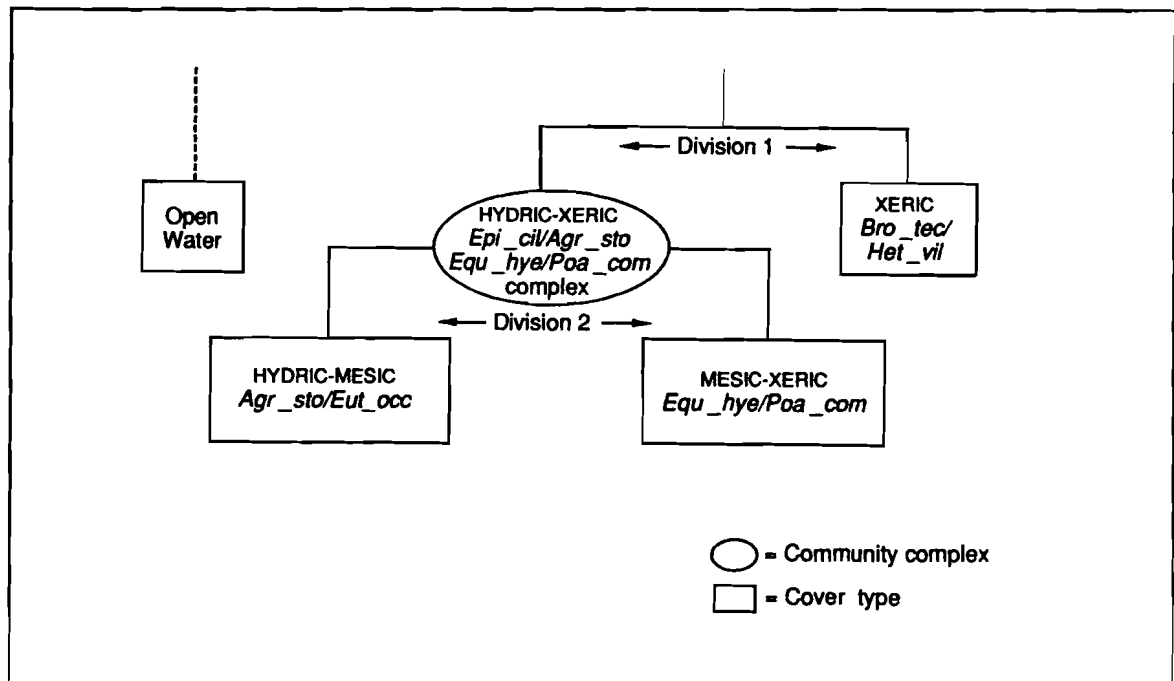


Fig. 18. Schematic depiction of cover-type classification.

Table 4. *TWINSPAN classification outline.*

Classification unit	Moisture regime	Dominant species (% occurrence)	Vegetation description	Classification criteria
Bro_tec/Het_vil	Xeric	Bro_tec (87) Het_vil (80) Spo_cry (73)	Low to medium height grasses and herbs	Distinguished from "Epi_cil/Agr_sto;Equ_hye/Poa_com Complex" by Presence of Het_vil, Bro_tec, Spo_cry Absence of Agr_sto, Eut_occ, Poa_com
"Epi_cil/Agr_sto; Equ_hye/Poa_com Complex"	Hydric-Xeric		Composed of Equ_hye/Poa_com and Agr_sto/Eut_occ types	Distinguished from Bro_tec/Het_vil by above criteria
Equ_hye/Poa_com	Mesic-Xeric	Poa_com (90) Equ_hye (90) Agr_sto (77) Eut_occ (75)	Medium to tall grasses and herbs	Distinguished from Agr_sto/Eut_occ by Presence of Equ_hye Absence of Ele_pal, Epi_cil, Poa_pal
Agr_sto/Eut_occ	Hydric-Mesic	Agr_sto (100) Eut_occ (96) Ele_pal (72) Pha_aru (72) Poa_com (64) Poa_pal (60) Epi_cil (60)	Low to tall herbs and grasses	Distinguished from Equ-Hye/Poa_com by above criteria

[illegible]

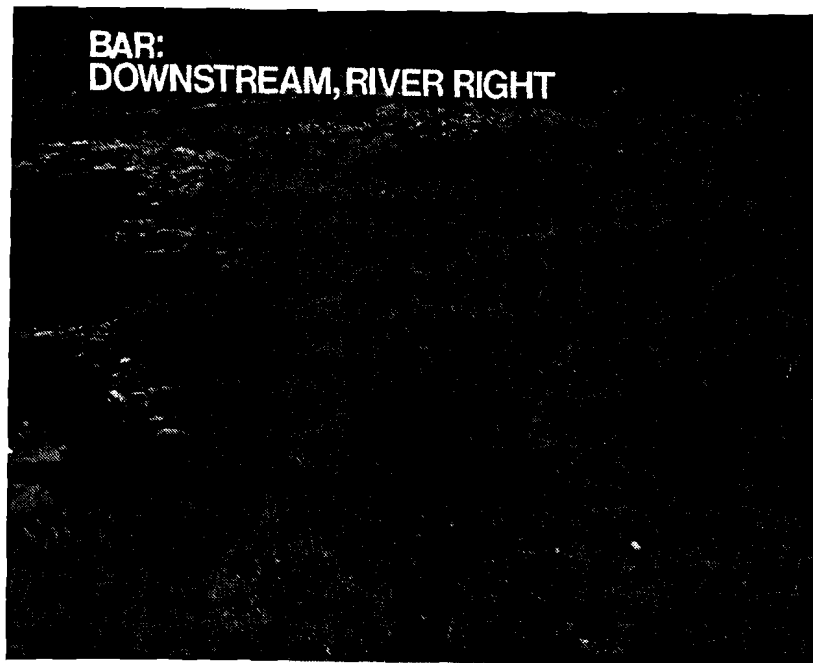


Fig. 19. Selected individual plots on Downstream, River Right bar.

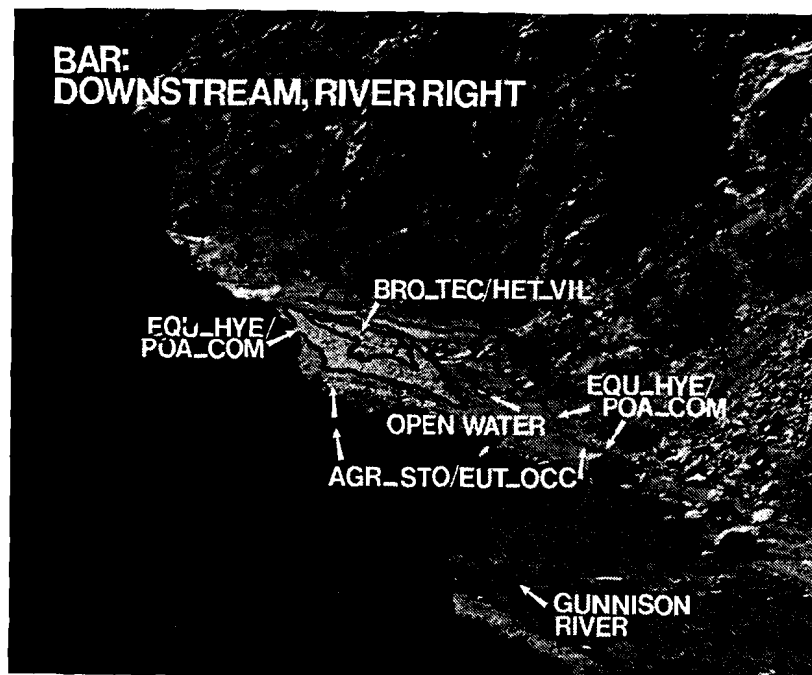


Fig. 20. General areas occupied by cover types on Downstream, River Right bar.

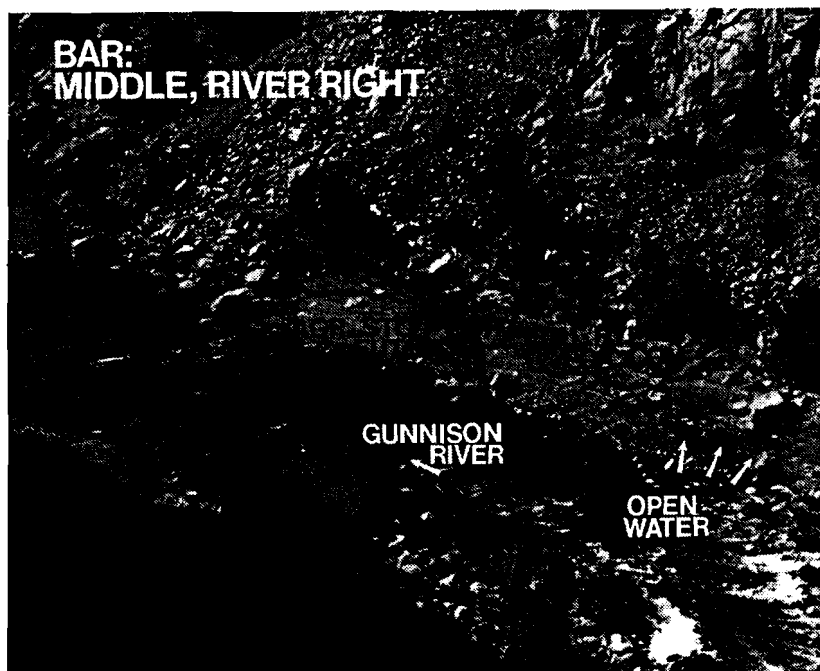


Fig. 21. General areas occupied by cover types on Middle, River Right bar.



Fig. 22. General areas occupied by cover types on Middle, River Left bar.

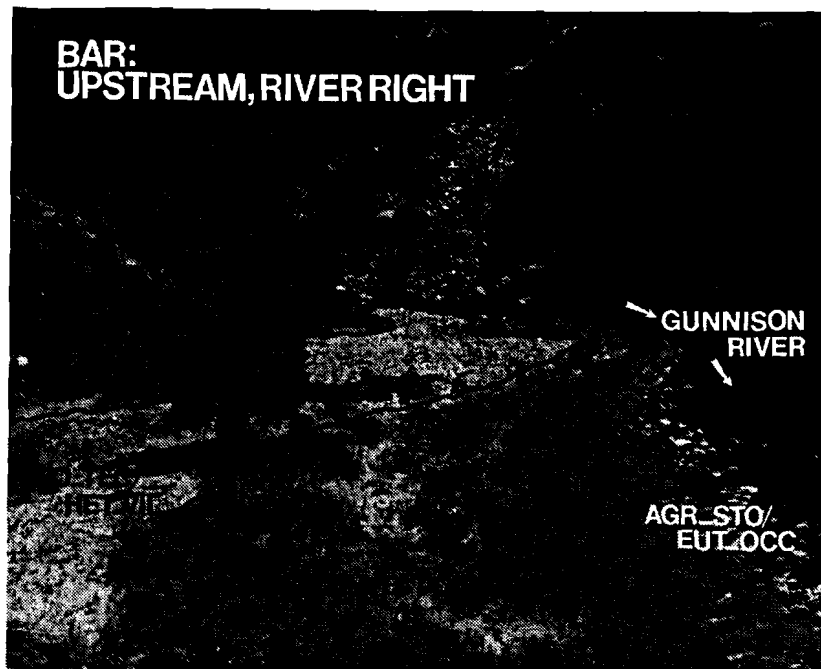


Fig. 23. General areas occupied by cover types on Upstream, River Right bar.

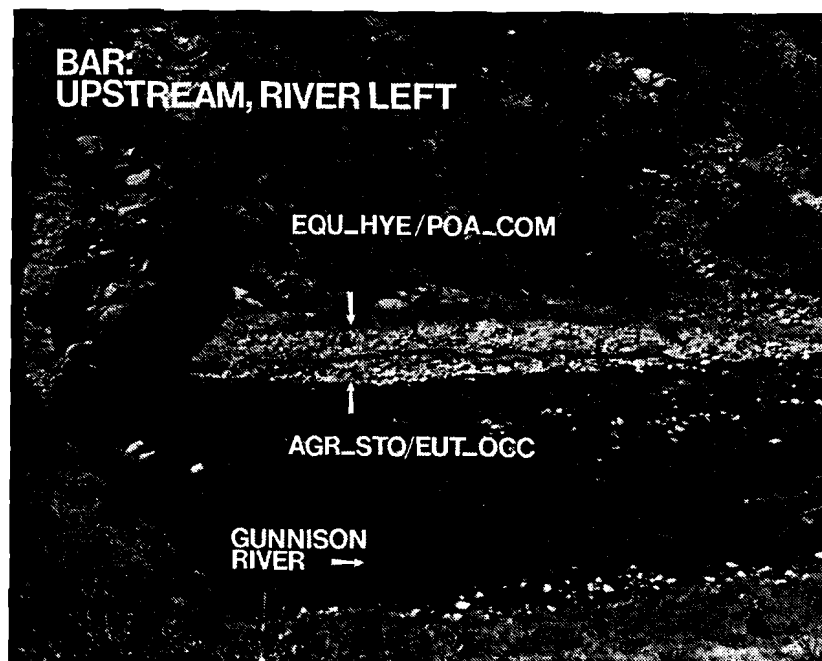


Fig. 24. General areas occupied by cover types on Upstream, River Left bar.

The three TWINSpan cover types differed significantly in the measured environmental variables (Table 6), suggesting that floristic differences across cover types are related to environmental gradients. The floristics, environmental conditions, and general characteristics of the cover types are summarized in Table 7. Cover types are identified by a moisture regime descriptor (e.g., xeric), followed by the names of the dominant species. The complete sets of indicator and preferential species for each cover type are listed in Appendix 3.

Table 6. *Wilcoxon scores and Kruskal-Wallis (Chi square approximation) test of differences in environmental variables across cover types. The Open Water type is excluded.*

Environmental variables	Wilcoxon rank sums by cover type (Observed / Expected)			Chi Square	Probability (p > Chi Square)
	Agr_sto/Eut_occ	Equ_hye/Poa_com	Bro_tec/Het_vil		
Hydroperiod	5362/3375	3484/4657	119/1012	94.8	0.0001
Cover	3943/3234	4228/4422	474/990	21.5	0.0001
Soil 1	4138/3258	3604/4522	1035/997	20.8	0.0001
Soil 2	2020/2408	3297/3192	898/616	12.0	0.0024

Xeric *Bro_tec/Het_vil*

This cover type consists of xeric grasses and herbs dominated by *Bromus tectorum*, *Heterotheca villosa*, and *Sporobolus cryptandrus*. Vegetative cover of living aboveground material was sparse and was predominantly in the range of 0 to 25%. The substrate consisted primarily of sands, cobbles, and boulders. This cover type was confined to the upper portions of the Upstream, River Right bar (Figs. 10 and 23). This was the driest cover type; its hydroperiod was generally less than 2%.

Table 7. *Physical and biological characteristics of cover types.*

Attributes	Cover types			
	Open Water	Agr_sto/Eut_occ	Equ_hye/Poa_com	Bro_tec/Het_vil
Moisture regime	Aquatic	Mesic-hydric	Mesic-xeric	Xeric
Geomorphic position	Channel and depressions	Overflow channels, and from edges of channel and depressions to low and middle elevations on bars	Middle and upper elevations on gravel and cobble bars	Upper portion of cobble bar
Dominant plants	Unvegetated	Agr_sto, Eut_occ, Epi_cil, Ele_pal, Pha_aru, Poa_pal, Poa_com	Equ_hye, Poa_com, Agr_sto, Eut_occ, Muh_rac	Bro_tec, Het_vil, Spo_cry
Physiognomy	Open water	Short to tall herbs and grasses	Medium to tall grasses and herbs	Short to medium grasses and herbs
Cover ^a				
Mean	--	2.8	2.4	1.5
Range	--	2 - 4	2 - 3	1 - 2
(% in range)	--	(91)	(75)	(87)
Soil 1 (predominant)	--	Primarily boulders with fractions of sands and organic matter	Organic matter, sands, and boulders	Sands and cobbles
Soil 2 (secondary)	--	Silts, organic matter, and sands	Sands and organic matter	Sands and cobbles
% of time inundated				
Mean	--	62	12	1
Range	> 98	50 - 89	0 - 18	0 - 1
(% in range)	(100)	(82)	(80)	(93)

^aCover codes: 1 = 0-25%, 2 = 25-50%, 3 = 50-75%, 4 = 75-100%

Mesic-Xeric *Equ_hye/Poa_com*

This cover type consisted of mesic to xeric herbs and grasses dominated by *Equisetum hyemale*, *Poa compressa*, *Agrostis stolonifera*, *Muhlenbergia racemosa*, and *Euthamia occidentalis*. Vegetative cover of living aboveground material had a broad range of values, but was primarily in the range of 25 to 75%. The substrate consisted primarily of organic matter and sands; however, some plots were dominated by boulders. This cover type was found typically on middle and upper elevation gravel and cobble bars. Generally, this was a relatively dry and infrequently inundated cover type. Hydroperiods ranged from approximately 2 to 60%, with most plots in the range of 2 to 20%.

Mesic-Hydric *Agr_sto/Eut_occ*

This cover type consists of mesic herbs and grasses dominated by *Agrostis stolonifera*, *Euthamia occidentalis*, *Eleocharis palustris*, *Phalaris arundinacea*, *Poa palustris*, *Epilobium ciliatum*, and *Poa compressa*. Vegetative cover of living aboveground material was highly variable, ranging from 25 to 100%. However, most plots had from 50 to 75% cover. The substrate was also variable and consisted primarily of cobbles and boulders with large fractions of silt, sand, and organic matter. This was the wettest vegetated cover type and was found from the channel edge and the edge of off-channel pools, up to low and middle elevation gravel bars. This cover type was inundated frequently. Although the overall range of inundation frequencies was broad, approximately 82% of the plots had hydroperiods from 50 to 89%.

Open Water

A final cover type was defined to account for the open water found in the river channel and in off-channel pools at the edges of the study sites. This cover type represented unsampled sites devoid of terrestrial riparian vegetation and inundated at the time of sampling. Based on stage-discharge information, this cover type was assigned a hydroperiod of greater than 98%.

Woody Vegetation

Tree Rings

For each of the three cored trees, significant positive correlations existed between ring widths of replicate cores (Table 8). Standardized ring widths are plotted in Figs. 25 and 26.

Table 8. *Pearson correlations of standardized ring widths from replicate cores.*

Tree	Correlation coefficient (R)	Probability
A1	0.554	0.014
A2	0.722	0.043
T1	0.870	< 0.001

Tree A1 (*Acer negundo*) dated to 1968, although only one core contained rings for the years 1968-1971. Neither core passed through the center. However, based on the patterns of the innermost rings and the average growth of the last five rings, it was estimated that the cores were within 1-2 rings of the center. Given that the cores were taken 30 cm above the ground, this tree was probably established in the mid-1960's.

Tree A2 (*Acer negundo*) dated to 1983 for both cores. Both cores passed through the center of the stem. Young trees typically do not produce distinct transitions between spring and summer wood and the two innermost rings of this tree were difficult to discern. The innermost ring was considered to be a true ring for both cores. If this ring is in fact false, then this tree was established in 1984.

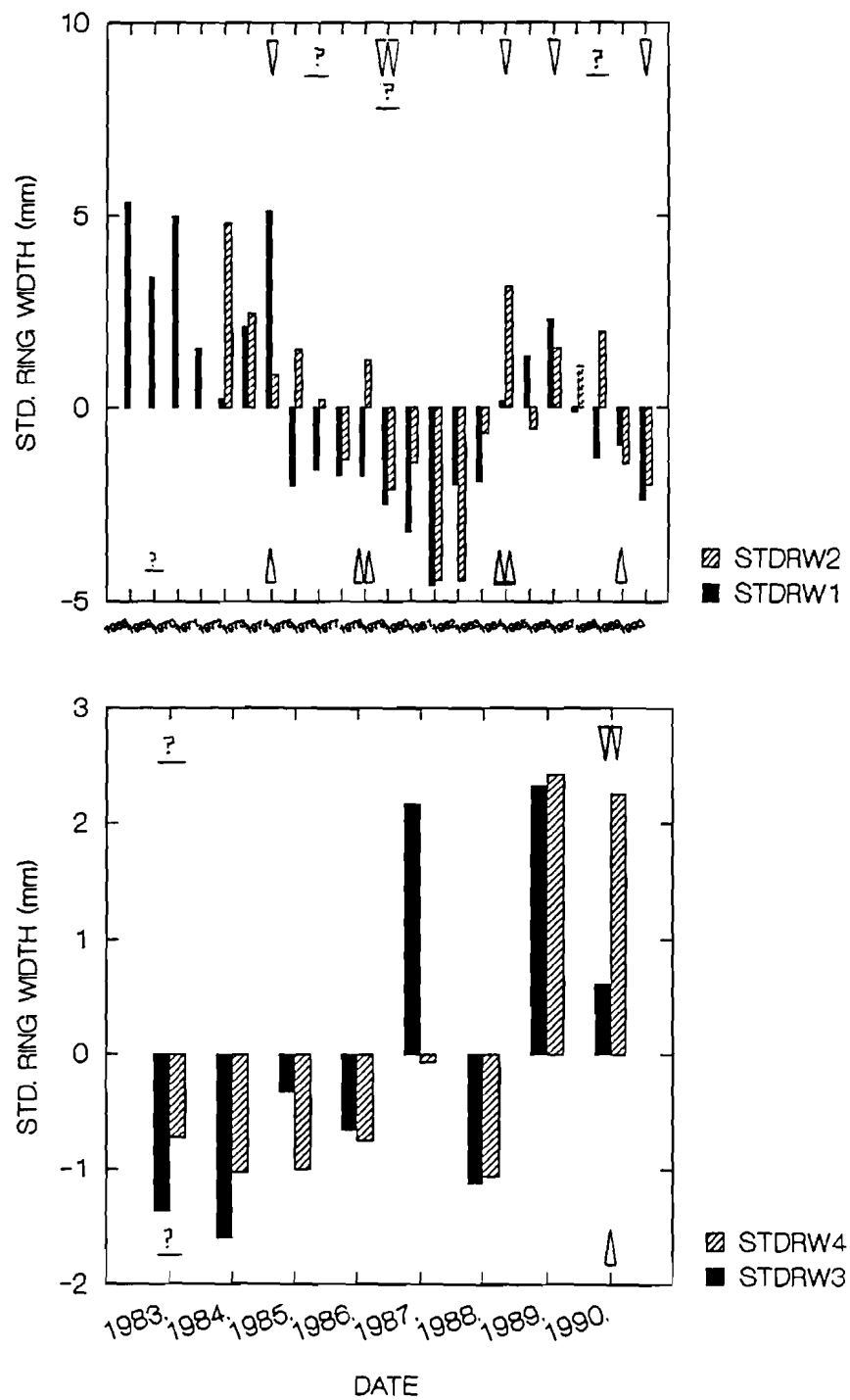


Fig. 25. Standardized ring widths from *Acer negundo*. STD. RING WIDTH (mm) & 2 are from A1, STD. RING WIDTH (mm) & 4 are from A2. Triangles indicate false rings, question marks indicate questionable true rings.

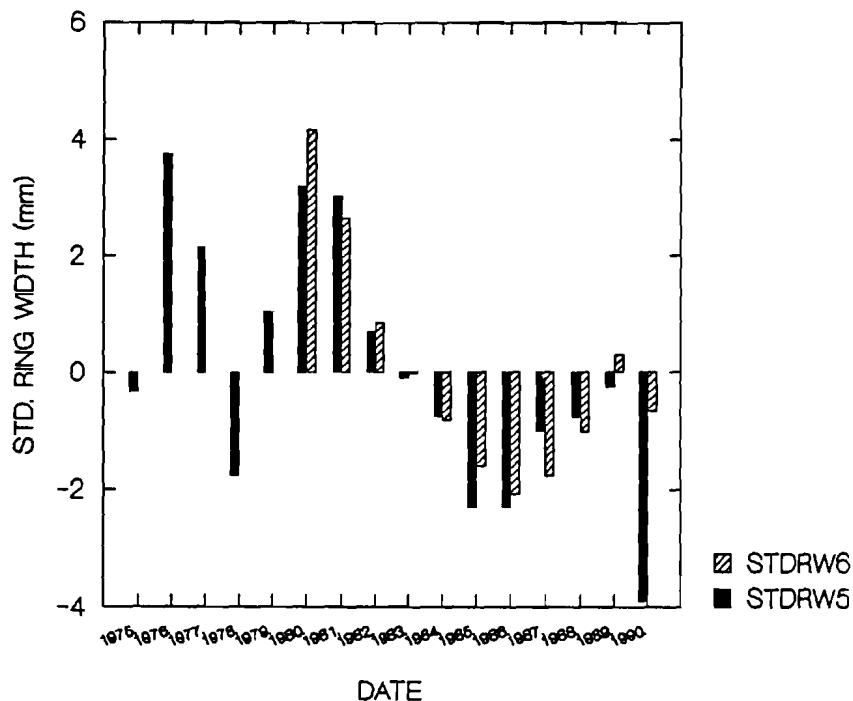


Fig. 26. Standardized tree ring widths from *Tamarix ramosissima*. STDRW5 & 6 are from T1. Triangles indicate false rings, question marks indicate questionable true rings.

Tree T1 (*Tamarix ramosissima*) showed no evidence of false rings and there was high correlation between cores. The lower core commences at 1975; the fact that the cores were taken at different heights above the ground accounts for the 5-year difference in the age of the cores. Both cores were determined to have passed through or directly adjacent to the center of the stem. The position of the lowest core, 30 cm above the ground, and the growth rate during the innermost years suggest that this tree was established in the period between the late 1960's and the early 1970's.

Woody Species Distribution

The two most abundant woody species within the study reach were box elder (*Acer negundo*) and saltcedar (*Tamarix ramosissima*). Sandbar willow

(*Salix exigua*), a shrub, was less abundant. Box elder was the only woody species with substantial recent reproduction (individuals less than 0.6 m tall).

Woody species of different size classes were distributed in three zones generally corresponding to the three cover types: a low area corresponding to the hydric-mesic *Agr_sto/Eut_occ* cover type and occupied by large numbers of box elder shorter than 2 feet, a middle area corresponding to the mesic-xeric *Equ_hye/Poa_com* cover type and occupied by box elder and saltcedar 2-10 feet tall, and a discontinuous fringe along the base of the canyon wall containing 2-30 foot tall box elders, and sometimes saltcedar (see Figs. 20 and 23). The clear spatial separation of size classes along the hydroperiod gradient is illustrated for box elder in Fig. 27.

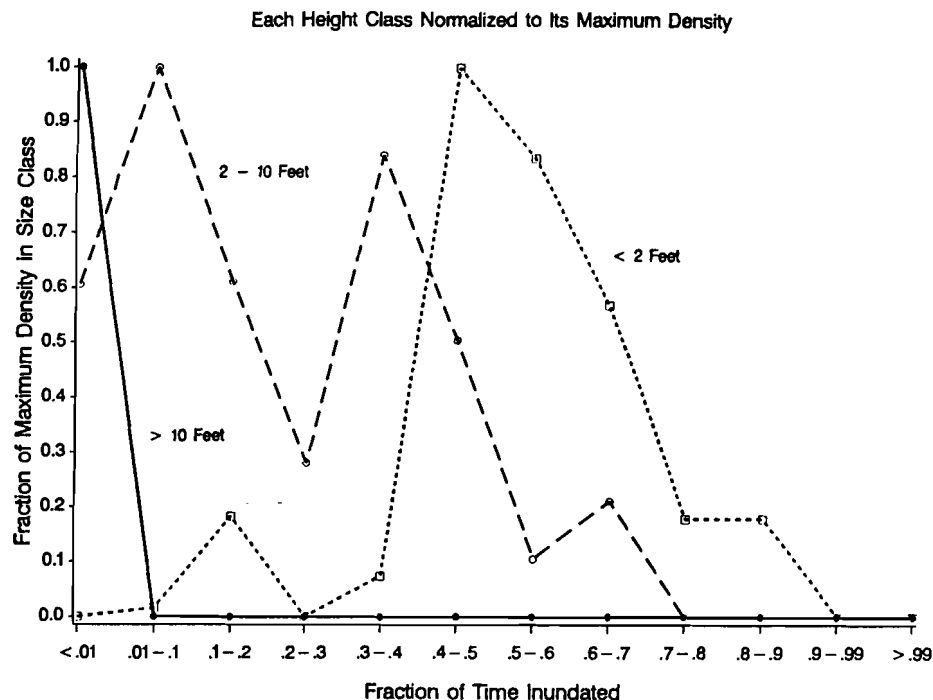


Fig. 27. Hydroperiod distribution of *Acer negundo* by size class.

This pattern is consistent with the hypothesis that establishment and persistence of woody vegetation in the study reach are determined largely by the sequence of hydrologic conditions. In the low area, seedlings established before 1986 were removed by the high flows of 1983, 1984, 1985, and 1986, all of which exceeded 4,000 cfs. The consistently low flows since 1987 have

allowed establishment of many box elders currently less than 2 feet tall. Examination of two of these box elders indicated that they were less than 3 years old. The absence of saltcedar and sandbar willow in this zone may be explained in part by seed size. Box elder has a relatively large seed with sufficient reserves to penetrate the layer of herbaceous foliage and litter in this zone. Saltcedar and sandbar willow both have small seeds that become successfully established only on bare substrate exposed by floods. Additionally, box elder has an abundant seed source from trees growing on talus slopes that descend from small side canyons to the river floodplain at the canyon bottom.

The box elders and saltcedars in the middle area were established on bare sediment following the spring flood of 1984. Individuals less than 2 feet tall were scarce in this zone at the time of sampling, probably because of low soil moisture associated with low flows in the last few years (Fig. 7). One box elder (A2) in this zone was aged and found to have established in 1983 or 1984. Trees in this zone that had become established prior to 1984 were removed by this flood, which peaked at 10,100 cfs. *The relative scarcity of sandbar willow in this zone may result in part from the timing of the 1984 flood.* Sandbar willow seed is produced in June; we observed individuals in fruit on June 18-19, but not July 18-31. Germination percentages of willow (*Salix*) seeds decrease rapidly over time, with seeds remaining viable for as little as one week (Brinkman 1974). The flood of 1984 did not subside below this zone until well into July. The lateness of the flood combined with the small population of adults may have resulted in a limited amount of viable seed present after the flood. Prior to the floods of 1983 and 1984 the most recent flood exceeding 3,500 cfs was in 1971. It is likely that the floods of 1983 and 1984 removed trees that were up to 12 years old.

The discontinuous fringe of larger box elder at the upper bar edges included individuals established following the 1984 flood and individuals that survived that flood. Trees in this fringe zone were protected from flood damage by their high relative elevation and their proximity to large boulders and the canyon wall. In addition, these trees were often rooted in angular talus material that the river had been unable to move from the point of introduction.

Only one box elder over 10 feet tall occurred streamward of this fringe. This tree (A1) was standing near the highest point of the highest bar in the study reach (Upstream, River Right). Scattered box elders occur above the maximum stage of the largest recorded flood along the edges of talus slopes on the lower canyon walls. In a trip down the canyon in 1934, Warner and Walker (1972) describe box elder as "... the prevalent tree of the canyon bottom, growing on the small benches and sandy places along the river bed." Therefore, even before construction of dams some box elders survived all floods and served as a seed source for new cohorts.

On the Middle, River Right and Left bay, and Downstream, River Right bars, the discontinuous fringe zone did not include any saltcedar. On the Upstream, River Left bar, this zone included a few saltcedar 2-10 feet tall. On the Upstream, River Right bar, this zone included many saltcedar 2-10 feet tall and a few saltcedars larger than 10 feet including the largest saltcedar in the study reach (27.5 feet in height). Coring indicated that this large saltcedar (T1) had become established in the late 1960's or early 1970's. The scarcity of large saltcedar probably has two causes. First, saltcedar is limited to the canyon bottom. Unlike box elder, it does not occur on talus slopes. Therefore, a flood that scours the entire canyon bottom could remove all saltcedars. The flood of 1958 which peaked at over 16,000 cfs may have been such an event. Second, saltcedar is an Eurasian introduction that was uncommon in the west until the 1920's (Everitt 1980). The patchy occurrence of saltcedar and the absence of large individuals may indicate that this species is a recent arrival with an increasing population in this part of the canyon.

The distribution of trees on the canyon bottom may be summarized as follows: (1) trees >10 feet in height date back to the early 1960's, roughly corresponding with cessation of historically highest peak flows (Fig. 2); (2) trees 2-10 feet in height date back to the high flow years of 1983 and 1984; and (3) trees <2 feet are 3 years old and were established in the period of relatively constant flow since 1987 (Figs. 2 and 7).

Future Woody Vegetation

Woody species were included in the TWINSpan-based cover types and thus are included as components of cover type changes estimated by the alternatives

analysis presented in the next section. However, the distributions of woody species like box elder are more related to specific flood events than to an aggregated measure of hydroperiod. The episodic nature of this relationship and the long-lived nature of trees means that our model's prediction of the responses to future changes in flow is less clear for individual tree species than for cover types based largely on herbaceous species composition.

However, some general comments on the future distribution of box elder and saltcedar can be made based on the observed distribution of stems and the historical hydrograph. The following summary should thus be considered as a qualification of the more aggregated results from the alternatives analysis based on cover types:

- (1) If relatively low flows, like those observed from 1988 through 1990, continue, then box elder stems of all size classes will continue to grow.
- (2) If future peak flows are intermediate between the low values of 1988 through 1990 and the high values of 1962-1965, 1970, and 1983-1984, then trees <2 feet in height will be removed and the remaining trees will continue to grow.
- (3) If future flows are high, including >10,000 cfs events such as occurred in 1962-1965, 1970, and 1983-1984, then trees <2 and 2-10 feet will likely be eliminated and trees >10 feet will continue to grow. It is also likely that trees will reestablish in similar densities and in similar hydraulic positions as those that established in 1984 following floods $\geq 10,000$ cfs.

Decreases in the magnitude, frequency, and duration of future floods would be expected to lead to further encroachment of trees into the channel, but detailed predictions of this response are beyond the scope of our analysis and would generally have to be based on specific, long-term sequences of future hydrologic events. We observed one recently abandoned beaver house in the study reach between the Middle and Lower, River Right bars. Most of the box elder and saltcedar in the middle area of the bars had been cut back by beavers. Some trees had been killed. Any prediction of the future woody vegetation is contingent on the number and distribution of beaver. Finally,

there is evidence to suggest that saltcedar is spreading along the canyon bottom in the Black Canyon of the Gunnison National Monument.

Alternatives Analysis

Calibration

The direct gradient assessment model was applied to the 13 hydrologic alternatives identified in Table 2 to estimate the proportional areal extent of cover types under each hydrologic alternative. The flow exceedance curves for the hydrologic alternatives, along with the 71-89 Mean Daily Flow historical regime, are depicted in Figs. 28-31. Summary statistics for the hydrologic alternatives are presented in Table 9. The flow scenarios were developed largely to explore potential responses to water development. Thus, it is not surprising that they generally make the hydrologic regime drier and more stable. The Power Generation alternative increases the mean flow, but dramatically reduces the variability and peak flow. The two moving average regimes have approximately the same mean flow as the 71-89 reference regime. All the other alternatives have lower mean flow, although alternatives that reduced only very high flows (e.g., 50% 71-89 >2,000) or combined general flow reduction with a high minimum flow (e.g., 80% 71-89, 600) produce relatively slight reductions in mean flow.

All the alternatives decrease flow variability in terms of standard deviation (Table 9). The flow exceedance curves and percentile table entries reveal substantial differences in how the alternatives change the distribution of flows. The 50% and 80% 71-89 alternatives produce comprehensive reductions in mean, peak, minimum, and median flows, as well as in flow variability. Two alternatives, 50% 71-89 >1,500 and 50% 71-89 >2,000, modify only higher flows, producing lower mean flow and peak flow but leaving the median and lower percentile flows unchanged. Alternatives that combine a general flow reduction with a minimum flow (e.g., 80% 71-89, 300 min) reduce higher flows while increasing lower flows. The percentile at which the effect shifts from increase to decrease is below the median for all these alternatives (i.e., the median flow goes down whereas the 5th percentile flow goes up in all of these regimes).

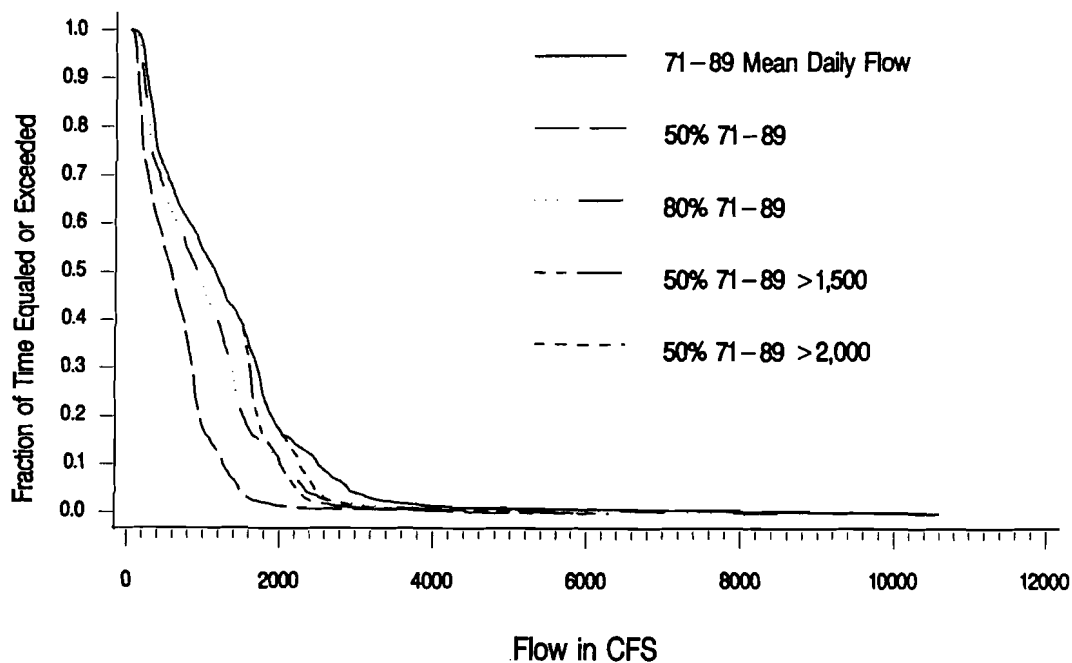


Fig. 28. Flow exceedance curves for selected hydrologic alternatives: 71-89 Mean Daily Flow; 50% 71-89; 80% 71-89; 50% 71-89 >1,500; and 50% 71-89 >2,000.

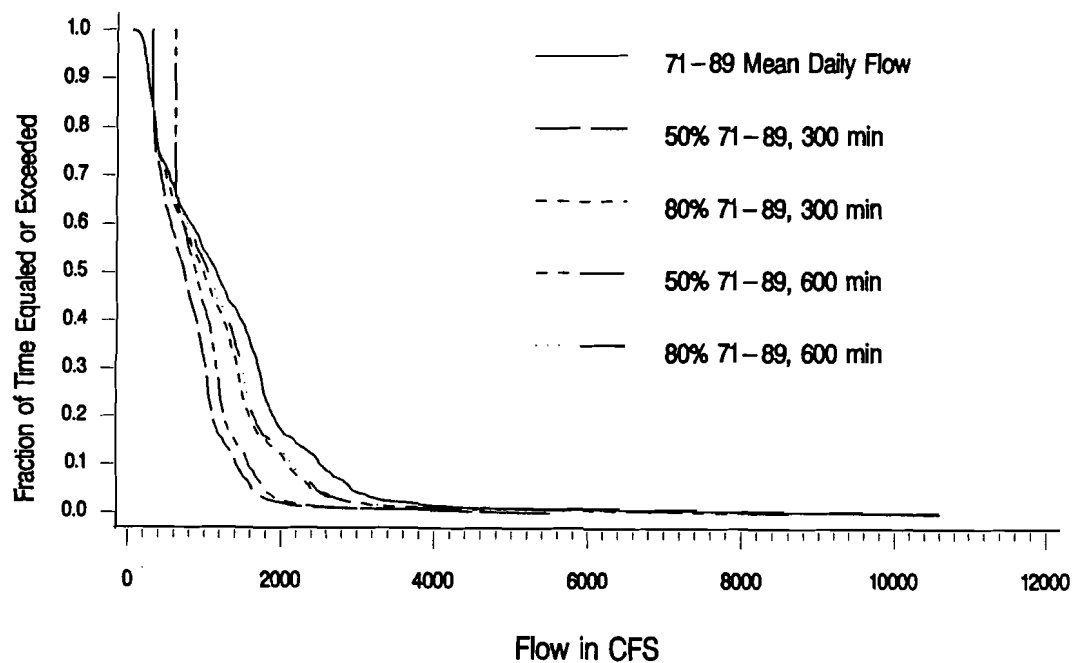


Fig. 29. Flow exceedance curves for selected hydrologic alternatives: 71-89 Mean Daily Flow; 50% 71-89, 300 min; 80% 71-89, 300 min; 50% 71-89, 600 min; and 80% 71-89, 600 min.

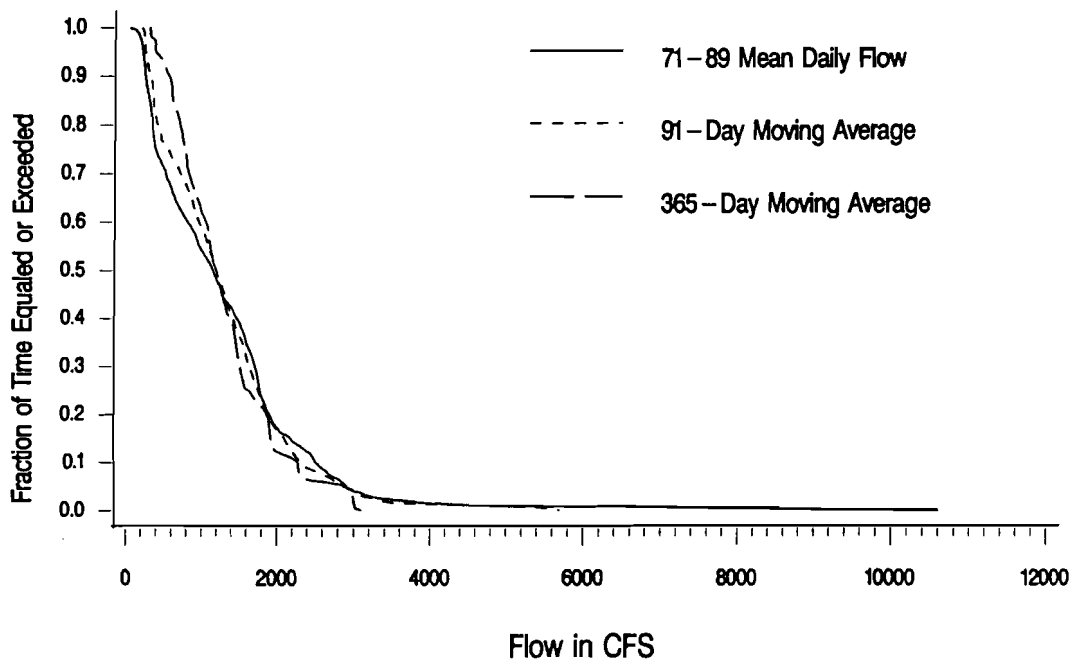


Fig. 30. Flow exceedance curves for selected hydrologic alternatives: 71-89 Mean Daily Flow; 91-day Moving Average; and 1-year Moving Average.

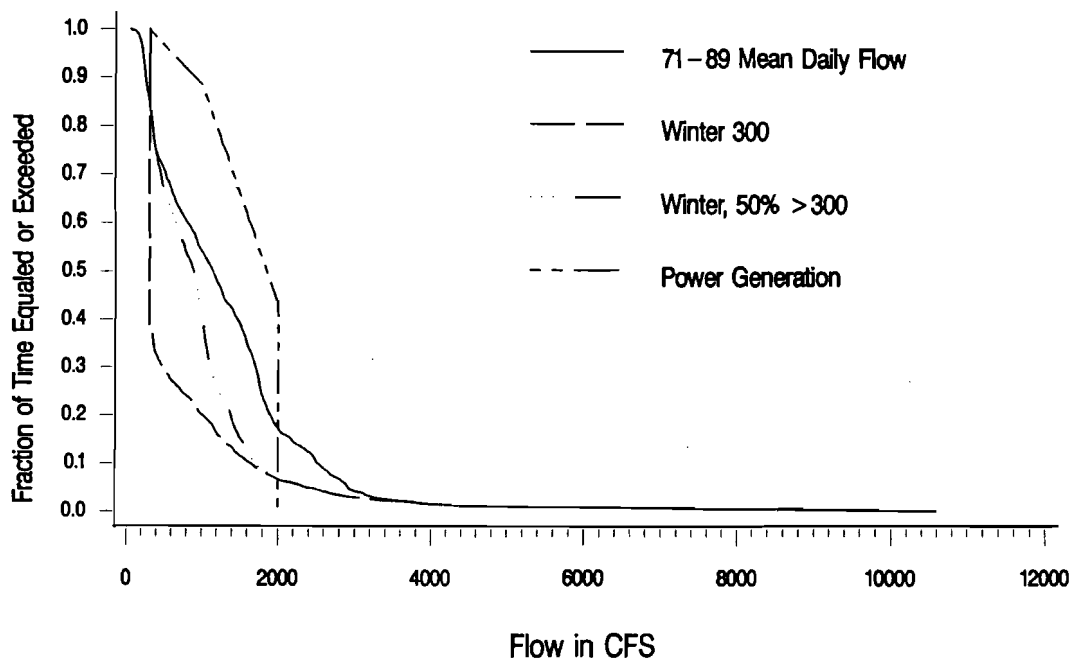


Fig. 31. Flow exceedance curves for selected hydrologic alternatives: 71-89 Mean Daily Flow; Winter 300; Winter, 50% >300; and Power Generation.

Table 9. *Summary statistics of hydrologic regimes.*

Regime	n	Mean	Standard deviation	Percentiles						
				0 (minimum)	5	20	50 (median)	80	95	100 (maximum)
71-89 Mean Daily Flow	6,940	1,280	1,085	37	206	342	1,140	1,890	2,900	10,600
50% 71-89	6,940	641	543	18	103	171	570	945	1,450	5,300
80% 71-89	6,940	1,024	868	30	165	274	912	1,510	2,320	8,480
50% 71-89 >1,500	6,940	1,131	761	37	206	342	1,140	1,700	2,200	6,050
50% 71-89 >2,000	6,940	1,198	842	37	206	342	1,140	1,890	2,450	6,300
50% 71-89, 300 min	6,940	797	537	300	300	321	720	1,100	1,600	5,450
80% 71-89, 300 min	6,940	1,094	858	300	300	334	972	1,570	2,380	8,540
50% 71-89, 600 min	6,940	987	504	600	600	600	870	1,250	1,750	5,600
80% 71-89, 600 min	6,940	1,218	805	600	600	600	1,030	1,630	2,440	8,600
91-day Moving Average	6,850	1,283	885	191	240	409	1,180	1,880	2,860	5,700
1-year Moving Average	6,576	1,284	662	297	379	703	1,180	1,850	2,910	3,100
Winter 300	6,940	714	985	300	300	300	300	997	2,330	10,600
Winter, 50% >300	6,940	1,002	947	300	300	334	886	1,380	2,337	10,600
Power Generation	365	1,352	605	300	300	1,000	1,000	1,000	2,000	2,000

The moving average regimes also decrease flow variability by increasing low flows and decreasing high flows. In these regimes, sites that were rarely inundated become drier (inundated less frequently) and sites that were frequently inundated become wetter (dry less frequently). The Winter 300 and Winter, 50% >300 alternatives stabilize low flows, but have no effect on the highest spring and summer flows. Finally, the Power Generation alternative strongly reduces high flows and flow variability, while actually increasing the average flow and thus the total discharge through the Black Canyon.

Stage-discharge relationships for the four hydraulic cross-sections are depicted in Fig. 32. The relationship of cover types to hydroperiod used to calibrate the model was determined from the sampled distribution of cover types in relation to the historical 71-89 Mean Daily Flow hydrologic regime (Fig. 33). The xeric *Bro_tec/Het_vil* cover type occurred on only the driest, most infrequently inundated sites and represented a small percentage of total bar area (10.5%). Over half the total bar area (52.6%) was in the mesic-xeric *Equ_hye/Poa_com* cover type occupying intermediate to dry sites. The remaining bar area (36.8%) was in the hydric-mesic *Agr_sto/Eut_occ* cover type occupying a relatively broad range of sites from the wettest vegetated locations to some more xeric sites. Some of the drier sites occupied by *Agr_sto/Eut_occ* may be locations where the hydraulic model overestimated inundating discharge. Localized depressions within the plot and side slope drainage are two sources of such error in using a simplified water surface profile model to estimate conditions at specific plots. The Open Water cover type did not occur in the set of sampled plots, but was defined based on the streamward limit of vegetation in order to support prediction about plots that might become much wetter under some alternative hydrologic regime.

The direct gradient assessment model assumes that the sampled vegetation and defined cover types are an adequate "quasi-equilibrium" expression of the longer term hydrologic regime. It does not require that the vegetation be absolutely constant, but it does require that the cluster of compositions over time at one hydraulic position be distinct from the cluster of compositions at a different hydraulic position. Conditions at the time of sampling were definitely dry relative to the overall range of conditions in the 1971-1989 hydrologic record. Since the calibration was made during a period of low flow, the model will tend to place cover types at incorrectly high hydroperiods. The magnitude of the error will depend on the flow conditions

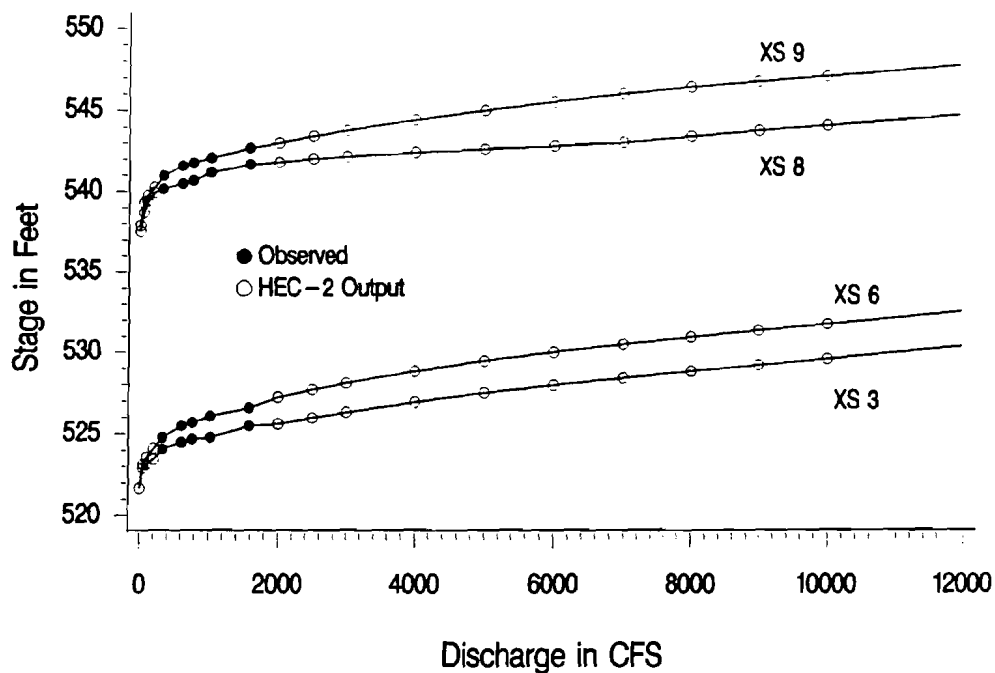


Fig. 32. Stage-discharge relationships for hydraulic cross sections.

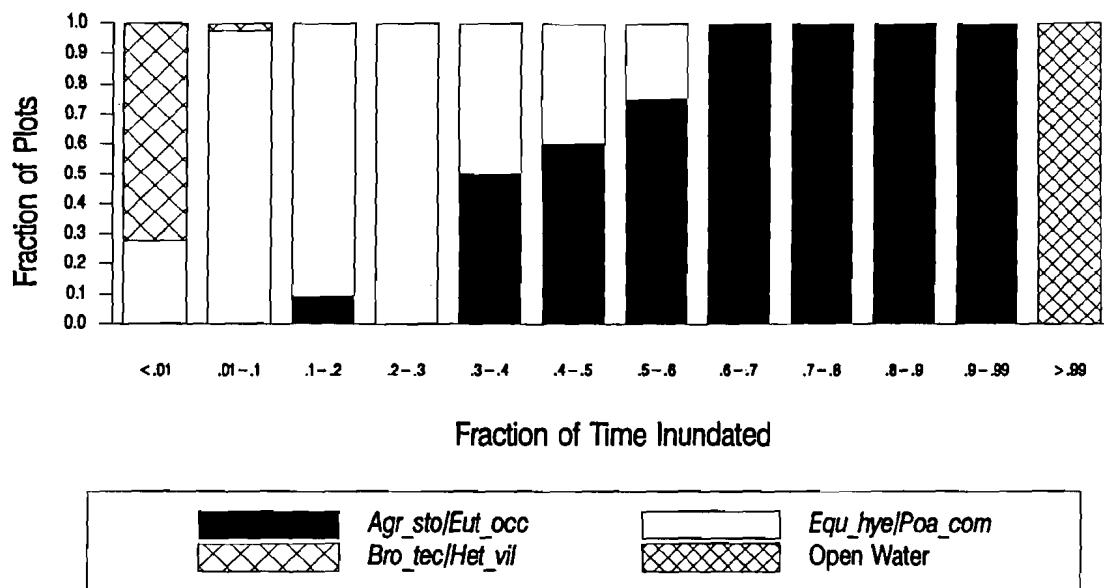


Fig. 33. Relative distribution of cover types along hydroperiod gradient used to calibrate direct gradient assessment model.

prior to the time in question. This source of error does not affect the relative analysis of alternatives like the ones presented here. However, caution should be exercised when using the model to predict the precise vegetation composition at a specific point in time.

Prediction

Table 10 summarizes the cover type composition for the various alternatives in terms of the fraction of total bar area predicted to be in each cover type. Departure in vegetation composition from that of 1990 is summarized as increases or decreases in the fraction of total bar area in each cover type (Table 11) and as percentage change in the area of each cover type (Table 12). Model output in terms of plots was converted to fraction of total bar area by assuming that the sampled plots were an adequate random sample of the total bar area.

Equ_hye/Poa_com remains the predominant cover type under all the alternatives (Table 10), except for the Winter 300 alternative in which both the wetter *Agr_sto/Eut_occ* (41.1%) and the drier *Bro_tec/Het_vil* (38.0%) exceed *Equ_hye/Poa_com* (16.3%). Only four of the alternatives result in a change of cover types on less than 10% of the total bar area (i.e., the row sum of absolute values in Table 11 is less than 20%). These four alternatives are 80% 71-89; 50% 71-89 >2,000; 80% 71-89, 300 min; and the 91-day Moving Average.

Five of the alternatives produce an increase or decrease in a single cover type corresponding to more than 20% of the total bar area (Table 11). These alternatives with the largest absolute changes in the area of a single cover type are the 50% 71-89; 50% 71-89, 300 min; 50% 71-89, 600 min; Winter 300; and Power Generation. Only the 91-day Moving Average alternative produces relative changes of less than 20% in all cover types.

Seven alternatives have vegetated cover types that increase or decrease by more than 50% of their initial area (Table 12). These alternatives are 50% 71-89; 50% 71-89 >1,500; 50% 71-89, 300 min; 50% 71-89, 600 min; 1-year Moving Average; Winter 300; and Power Generation. Higher low flows result in the Open Water cover type replacing vegetated cover types in the following

Table 10. *Cover type composition of bars under hydrologic alternatives. Rows may not sum to 100% due to rounding error.*

Hydrologic alternative	Cover types (% of total bar area)			
	Open Water	<i>Agr_sto/Eut_occ</i>	<i>Equ_hye/Poa_com</i>	<i>Bro_tec/Het_vil</i>
71-89 Mean Daily Flow	0.0	36.8	52.6	10.5
50% 71-89	0.0	17.2	48.2	34.6
80% 71-89	0.0	29.9	55.8	14.4
50% 71-89 >1,500	0.0	34.9	40.8	24.4
50% 71-89 >2,000	0.0	36.4	44.1	19.6
50% 71-89, 300 min	2.3	18.5	46.7	32.5
80% 71-89, 300 min	2.3	28.7	55.3	13.8
50% 71-89, 600 min	13.5	14.0	42.7	29.8
80% 71-89, 600 min	13.5	19.6	53.0	13.8
91-day Moving Average	0.0	36.0	52.3	11.7
1-year Moving Average	2.3	33.4	36.9	27.5
Winter 300	4.5	41.1	16.3	38.0
Winter, 50% >300	2.3	23.7	63.2	10.8
Power Generation	4.5	41.1	16.3	38.0

Table 11. *Vegetation departure under hydrologic alternatives as percent of total bar area.*

Hydrologic alternative	Cover type change from sampled condition (% of total bar area)			
	Open Water	<i>Agr_sto/Eut_occ</i>	<i>Equ_hye/Poa_com</i>	<i>Bro_tec/Het_vil</i>
71-89 Mean Daily Flow	0.0	0.0	0.0	0.0
50% 71-89	0.0	-19.7	-4.4	24.1
80% 71-89	0.0	-7.0	3.1	3.9
50% 71-89 >1,500	0.0	-2.0	-11.9	13.8
50% 71-89 >2,000	0.0	-0.5	-8.6	9.1
50% 71-89, 300 min	2.3	-18.3	-5.9	22.0
80% 71-89, 300 min	2.3	-8.2	2.6	3.3
50% 71-89, 600 min	13.5	-22.9	-9.9	19.2
80% 71-89, 600 min	13.5	-17.2	0.4	3.3
91-day Moving Average	0.0	-0.8	-0.3	1.1
1-year Moving Average	2.2	-3.4	-15.8	16.9
Winter 300	4.5	4.3	-36.3	27.5
Winter, 50% >300	2.3	-13.1	10.6	0.3
Power Generation	4.5	4.3	-36.3	27.5

Table 12. *Vegetation departure under hydrologic alternatives as percent change in each cover type. A "+" indicates that the change was positive, but that the initial area of the cover type was zero.*

Hydrologic alternative	Cover type change from sampled condition (% of each cover type)			
	Open Water	<i>Agr_sto/Eut_occ</i>	<i>Equ_hye/Poa_com</i>	<i>Bro_tec/Het_vil</i>
71-89 Mean Daily Flow	0.0	0.0	0.0	0.0
50% 71-89	0.0	-53.4	-8.4	229.1
80% 71-89	0.0	-19.0	5.9	36.6
50% 71-89 >1,500	0.0	-5.4	-22.5	131.4
50% 71-89 >2,000	0.0	-1.3	-16.3	86.0
50% 71-89, 300 min	+	-49.7	-11.2	208.6
80% 71-89, 300 min	+	-22.2	5.0	31.3
50% 71-89, 600 min	+	-62.1	-18.8	182.8
80% 71-89, 600 min	+	-46.7	0.8	31.1
91-day Moving Average	0.0	-2.3	-0.6	10.8
1-year Moving Average	+	-9.3	-30.0	160.8
Winter 300	+	11.6	-68.9	261.1
Winter, 50% >300	+	-35.6	20.2	2.4
Power Generation	+	11.6	-68.9	261.1

eight alternatives: 50% 71-89, 300 min; 80% 71-89, 300 min; 50% 71-89, 600 min; 50% 71-89, 600 min; 1-year Moving Average; Winter 300; Winter, 50% >300; and Power Generation.

The 50% 71-89 and 80% 71-89 alternatives are multiplicative reductions in all flows (Tables 2 and 9, Fig. 28). Total bar area in the xeric *Bro_tec/Het_vil* cover type increases in both these alternatives (Table 10), more than doubling the area of this cover type in the 50% 71-89 alternative (Table 12). The systematic flow reductions in these alternatives produce declines in the area of the wettest vegetated cover type, *Agr_sto/Eut_occ*, and mixed results on the intermediate *Equ_hye/Poa_com*. Under a 50% reduction there is a net decrease in *Equ_hye/Poa_com*. However, with only an 80% reduction, there are more former *Agr_sto/Eut_occ* plots becoming drier and shifting to *Equ_hye/Poa_com* than there are *Equ_hye/Poa_com* plots becoming so dry that they shift to *Bro_tec/Het_vil*, resulting in a small net increase in *Equ_hye/Poa_com* area.

The 50% 71-89 >1,500 and 50% 71-89 >2,000 alternatives reduce only those high flows above the respective threshold values (Tables 2 and 9, Fig. 28). These alternatives produce a shift from wetter to drier cover types with increases in *Bro_tec/Het_vil* and decreases in *Agr_sto/Eut_occ* and *Eut_hye/Poa_com* (Table 11). The magnitude of the shift toward drier cover types decreases as the threshold value increases and the regime more closely approximates an unmodified 71-89 Mean Daily Flow distribution. The increase in the xeric *Bro_tec/Het_vil* goes from 24.1% of total bar area under 50% 71-89, to 13.8% under 50% 71-89 >1,500, to 9.1% under 50% 71-89 >2,000 (Table 11).

Four alternatives combine a multiplicative flow reduction (50 or 80%) with a fixed minimum flow (300 or 600 cfs). All of these alternatives produce an increase in the xeric *Bro_tec/Het_vil* cover type, and an increase in the Open Water cover type from the increased low flows, and a net decrease in the hydric-mesic *Agr_sto/Eut_occ* (Table 11). Net changes in the area of mesic-xeric *Equ_hye/Poa_com* are mixed, depending on the balance of area moving in and out of this cover type.

The two alternatives formed by moving average calculations (Tables 2 and 9, Fig. 30) produce decreases in the area of the intermediate *Equ_hye/Poa_com*

and increases in both the drier *Bro_tec/Het_vil* and the wetter *Agr_sto/Eut_occ* and Open Water cover types (Table 11). As the extreme flow events are moderated by a moving average calculation, sites that are frequently inundated become wetter (dry even less frequently) and sites that are rarely inundated become drier (inundated even less frequently). Thus, in this case, a systematic reduction in the range of flow conditions towards the middle of the distribution actually increases the dispersion of cover types by producing increases in the area of cover types at the edges of the gradient. Using a longer interval in the moving average (i.e., 365 compared to 91 days) produces a stronger effect.

The Winter 300 alternative establishes a fixed flow of 300 cfs during the winter with a 300 cfs minimum flow throughout the year. The Winter, 50% >300 alternative reduces winter flows in excess of 300 cfs by 50% with a minimum of 300 cfs throughout the year (Tables 2 and 9, Fig. 31). The Winter 300 alternative produces a large increase in the xeric *Bro_tec/Het_vil* cover type, smaller increases in the Open Water and mesic-hydric *Agr_sto/Eut_occ*, and a large decrease in the intermediate *Equ_hye/Poa_com* (Table 11). The Winter, 50% >300 alternative involves a less severe reduction in winter flows and essentially eliminates the increase in area of xeric *Bro_tec/Het_vil* seen under the Winter 300 alternative.

Finally, the Power Generation alternative consists of a combination of three fixed flows (300, 1,000, and 2,000 cfs) producing an average flow of 1,353 cfs. This alternative results in a large increase in the xeric *Bro_tec/Het_vil* cover type, a large decrease in the intermediate *Equ_hye/Poa_com*, and small increases in the wetter *Agr_sto/Eut_occ* and Open Water. However, the rapid fluctuations associated with this type of peaking operation are outside the range of hydrologic conditions used to calibrate the model. Differences in the flow duration curves used in our direct gradient do not fully capture the differences between rapid flow fluctuations and non-rapid natural or regulated hydrographs. Thus, results from the Power Generation alternative, or other hydro-peaking scenarios, are considerably less reliable than those for the other alternatives.

Valuation of the vegetation differences described above and the combination of these values with other attributes of the alternatives are the next steps in an overall framework of water management decisionmaking

(Fig. 8). Although these steps are generally beyond the scope of this analysis, there are several points that should be considered in using our results. First, there are limitations and uncertainty involved in the assessment model. These include specific situations that are poorly represented (e.g., hydropower peaking operations) and more general simplifying assumptions about hydrology, hydraulics, and vegetation dynamics. The model results are best viewed as indications of the direction and magnitude of expected change, rather than precise predictions about the vegetation at any particular time.

Finally, special attention should be given to alternatives involving changes to flow boundaries. This includes both effectively implemented minimum flows and substantial reductions in peak flows. There are several reasons for being concerned about these hydrologic changes with respect to riparian vegetation. Changing the boundaries of the flow distribution creates new zones that are either always inundated or that are never inundated. These zones generally have the highest certainty in model predictions because there are fewer overlapping riparian cover types at the edges of the gradient. Cover types in these zones (e.g., Open Water) are generally the most structurally distinct from other cover types and exhibit little temporal fluctuation because of the constant conditions. In addition, some important establishment and mortality processes of riparian vegetation are episodic. Changing the boundary flows may eliminate the infrequent establishment opportunities in areas that are highly suitable for survival, but not generally suitable for establishment, or may critically reduce the normal resetting influence of episodic flooding.

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Literature Cited

- Bovee, F.D. 1982. A guide to stream habitat analysis using the Instream Flow Incremental Methodology. Instream Flow Information Paper 12. U.S. Department of the Interior, Fish and Wildlife Service, Office of Biological Services. FWS/OBS-82/26. 248 pp.
- Brown, S. 1981. A comparison of the structure, primary productivity, and transpiration of cypress ecosystems in Florida. Ecological Monographs 51:403-427.
- Brinkman, K. 1974. Salicaceae -- Willow family, *Salix* L., Willow. Pages 746-750 in C.S. Schopmeyer, ed. Seeds of woody plants in the United States. U.S. Department of Agriculture, Forest Service. Agriculture Handbook 450. 883 pp.
- Colorado Climate Center. 1984. Colorado average annual precipitation 1951-1980. Colorado State University, Fort Collins. Map.
- EarthInfo. 1991. Hydrodata daily values, West 1, vol. 4. EarthInfo, Boulder, CO. (Compilation of USGS records on optical disc formerly published by US West.)
- Everitt, B.L. 1980. Ecology of saltcedar--a plea for research. Environmental Geology 3: 77-84.
- Franz, E.H., and F.A. Bazzaz. 1977. Simulation of vegetation response to modified hydrologic regimes: a probabilistic model based on niche differentiation in a floodplain forest. Ecology 58:176-183.
- Hansen, W.R. 1987. The Black Canyon of the Gunnison in depth. Southwest Parks and Monuments Association, Tucson. 58 pp.

- Harris, R.R., R.J. Risser, and C.A. Fox. 1985. A method for evaluating streamflow discharge -- plant species occurrence patterns on headwater streams. Pages 87-90 in R.R. Johnson, C.D. Ziebell, D.R. Patton, P.F. Ffolliott, and R.H. Hamre, eds. Riparian ecosystems and their management: reconciling conflicting uses. U.S. Department of Agriculture, Forest Service. General Technical Report RM-120.
- Hill, M.O. 1979. TWINSpan--A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes. Cornell University, Ithaca, NY. 90 pp.
- Hoggan, D.H. 1989. Computer-assisted floodplain hydrology and hydraulics. McGraw-Hill, New York. 518 pp.
- Hupp, C.R., and W.R. Osterkamp. 1985. Bottomland vegetation distribution along Passage Creek, Virginia, in relation to fluvial landforms. Ecology 66:670-681.
- Hydrologic Engineering Center. 1982. HEC-2 water surface profiles, user's manual. U.S. Army Corps of Engineers, Davis, CA.
- Johnson, W.C. 1988. Dams and riparian forest ecosystems. Supplement to K.M. Mutz, D.J. Cooper, M.L. Scott, and L.K. Miller, eds. Restoration, creation and management of wetland and riparian ecosystems in the American West. Rocky Mountain Chapter of the Society of Wetland Scientists.
- Jongman, R.H.G., C.J.F. ter Braak, and O.F.R. van Tongeren, eds. 1987. Data analysis in community and landscape ecology. Pudoc Wageningen Wageningen, the Netherlands.
- Klimas, C.V., C.O. Martin, and J.W. Teaforde. 1981. Impacts of flooding regime modification on wildlife habitats of bottomland hardwood forests in the Lower Mississippi Valley. U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS. Technical Report EL-81-13. 200 pp.

- Lichvar, R. 1987. Riparian vegetation reconnaissance of the Black Canyon of the Gunnison, spring 1987. Mariah Associates, Inc. Prepared for EMANCO, Inc., Houston, Texas.
- Pearlstine, L., H. McKellar, and W. Kitchens. 1985. Modelling the impacts of a river diversion on bottomland forest communities in the Santee River floodplain, South Carolina. *Ecological Modelling* 29:283-302.
- Reed, P.B. 1988. National list of plant species that occur in wetlands: national summary. U.S. Department of the Interior, Fish and Wildlife Service. Biological Report 88(24). 244 pp.
- Reed and Norton. 1963. Title unknown. Excerpt copied as "Appendix C. Algae of Black Canyon of the Gunnison National Monument" and "Appendix D. Vascular plants below high water mark in the Black Canyon of the Gunnison National Monument". National Park Service.
- Rominger, J.M. 1963. Preliminary studies of the agrostology of Black Canyon of the Gunnison National Monument, 1962-1963. Unpublished report to National Park Service.
- Stanford, J.A., and J.V. Ward. 1983. The effects of mainstem dams on physicochemistry of the Gunnison River, Colorado. *In*: V.D. Adams and V.A. Lamarra, eds. Proceedings of the 1981 symposium on the Aquatic Resources Management of the Colorado River Ecosystem. Ann Arbor Science Publishers, Inc., Ann Arbor, Michigan.
- Stanford, J.A., and J.V. Ward. 1985. The effects of regulation on the limnology of the Gunnison River: a North American case history. Pages 467-480 *in* A. Lillehammer and S. Saltveit, eds. Regulated Rivers. Universitetsforlaget As. Oslo, Norway.
- Stokes, M.A., and T.L. Smiley. 1968. An introduction to tree-ring dating. University of Chicago Press. 73 pp.

- Teskey, R.O., and T.M. Hinckley. 1977. Impact of water level changes on woody riparian and wetland communities, vol. 1: plant and soil responses to flooding. U.S. Department of the Interior, Fish and Wildlife Service, Office of Biological Services. FWS/OBS-77/58. 31 pp.
- Ugland, R.C., B.J. Cochran, R.G. Kretschman, E.A. Wilson, and J.D. Bennett. 1989. Water resources data for Colorado, water year 1988, vol. 2. Colorado River Basin. U.S. Geological Survey, Water Resources Division. Water Data Report CO-88-2. Denver, CO.
- U.S. Department of Agriculture. 1982. National list of scientific plant names. U.S. Department of Agriculture, Soil Conservation Service. SCS-TP-159. 1984-455-155/20049.
- U.S. Department of the Interior. 1990. Final Environmental Impact Statement: AB Lateral hydropower facility, Uncompahgre Valley Reclamation Project, Montrose and Delta Counties, Colorado. 2 volumes. U.S. Department of the Interior, Bureau of Reclamation.
- Walker, D.B. 1967. Copyrighted photographs of 1934 trip through Black Canyon of Gunnison. Reproduced in Warner and Walker (1972).
- Warner, M.T., and D.B. Walker. 1972. Through the Black Canyon. Braun-Brumfield, Inc., Ann Arbor, MI. 46 pp.
- Weber, W.A. 1983. Checklist of vascular plants, Black Canyon of the Gunnison National Monument. University of Colorado Museum, Boulder. 35 pp.
- Weber, W.A. 1987. Colorado flora: western slope. Colorado Associated University Press, Boulder. 530 pp.
- Wells, B.W. 1928. Plant communities of the coastal plain of North Carolina and their successional relations. *Ecology* 9:230-242.
- Whittaker, W.H. 1967. Gradient analysis of vegetation. *Biological Reviews* 49:207-264.

Appendix 1. Mathematical outline of reciprocal averaging or two-way weighted averaging (after Jongman et al. 1987).

A. Iterative steps of the algorithm.

1. Start with arbitrary and unequal site scores (x_i).
2. Calculate new species scores (u_k) by weighted averaging of site scores:

$$u_k = \sum_{i=1}^n y_{ki} x_i / \sum_{i=1}^n y_{ki}$$

where: y_{ki} is the abundance of species k at site i .

3. Calculate new site scores (x_i) by weighted averaging of the species scores:

$$x_i = \sum_{k=1}^m y_{ki} u_k / \sum_{k=1}^m y_{ki}$$

4. Standardize site scores (x_i) to a weighted mean of 0 and a variance of 1:

1. Calculate the centroid (z) of the site scores (x_i):

$$z = \sum_{i=1}^n y_{xi} x_i / y_{xx}$$

where: y_{xi} = overall total of site i , and
 y_{xx} = the overall total of sites.

Appendix 1. Concluded.

2. Calculate the dispersion of the site scores (s^2):

$$s^2 = \sum_{i=1}^n y_{xi} (x_i - z)^2 y_{xx}$$

3. Calculate new site score ($x_{i,\text{new}}$):

$$x_{i,\text{new}} = (x_{i,\text{old}} - z/s)$$

5. Stop when the new site scores are close to the site scores of the previous run through the iteration, or else return to Step 2.

NOTE: When the site scores converge, s will equal the eigenvalue, or the value that represents the maximized dispersion of species scores on the ordered axis.

Appendix 2. Distribution of individual species on hydroperiod gradient. Hydroperiod is defined as fraction of time inundated. Class intervals differ from the larger number of classes used in the cover type assessment. Number of plots in each hydroperiod class is given in parentheses.

Species	Fraction of plots with species by hydroperiod class							
	<.01	.01-.1	.1-.2	.2-.4	.4-.6	.6-.8	.8-.99	>.99
(n)	(18)	(42)	(11)	(9)	(26)	(21)	(6)	(1)
<i>Ace_neg</i>	0.11	0.05	0.18	0.22	0.69	0.52	0.17	0.00
<i>Agr_spe</i>	0.06	0.38	0.18	0.22	0.04	0.00	0.00	0.00
<i>Agr_sto</i>	0.11	0.76	0.73	1.00	0.96	1.00	1.00	0.00
<i>Alo_aeq</i>	0.00	0.00	0.00	0.00	0.00	0.19	0.17	0.00
<i>Apo_spe</i>	0.17	0.17	0.36	0.11	0.31	0.19	0.50	0.00
<i>Ari_pur</i>	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Art_lud</i>	0.22	0.19	0.18	0.33	0.69	0.43	0.33	0.00
<i>Asc_spe</i>	0.06	0.17	0.09	0.00	0.00	0.00	0.00	0.00
<i>Ast_hes</i>	0.06	0.07	0.27	0.11	0.15	0.00	0.00	0.00
<i>Bri_cal</i>	0.00	0.00	0.00	0.00	0.12	0.00	0.00	0.00
<i>Bro_jap</i>	0.06	0.07	0.18	0.22	0.00	0.00	0.00	0.00
<i>Bro_tec</i>	0.72	0.19	0.27	0.00	0.00	0.05	0.00	0.00
<i>Cal_neg</i>	0.00	0.02	0.00	0.00	0.04	0.00	0.00	0.00
<i>Car_ath</i>	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00
<i>Car_lan</i>	0.11	0.64	0.55	0.11	0.46	0.38	0.17	0.00
<i>Car_mic</i>	0.00	0.02	0.00	0.11	0.08	0.19	0.00	0.00
<i>Car_neb</i>	0.17	0.26	0.18	0.11	0.12	0.05	0.00	0.00
<i>Car_pra</i>	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00
<i>Car_ros</i>	0.00	0.00	0.09	0.22	0.12	0.05	0.00	0.00
<i>Cel_ret</i>	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00
<i>Cha_spe</i>	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00
<i>Che_fre</i>	0.11	0.12	0.09	0.00	0.00	0.00	0.00	0.00
<i>Chr_lin</i>	0.06	0.00	0.00	0.00	0.23	0.14	0.00	0.00
<i>Cir_arv</i>	0.22	0.26	0.09	0.11	0.12	0.19	0.00	0.00
<i>Cir_vul</i>	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00
<i>Con_arv</i>	0.00	0.02	0.09	0.00	0.00	0.00	0.00	0.00
<i>Con_can</i>	0.00	0.02	0.00	0.33	0.27	0.57	0.67	0.00

Appendix 2. Continued.

Species	Fraction of plots with species by hydroperiod class							
	<.01	.01-.1	.1-.2	.2-.4	.4-.6	.6-.8	.8-.99	>.99
<i>Ech_cru</i>	0.00	0.00	0.00	0.00	0.00	0.10	0.17	0.00
<i>Ele_pal</i>	0.00	0.10	0.09	0.33	0.42	0.81	0.83	0.00
<i>Ely_can</i>	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00
<i>Epi_cil</i>	0.00	0.00	0.00	0.00	0.35	0.71	1.00	0.00
<i>Equ_arv</i>	0.00	0.05	0.18	0.11	0.12	0.24	0.50	0.00
<i>Equ_hye</i>	0.33	0.88	0.82	0.67	0.42	0.24	0.17	0.00
<i>Equ_lae</i>	0.39	0.64	0.64	0.33	0.35	0.29	0.17	0.00
<i>Eup_ser</i>	0.00	0.07	0.18	0.00	0.00	0.24	0.00	0.00
<i>Eut_occ</i>	0.17	0.62	1.00	1.00	0.96	1.00	0.67	0.00
<i>Fes_aru</i>	0.06	0.05	0.00	0.00	0.04	0.00	0.00	0.00
<i>Fra_ano</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00
<i>Gly_gra</i>	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00
<i>Gut_sar</i>	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00
<i>Her_sph</i>	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00
<i>Het_vil</i>	0.61	0.12	0.00	0.00	0.15	0.00	0.00	0.00
<i>Hor_jub</i>	0.00	0.00	0.00	0.11	0.04	0.33	0.17	0.00
<i>Jun_bal</i>	0.11	0.17	0.55	0.44	0.08	0.05	0.00	0.00
<i>Jun_ens</i>	0.00	0.00	0.00	0.00	0.00	0.14	0.00	0.00
<i>Jun_ten</i>	0.00	0.00	0.00	0.00	0.08	0.24	0.17	0.00
<i>Lac_ser</i>	0.00	0.02	0.09	0.22	0.04	0.14	0.33	0.00
<i>Med_lup</i>	0.00	0.00	0.00	0.11	0.08	0.19	0.00	0.00
<i>Mel_alb</i>	0.00	0.02	0.00	0.11	0.31	0.14	0.17	0.00
<i>Mel_off</i>	0.00	0.00	0.00	0.11	0.15	0.19	0.00	0.00
<i>Mel_spe</i>	0.11	0.24	0.09	0.56	0.23	0.52	0.50	0.00
<i>Men_arv</i>	0.00	0.10	0.00	0.11	0.19	0.10	0.00	0.00
<i>Muh_rac</i>	0.06	0.52	0.45	0.33	0.69	0.67	0.50	0.00
<i>Pan_fle</i>	0.00	0.00	0.18	0.00	0.04	0.24	0.50	0.00
<i>Pha_aru</i>	0.06	0.24	0.36	0.22	0.62	0.81	0.17	0.00
<i>Phl_pra</i>	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00
<i>Pla_maj</i>	0.00	0.02	0.00	0.00	0.38	0.71	0.17	0.00
<i>Poa_com</i>	0.39	0.90	1.00	0.67	0.73	0.67	0.33	0.00

Appendix 2. Concluded.

Species	Fraction of plots with species by hydroperiod class							
	<.01	.01-.1	.1-.2	.2-.4	.4-.6	.6-.8	.8-.99	>.99
<i>Poa_pal</i>	0.00	0.00	0.27	0.33	0.50	0.62	0.33	0.00
<i>Pol_spe</i>	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00
<i>Pop_del</i>	0.00	0.00	0.00	0.11	0.04	0.00	0.00	0.00
<i>Pot_pec</i>	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00
<i>Pot_spe</i>	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00
<i>Ran_cir</i>	0.00	0.00	0.00	0.00	0.00	0.10	0.17	0.00
<i>Ran_cym</i>	0.00	0.00	0.00	0.22	0.15	0.48	0.50	0.00
<i>Rhu_tri</i>	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00
<i>Ror_ter</i>	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00
<i>Rum_spe</i>	0.00	0.02	0.09	0.11	0.08	0.05	0.00	0.00
<i>Sal_exi</i>	0.06	0.12	0.09	0.11	0.04	0.00	0.00	0.00
<i>Sci_spe</i>	0.00	0.00	0.00	0.11	0.04	0.05	0.00	0.00
<i>Sol_spa</i>	0.00	0.05	0.00	0.00	0.27	0.10	0.33	0.00
<i>Spo_cry</i>	0.61	0.05	0.09	0.00	0.00	0.00	0.00	0.00
<i>Sta_pal</i>	0.00	0.02	0.09	0.11	0.08	0.00	0.00	0.00
<i>Tam_ram</i>	0.06	0.07	0.18	0.00	0.04	0.00	0.00	0.00
<i>Tar_spe</i>	0.00	0.00	0.09	0.00	0.04	0.14	0.00	0.00
<i>Tox_ryd</i>	0.00	0.12	0.09	0.00	0.00	0.00	0.00	0.00
<i>Tra_spe</i>	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Tri_spe</i>	0.00	0.00	0.00	0.11	0.38	0.48	0.00	0.00
<i>Typ_spe</i>	0.00	0.00	0.00	0.00	0.04	0.00	0.17	0.00
<i>Urt_dio</i>	0.00	0.00	0.00	0.00	0.04	0.10	0.00	0.00
<i>Ver_ana</i>	0.00	0.00	0.00	0.00	0.04	0.33	0.50	0.00
<i>Ver_bra</i>	0.00	0.07	0.00	0.11	0.35	0.14	0.00	0.00
<i>Ver_tha</i>	0.00	0.07	0.00	0.00	0.31	0.33	0.00	0.00

Appendix 3. Annotated TWINSpan output summarizing divisions, indicator species, and preferential species. Output has been truncated to include just those divisions used in this analysis. Negative groups refer to plot groups to the left of the division and positive groups refer to the group of plots to the right of the division.

DIVISION 1 (N = 134) I.E. GROUP *

EIGENVALUE .494 AT ITERATION 2

INDICATORS, TOGETHER WITH POA_COM COMPLEX) = INDICATOR SPECIES FOR HYDRIC-XERIC-- Epi_cil/Agr_sto,
(+) = INDICATOR SPECIES FOR XERIC-- Bro_tec/Het_vil COVER TYPE

AGR_STO 1(-) EUT_OCC 1(-) HET_VIL 1(+) BRO_TEC 1(+) SPO_CRY 1(+) POA_COM 1(-)

MAXIMUM INDICATOR SCORE FOR NEGATIVE GROUP 0 MINIMUM INDICATOR SCORE FOR POSITIVE GROUP 1

```

1 2 3 4** 5 6 7 8** 9 10 11 12 13 14 15 16****
*****
0 0 0 0** 0 0 0 0** 0 0 0 0 0 0 1 4** 3
0 0 0 0** 0 0 0 0** 0 0 0 0 2 1 1 2** 2
0 0 0 0** 2 0 0 0** 0 1 0 0 0 0 0 1** 1
*****
0 0 2 4** 0 0 1 0** 0 0 0 0 0 0 0 0** 0
0 1 8 3** 0 1 0 0** 0 0 0 0 0 0 0 0** -1
51315 3** 0 0 0 0** 0 0 0 0 0 0 0 0** -2
153810 0** 0 0 0 0** 0 0 0 0 0 0 0 0** -3

```

PLOTS IN NEGATIVE GROUP (N = 119); I.E. HYDRIC-XERIC-- Epi_cil/Agr_sto, Equ_hye/Poa_com COMPLEX; (GROUP *0)

101	102	103	104	105	106	107	108	109	110	111	113
114	115	116	117	118	119	120	121	122	123	124	125
126	129	130	133	134	136	137	139	140	142	148	149
152	153	154	155	156	157	158	159	160	161	162	164
165	201	202	203	204	205	206	207	208	209	210	211
212	213	214	215	216	217	218	219	220	221	222	223
224	225	226	227	228	229	230	231	232	233	234	235
236	237	238	239	240	241	242	243	244	245	301	302
303	304	305	306	307	308	309	310	311	312	313	314
315	316	317	318	319	320	321	322	323	324	325	

BORDERLINE NEGATIVES (N = 2)

149 235

PLOTS IN POSITIVE GROUP (N = 15); I.E. XERIC-- Bro_tec/Het_vil; (GROUP *1)

127	128	131	132	135	138	141	143	144	145	146	147
150	151	163									

BORDERLINE POSITIVES (N = 2)

127 147

NEGATIVE PREFERENTIAL SPECIES (# of occurrences in negative group, # of occurrences in positive group)

ACE_NEG 1(38, 1) AGR_STO 1(103, 1) APO_SPE 1(30, 0) CAR_LAN 1(57, 1) CIR_ARV 1(25, 0) CON_CAN 1(27, 0)
ELE_PAL 1(42, 0) EPI_CIL 1(31, 0) EQU_RYE 1(73, 3) MEL_SPE 1(38, 1) MUH_RAC 1(65, 1) PHA_ARU 1(52, 0)
PLA_MAJ 1(28, 0) POA_COM 1(94, 4) POA_PAL 1(35, 0) EUT_OCC 1(100, 0)

POSITIVE PREFERENTIAL SPECIES (# of occurrences in negative group, # of occurrences in positive group)

ARI_PUR 1(0, 6) BRO_TEC 1(12, 13) HET_VIL 1(8, 12) SPO_CRY 1(3, 11)

NON-PREFERENTIALS (# of occurrences in negative group, # of occurrences in positive group)

ART_LUD 1(42, 4) EQU_LAE 1(54, 6)

Appendix 3. Concluded.

DIVISION 2 (N = 119) I.E. GROUP *0

EIGENVALUE .326 AT ITERATION 1

INDICATORS, TOGETHER WITH THEIR SIGN: (-) = INDICATOR SPECIES FOR HYDRIC-MESIC-- Agr_sto/Eut_occ COVER TYPE

(+) = INDICATOR SPECIES FOR MESIC-XERIC-- Equ_hye/Poa_com COVER TYPE

EQU_HYE 1(+) ELE_PAL 1(-) EPI_CIL 1(-) POA_PAL 1(-)

MAXIMUM INDICATOR SCORE FOR NEGATIVE GROUP -1 MINIMUM INDICATOR SCORE FOR POSITIVE GROUP 0

1 2 3 4** 5 6 7 8** 9 10 11 12 13 14 15 16**

 0 0 0 0** 1 0 0 0** 2 1 0 2 1 2 1 3 4** 1
 0 0 3 1** 0 1 0 0** 0 1 0 2 2 7 3 0** 0

 0 210 7** 0 0 0 0** 0 0 0 0 1 0 0 0** -1
 1 6 4 3** 0 0 0 0** 0 0 0 0 0 0 0 0** -2
 6 3 3 1** 0 0 0 0** 0 0 0 0 0 0 0 0** -3

PLOTS IN NEGATIVE GROUP (N = 50); I.E. HYDRIC-MESIC-- Agr_sto/Eut_occ; (GROUP *00)

103	109	118	119	120	121	129	148	152	153	156	159
165	201	203	204	210	211	212	214	216	220	221	222
226	227	228	230	231	232	234	236	239	242	245	301
304	305	307	310	311	312	313	314	320	321	322	323
324	325										

MISCLASSIFIED NEGATIVES (N = 4)

222 226 227 239

PLOTS IN POSITIVE GROUP (N = 69); I.E. MESIC-XERIC-- Equ_hye/Poa_com; (GROUP *01)

101	102	104	105	106	107	108	110	111	113	114	115
116	117	122	123	124	125	126	130	133	134	136	137
139	140	142	149	154	155	157	158	160	161	162	164
202	205	206	207	208	209	213	215	217	218	219	223
224	225	229	233	235	237	238	240	241	243	244	302
303	306	308	309	315	316	317	318	319			

BORDERLINE POSITIVES (N = 2)

106 225

MISCLASSIFIED POSITIVES (N = 1)

219

NEGATIVE PREFERENTIAL SPECIES (# of occurrences in negative group, # of occurrences in positive group)

ACE_NEG 1(28, 10) ART_LUD 1(27, 15) CON_CAN 1(24, 3) ELE_PAL 1(36, 6) EPI_CIL 1(30, 1) MEL_ALB 1(10, 4)
 PHA_ARU 1(36, 16) PLA_MAJ 1(26, 2) POA_PAL 1(30, 5) RAN_CYM 1(18, 2) SOL_SPA 1(11, 1) TRI_SPE 1(20, 2)
 VER_THA 1(15, 1) VER_BRA 1(11, 4) VER_ANA 1(11, 0)

POSITIVE PREFERENTIAL SPECIES (# of occurrences in negative group, # of occurrences in positive group)

AGR_SPE 1(3, 19) CAR_NEB 1(4, 17) EQU_HYE 1(10, 63) EQU_LAE 1(12, 42) JUN_BAL 1(4, 18)

NON-PREFERENTIALS (# of occurrences in negative group, # of occurrences in positive group)

AGR_STO 1(50, 53) APO_SPE 1(11, 19) CAR_LAN 1(18, 39) CIR_ARV 1(9, 16) MEL_SPE 1(22, 16) MUH_RAC 1(28, 37)
 POA_COM 1(32, 62) EUT_OCC 1(48, 52)

END OF DIVISIONS

