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DISSERTATION

RIPARIAN WILLOW DYNAMICS AND THEIR INTERACTION WITH ENVIRONMENTAL AND BIOLOGICAL FACTORS IN THE ELK WINTER RANGE OF ROCKY MOUNTAIN NATIONAL PARK (COLORADO) - A MULTI-SCALE ANALYSIS.

Submitted by

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Rangeland and Ecosystem Science

In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Fort Collins, Colorado

Spring 2000

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February 24, 2000

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY HECTOR RAUL PEINETTI ENTITLED "RIPARIAN WILLOW DYNAMICS AND THEIR INTERACTION WITH ENVIRONMENTAL AND BIOLOGICAL FACTORS ON THE ELK WINTER RANGE OF ROCKY MOUNTAIN NATIONAL PARK (COLORADO) - A MULTI-SCALE ANALYSIS" BE ACCEPTED AS FULLFILLING IN PART REQUIREMENTS FOR THE DEGRE OF DOCTOR OF PHILOSOPHY.

Committee on Graduate Work

Michael B. Coughenour
Adviser

Department Head

ABSTRACT OF DISSERTATION

RIPARIAN WILLOW DYNAMICS AND THEIR INTERACTION WITH ENVIRONMENTAL AND BIOLOGICAL FACTORS IN THE ELK WINTER RANGE OF ROCKY MOUNTAIN NATIONAL PARK (COLORADO)- A MULTI-SCALE ANALYSIS.

Changes in willow populations and their association with different causative factors were evaluated in two valleys of the elk winter range of Rocky Mountain National Park (Colorado). Studies at the individual, population, and landscape scale were conducted, and results from these studies were incorporated into a spatial, process based model (SAVANNA). Morphological and physiological characteristic of willows protected and unprotected from elk browsing were compared. Browsing induced plant canopy changes and reduced the relative amount of carbon allocated belowground, but aboveground productivity was not changed. By suppressing height growth, elk browsing induced short willow morphotypes (< 1.5 m), which contrasted with tall willow plants (> 2 m) that grew in the same valley. Short willows that grew under protection from elk increased plant height compared to unprotected willows, but 5 years of protection was not long enough for these willows to acquire the height frequency distribution of a tall willow population. Landscape change analysis of willow cover was conducted by photo-interpretation of historic (1937/1946) and recent (1996) aerial photos. A decrease of willow cover of approximately 20% and more than 50% reduction in river length and water surface area were determined in this period. Deeper water tables that were produced by a decline of beavers and by human made ditches seem to explain most of the willow decline. The model estimated that the transition from short to tall willow population could occur in approximately 10 years, under no elk herbivory. This transition was inhibited at elk densities higher than 50 elk/km^2. Interaction between water table depth and elk density was predicted in the model. The beaver decline appeared to play the most significant role in the decline in willow. The increases in elk density that have occurred since the mid-1960's could have contributed to this decrease, but the major effect of elk was apparently an increase in the proportion of short willow morphotypes.

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TABLE OF CONTENTS

INTRODUCTION

In a series of studies included in this dissertation I evaluate willow population dynamics in two of the main valleys of the elk winter range of Rocky Mountain National Park (RMNP), and their relationships with causative factors. Independent studies at the individual, population, and landscape scale were conducted. Results were incorporated into a spatial, process-based model (SAVANNA) (Coughenour 1993). Modeling was used to integrate information taken at different scales, and to make prediction of willow dynamic under different climatic conditions or levels of herbivory.

Riparian ecosystems are a dynamic area of the landscape in the transition zone between terrestrial and aquatic ecosystems (Gregory et al 1991). These ecosystems are important in controlling landscape energy and material fluxes, supporting high biodiversity, and maintaining critical habitat for rare and threatened terrestrial and aquatic species (Naiman and Decampus 1997, Patten 1998a). Environmental and biotic characteristics of riparian ecosystems on the elk winter range of (RMNP), Colorado have been extensively modified. Changes include a decline in willows (*Salix spp*) (Hess 1993, Singer et al, 1998a), an increase in the elk (*Cervus elaphus*) population (almost 3-fold) (Singer et al. 1998 a, b), a beaver (*Castor cannadensis*) decline to almost disappearance (Zeigenfuss et al 2000), a reduction in river meanders, and a drying trend in climatic conditions (Singer et al, 1998a). Evidence of willow decline includes areas with a high proportion of dead willow plants, as well as areas dominated by short (<1.5m) willow, which in contrast to other areas dominated by tall willow (>2 m), reflect disturbed conditions. Several causative factors have been associated with willow decline (Singer et al, 1998a). However the extent of willow decline has not been quantitatively evaluated, and little is known about the relative importance of the factors that could produce willow decline or their mechanisms and interactions.

Large herbivores bring about changes in ecosystem structure and function directly by modifying plant physiology and morphology, or indirectly by inducing changes in species composition and nutrient cycling (Detling 1988, Naiman 1988,, Pastor and Naiman 1992, Briske and Richards 1995, Hobbs 1996). Previous studies on these willows indicated that in the short-term, plant physiological performance is improved in browsed willow compared to unbrowsed controls (Alstad et al 1999). These willows also maintain aboveground productivity for 3 years under severe clipping treatment (Singer et al. 1998). In the first Chapter of this dissertation I evaluate the mechanism of response of plants to elk browsing by integrating plant-level carbon, water and nitrogen dynamics with aboveground production. Different physiological process and plant morphological characteristics of unbrowsed and browsed willow are evaluated. This information is used to infer how elk will change the competitive ability and survivorship of plants over the long-term, particularly under drier climatic conditions and with deeper water tables.

In Chapter 2 I evaluate the hypothesis that short willows are primarily the result of the removal of the current annual growth by elk. If elk browsing is the primary factor producing short willow morphotypes, then willow should shift to a tall morphotype when elk browsing is prevented. I compare individual and population characteristics of short and tall browsed willows, with short willows that have been protected from elk herbivory for a period of 5 years. Plant growth is evaluated by considering the size and number of metamerics units (Harper and Bell 1979, White 1979) that are generated by the extension growth of the apical meristems (Alliende and Harper 1989, Raven 1992). This method allows me to reconstruct the temporal dynamics of growth of individuals with different histories of browsing. At the population level the height frequency distributions of short and a tall willow population are used as a baseline to compare the response of a short willow to protection from elk browsing.

In Chapter 3 I focus on the long-term change in spatial distribution of willow cover in the valleys. The study has the goals of providing a quantitative estimate of willow decline, and gathering information that help us to infer the relative importance of factors that could cause willow to decline. The interpretation of historic aerial photos with a medium level of resolution is a reliable, quantitative method for analyzing long-term changes in vegetation, in particular when combined with geographic information systems analyses

(Johnson and Naiman 1990c, Ustin et al 1993, Johnzon and Cage 1997). Long-term changes in willow cover are inferred from interpretation of historic (1935 or 1946) and recent (1996) aerial photos. Historic and recent spatial river channels patterns are used as an indication of areas of high plant water availability in riparian areas .The spatial association between willow decline and the disappearance of river meanders is analyzed. The spatial associations between short willow morphotypes, river changes, and the geomorphic characteristic of the valleys are also included in the analysis. In addition, the temporal and spatial pattern of willow vegetation changes is interpreted by considering historical changes in elk and beaver populations and human activities.

In the last chapter simulation modeling is used to synthesize the information generated in this study, as well as information from other studies recently conducted on willow in RMNP (Alstad et al 1999, Menezes 1999, Zeigenfuss et al 2000). Modeling is the most suitable tool for translating knowledge taken at the scale of the individual or plot to the scale of landscape (Ehleringer and Field. 1993). Modeling is used to evaluate the quantitative relationships between different variables that control willow population dynamics, and to infer the behavior of the system beyond the range of the experimental data.

CHAPTER 1

Changes induced by elk browsing on the aboveground biomass production and distribution of willow (*Salix monticola*): their relationship with plant water, carbon, and nitrogen dynamics.

Abstract. An increase in elk population on the winter range of Rocky Mountain National Park (RMNP) could negatively affect willow populations. Nevertheless, short-term physiological performance of *Salix monticola*, one of the most common willow species in this area, was improved under elk browsing. I hypothesized that elk browsing would produce long-term changes in willow morphology that would interact with physiological processes determining changes in productivity and survivorship. Browsed and unbrowsed treatments were established on 2 watersheds in the elk winter range of RMNP during the 1997 growing season (May to October). I used 8 long-term exclosures built in the fall of 1994 (4 in each watershed). Plants in the unbrowsed treatment were in the areas open to browsing, but they were protected from grazing during the time of the experiment, by small exclosures. Almost all shoots in the unbrowsed plants developed from buds of the previous year's shoots, but many shoots of the browsed plants were produced from buds older than one year. This morphological pattern is interpreted as an adaptive response to herbivory under the constraint of limitation in the number of axilary meristems required for shoot and leaf development. A limitation of the number of axilary meristems of the previous year's shoot could also be the reason for reduced flower production observed in browsed plants. Browsed plants produced more shoot biomass per unit of woody plant biomass, and shoot biomass per unit of leaf biomass than unbrowsed plants. Since no differences in carbon input per unit of leaf area and leaf specific area were found between treatments, I conclude that browsed willows allocated relatively more carbon aboveground than unbrowsed willows.

Transpiration rate and water use efficiency were not different between treatments. Plants allocated a high proportion of total aboveground nitrogen to leaves and shoots. Browsed plants allocated a higher proportion of nitrogen to new shoots than did unbrowsed plants. Elk browsing constrained plant size growth and development. Willows compensated for this constraint through morphological changes. However, reduced flower development was not compensated. Reduction in belowground carbon allocation will reduce root development, which will make willow less able to obtain water under deeper water table conditions. Elk browsing could therefore reduce the competitive ability and survivorship of willow in a long-term under drier environmental conditions.

INTRODUCTION

Ungulate activities modify ecosystem structure and function (Naiman 1988). Large herbivores directly affect plants through tissue removal, but they can also induce long term changes in nutrient cycling (Delting 1988, Pastor and Naiman 1992, Huntly 1991, Hobbs 1996). These direct and indirect effects could modify the competitive ability of a particular plant species or functional group (Bryant 1987, Pastor and Naiman 1992). At the plant level, removal of plant tissues by ungulates causes plant morphological and physiological changes over a broad range of temporal scales (Briske and Richards 1995). However, most information regarding plant response to herbivory is based on studies conducted on grasses, and a limited literature exists on the response of woody plant to defoliation. Several differences are expected between graminoids and woody plant response because of differences in plant characteristics, and because of the differences in patterns of ungulate tissue removal. Since woody plants are built up of segments produced over several years, biomass removal could induce long-term morphological changes (Bergström and Danell 1987). Woody plants have a juvenile and a mature state of development, with an age trend in the aboveground annual woody biomass production, and tissue removal could induce changes in this development pattern (du Toit et al. 1990). Strategies to avoid browsing in woody plants are different form those of herbaceous plants (Rohner and Ward, 1997), involving physical responses such as the production of thorns (Gowda 1996, Cooper and Ginnett 1998), chemical defenses by increasing the level of secondary metabolites (Herms and Mattson 1992, Bergström 1992) and unique growth strategies (Bergström 1992). Many woody plants are browsed during the period of dormancy, with a lag phase between the time browsing occurs and when plant response is observed (Bergström and Danell 1987). Finally, browser foraging selectivity is higher than that of grazers (Hofmann 1989, Bergström 1992). Plant responses depend on the type of tissues removed and the pattern of this removal (du Toit et al. 1990, Bergström 1992). These characteristics could result in important differences between woody and graminoid plant responses to defoliation.

This paper is focused on changes induced by elk (*Cervus elaphus*) browsing on willow plants (*Salix monticola*) in the riparian areas of the eastern slope of Rocky Mountain National Park (RMNP), Colorado. Elk browse on willow mainly during the winter on new shoots developed in the last growing season. Increases in elk population density that have occurred in the last 30 years could have negatively affected willow (Singer et. al. 1998). Previous studies on this willow community indicate that winter browsing by elk improved *S. monticola* physiological performance. Higher water potential and leaf carbon isotope discrimination were found in browsed willow compared to unbrowsed controls, which could improve willow regeneration and survivorship (Alstad et al. 1999). These willows were able to maintain aboveground production during 3 years of severe clipping treatment (Singer et al. 1998). However, it is not clear how physiological processes altered by browsing are linked to changes in plant productivity, and how these changes affect the competitive ability of willow under the drier and warmer conditions that have been observed in this area (Singer et al. 1998). I hypothesize that elk browsing on willow produces long-term changes in plant morphology that will interact with physiological processes determining changes in willow productivity and survivorship. In this study I had the following primary objectives: 1.) Determine aboveground biomass production and distribution in willows under browsing and non-browsing conditions. 2.) Associate biomass production and morphological changes induced by browsing with physiological plant performance such as photosynthesis or transpiration rate. 3.) Infer how elk browsing changes plant survivorship under drier environmental conditions.

MATERIALS AND METHODS.

The experiment was carried out during the 1997 growing season (May to October) in RMNP at two sites: the Moraine Park area in the Big Thompson River watershed (2481 m of altitude), and the Horseshoe Park area in the Fall River watershed (2598 m of altitude). A total of twelve large elk exclosures (30 m x 46 m) were built in Moraine and Horseshoe parks (six in each park) between August and November of 1994. Next to each exclosure, 30 m x 46 m plots were chosen and marked off as paired plots open to grazing (grazed plots). This study was conducted on the 8 exclosures and paired grazed areas (four in each park), that were located in the short willow communities. Two treatments were established: the unbrowsed treatment consisted of 2 willow plants inside exclosures that had been protected from elk browsing since 1994, and the browsed treatment consisted of 2 plants of the paired-plot open to grazing until May 1997. At this time, small exclosures were built around each selected individual plant in the browsed treatment to prevent offtake of new tissues formed during the 1997-growing season. Only the selected individual was included within the exclosure. However, elk browsing during the period of willow growth is not significant, because most elk move to higher elevation summer ranges at this time of the year. In each plot (exclosure or paired grazed area) I identified all *S. monticola* plants, that represented the most frequent size type (canopy volume and height) within the plot. From this subset, I randomly chose for measurements, two plants per plot, giving a total of thirty-two plants among all treatments.

Soil moisture was monitored during the growing season by taking measurements on a weekly basis in all plots in both watersheds with a time domain refractometer, Trase System model 6050x1. Due to soil depths, measurements were made between 0 and 28 cm in Moraine Park and 0 and 58 cm in Horseshoe Park. All soil moisture measurements were taken under *Salix spp.* canopies and in the grazed area adjacent to *Salix spp.* plants. Additional information on the hydrological conditions during the 1997-growing season was obtained by measuring ground water depths monthly in sampling wells installed inside the exclosures and in the grazed areas (Zeigenfuss et al. 2000). During the growing season measurements made on the selected willow plants included: phenological phase, leaf area dynamics, gas exchange variables (photosynthesis and transpiration), leaf and woody biomass, and percentage of carbon and nitrogen in leaves and woody biomass. The time periods of the phenological phases were determined by repeated qualitative observations and measurements on 6 to 8 target stems per plant, on the 32 sampled plants. To select stems, 4 equal quadrants were delimited in each plant. All stems in two opposite quadrants were identified, and their height and diameter were measured. Groups of stems were visually delimited in a x-y scatter plot of height vs diameter. From each group I randomly selected one stem, or two in the case of groups with a high number of stems. Plants were visited every two weeks from May 10 until the last week of August. The start of bud break and the time period of flowering, seed dispersion, and leaf shedding were determined by visual observation of the target stems. The phenological phase was considered initiated when more than 50% of the marked stems were in this phase. Approximately every two weeks, shoots on each marked stem were counted to monitor vegetative growth. In addition, one 1997 shoot per marked stem was identified on the top part of the stem, and shoot morphological variables were measured at every sample date. I determined shoot length, number of leaves per shoot and the length of the longest leaf on a shoot. These variables were also used to infer the temporal dynamics of plant leaf area. In this case, several 1997 shoots with leaves from adjacent *S. monticola* plants were collected on each date when phenological data were determined. In each shoot, the morphological variables described previously and the total leaf area of shoots were determined. Leaf areas were measured with a LI-3000, LI-COR leaf area meter. These data were used to create a multiple linear regression model that predicted leaf area per shoot using shoots and leaf morphological variables as predictors. For each target stem and date, shoot and leaf morphological variables were transformed to leaf area. Values were then multiplied by the total number of 1997 shoots per stem and expressed as a proportion.

Gas exchange measurements were performed on selected plants three times during the growing season. The first measurements were made during the second week of June (plants of one site were not measured because leaves of one of the browsed plants were small and difficult to manipulate). The second set of data was collected to measure gas exchange variables in response to changes in light intensity. Repeated measurements were performed on two plants growing in the same exclosure and two plants in the associated grazing plot. Two plants per treatment, growing in close proximity to one another, were chosen, with the goal of reducing variability due to different growing conditions. Gas exchange of fully developed leaves in the upper portion of the canopy was measured during the second week of July throughout the day, on 2 days. Between the dates of July 17-22 a third set of measurements was made on 5 plants per treatment on leaves located at different positions in the canopy. To select leaves for measurement, two opposite quadrants were identified in the canopy. Each quadrant was divided horizontally into two sections (outside and inside), and vertically into two layers (upper and lower). One leaf in each delimited part of the canopy was chosen for measurements. All gas measurements were made with a Licor LI-6200 portable photosynthesis system (LI-COR, Inc., Lincoln, Neb.) equipped with 0.25-L leaf chamber. The accuracy of the data was checked, and data that presented a strong deviation from a steady state were discarded. I discarded data from any run in which the standard error of the slope of the CO_2 concentration over time was greater than 10% of the value of the slope (LI-COR 1990). In addition, data that had an error higher than 20% between the estimation of transpiration using the relative humidity method, compared to the estimate using leaf energy balance, were also discarded (LI-COR 1990).

At the end of the season, eight plants of the sixteen selected plants per treatment (one in each plot), were harvested to measure stem and leaf biomass. Plants were harvested on the first week of September, before leaf shedding started._Total dry weight of woody and leaf biomass of the harvested plants, and leaf area and leaf dry weight of the marked stems were measured. These data were used to construct a regression model of leaf area on leaf dry weight to estimate plant leaf area. For each stem, shoots (segments of the stem produced each year) of different ages were separated. The age of each shoot of the stem was identified based on the position of the shoot according to the sympodial ramification pattern of willows, or the scar marks of the stems in the case of older shoots (chapter 2). All shoots of the same age of the different stems of the same plant were grouped. Total dry weight was determined in each shoot cohort.

Nitrogen dynamics on different parts of the plants were determined by using a LECO CHN analyzer. The percentage of nitrogen in leaves, 1997 and 1996 shoots was measured four times during the growing season on samples taken on all of the selected plants of both treatments, and additionally, during the first week of September on the 16 harvested plants. The same variables were measured on 1997 and 1996 shoots in each of the 16 unharvested plants, in October 1997 after leaf senescence. The percentage of nitrogen was also determined on leaves that were collected from the soil surface litter in October 1997. Nitrogen retranslocated back to the plant from the leaves during senescence and lost through litterfall were estimated based on the difference between nitrogen in leaves prior to and after literfall (September and October samples, respectively). Finally, nitrogen percentages were determined on shoots of different ages (cohort), on one of the marked stems of the 16 harvest plants. Total plant nitrogen was estimated as the sum of values obtained by multiplying the biomass of each shoot cohort by its nitrogen percentage.

Statistical analysis. A complete randomized block design ANOVA for comparison of experiments was used to analyze most of the measured variables. The exclosure and paired grazed plot were considered as a block, and the ANOVA test was used to check for differences between sites (Moraine and Horseshoe Park), treatments or interactions. A nested mixed model was used to analyze the gas exchange variables on the second set of measurements. A covariance (ANCOVA) analysis was used to compare treatments in the case of biomass variables.

RESULTS

Hydrological conditions for willow growth. A trend of decreasing water availability for willow growth during the growing season normally occurs because of the influence of the snowmelt on the groundwater levels (Zeigenfuss et al. 2000). Water tables under the selected willow plants were not deeper than 0.5 m during June and July, and not deeper than 1 m during the entire growing season. The volumetric soil moisture followed the same negative trend as groundwater levels during the growing season, but it was more affected by rain events occurring at the end of July 1997 (Fig. 1). Soils were saturated at the beginning of the season and become drier as the season progressed. Lower values were close to 35%, which corresponds to high soil water potentials considering that these are relatively coarse soils (Menezes 1999). No differences were found between soil water content between and under willow canopies.

Phenology and leaf area dynamics. The growth period lasted approximately three months, from June through August (Fig. 2). Leaves started to develop two weeks later in *S. monticola* than S. *planifolia*, the other co-dominant willow species. Flowers began to form from buds of the previous year's shoots just prior to bud break, and seed dispersion occurred early in the growing season. It is important to note that no flowers were found in the browsed plants. This was not only the case for the selected plants but also in all of the short willow plants that I sampled at the different sites of both watersheds. Most shoots were differentiated early in the growing season in unbrowsed plants, and few developed thereafter (Fig. 3a). Plants in the browsing treatment began growth a few days later than unbrowsed willows, and the number of shoots at the second measurement date (June 19) approximately doubled by the end of the season. Leaves were formed during the season at the same time the increase in shoot length occurred since all leaves are developed on new shoots (Fig. 3b, c). After mid-August, changes in the measured variables were minor, indicating that vegetative growth ended during this month. Browsed plants produced fewer shoots per stem than the unbrowsed plants (Fig. 3a) but these shoots were significantly longer than in unbrowsed plants ($P < 0.01$) (Fig. 3c). In addition, browsed plants produced fewer leaves compared with browsed plants (411 and 228 mean number of leaf/stem, $P=0.035$), but leaves were larger (3.7 and 5.1 $cm^2 leaf^{-1}$, $P=0.015$). No differences between treatments were found in specific leaf area (77.1 and 74.2 $cm^2 g^{-1}$, $P = 0.83$, for unbrowsed and browsed treatments, respectively). Regression models using shoot and leaf morphological variables to predict leaf area per shoot showed a highly significant linear relationship (Table 1). Total plant leaf area steadily increased during the growing season in a similar manner for both treatments (Fig. 3d). Differences between treatments were significant only on the first date of measurement, which was probably a result of the fact that unbrowsed plants started growing earlier than browsed plants.

Plant biomass. Unbrowsed and browsed plants displayed similar variation in total woody biomass at the end of the growing season (470 to 2,719 g, and 382 to 3,109 g for unbrowsed and browsed treatment, respectively). Nevertheless, at the beginning of the experiment, plants were taller (1.71 m and 0.92 m, $P = 0.001$) and larger (3.19 m^3 and 1.36 m^3, $P = 0.03$) in the unbrowsed treatments. These differences in plant morphology were also observed at the end of the experiment (1.97 and 1.20 m $P = 0.0003$, mean height of browsed and unbrowsed plants, respectively). Aside from initial differences in plant volume, total dry weights of woody biomass, leaves, and 1997 shoots were not different at the end of the experiment (Fig. 4a). Total plant leaf areas obtained based on linear regression (Table 1) were not different between treatments ($P = 0.4$). The range of variation in total leaf area was 1.7 to 9.4 m^2 for the unbrowsed, and 1.3 to 6.9 m^2 for the browsed treatment. The unbrowsed treatment had significantly higher biomass in 1994 and 1995 shoot cohorts, but biomass of the 1996-shoot cohort was not significantly different between treatments (Fig. 4a) (shoot biomass of all years except 1997 were affected by browsing, since the plans were protected form browsing only in 1997). The biomass of shoots older than 1994 appeared higher in the browsed plants the difference was not significant.

To reduce the effect of plant size differences, biomass variables were expressed relative to the total plant woody biomass (Fig. 4b). Plants in the browsed treatment produced a significantly higher relative shoot biomass compared to the unbrowsed treatment during the growing season of 1997. Since total leaf biomass was similar in both treatments, the ratio of 1997 shoot biomass to leaf biomass was higher in the browsed treatment (P = 0.006). Relative 1996 shoot biomass was not different between treatments. Mean plant biomass at the end of the experiment was higher in Horseshoe Park than in Moraine Park (1,830 g and 830 g, respectively, P = 0.05). Plants in Moraine Park produced more shoots per unit of biomass than Horseshoe Park (0.17 and 0.11, respectively, P = 0.02), and leaves per unit of plant biomass (0.28 and 0.19 respectively, P = 0.01), but the 1997-shoot: leaf dry weight ratio was not different between watersheds (P = 0.6).

Linear relationships between different biomass variables were found in both treatments (Table 2). The production of leaves, 1997 shoots, and 1996 shoots as a function of total dry weight was not statistically different between treatments. Treatment differences were found in the 1997 shoot biomass as a function of the previous year's shoot biomass. Browsed plants produced a greater amount of 1997 biomass per unit of 1996 biomass (P=0.009). This result is probably related to the observed difference in the branching pattern of plants of different treatments. Almost all shoots formed by the unbrowsed plants were developed from the previous year's shoots (1996), but in the browsed treatment many 1997 shoots were developed from shoots older than one year.

Gas exchange. Gas exchange values obtained at the beginning of the season were not different between treatments but the block (site) effect was significant for most of the variables. The environmental conditions under which measurements were performed included a range of light intensities from 1000 to 2100 μmol m^{-2} s^{-1}. Light intensity was positively correlated with temperature ($r = 0.58$, $P = 0.02$), and was not correlated with relative humidity or vapor pressure deficit. A linear relationship was found between light intensity and transpiration rate and water use efficiency (WUE) within the range of 1000 to 2100 μmol m^{-2} s^{-1} (Fig. 5). Photosynthesis rate was not correlated with light intensity ($P = 0.2$), but transpiration was positively correlated ($P = 0.03$). Consequently WUE tended to decrease with higher light intensity. None of the above gas exchange variables were significantly correlated with temperature.

In the second series of measurements, in which a wider range of microclimatic conditions were covered, light intensity, temperature, and relative humidity were positively correlated. Photosynthesis rates increased with increasing light intensity up to approximately 1500 μmol m^{-2} s^{-1}, but beyond this level photosynthesis rates tended to decrease (Fig. 6a). Photosynthesis rates did not show any clear trend with the variation of temperature under the conditions of the experiment (Fig. 7a). Conversely, transpiration followed a linear increase with light intensity, and an exponential increase with temperature (Fig. 6b and 7b). The two variables combined in WUE showed a pattern of response to increase in light intensity similar to that of photosynthesis, but with a higher rate of increase until 1000 μmol m^{-2} s^{-1}, and a higher rate of decrease at higher light intensity (Fig. 6c). WUE displayed a negative linear relationship with temperature (Fig. 7c). Values of WUE at light intensities lower than 100 μmol m^{-2} s^{-1} were erratic and difficult to interpret, but photosynthesis tended to be low at this light intensity. High values of WUE were obtained due to very low values of transpiration. No treatment effects were found in any of the gas exchange variables when data were analyzed using a nested ANOVA design. The nested factor (plants) was not significant in photosynthesis ($P = 0.8$) and WUE ($P = 0.8$) variables. However, it was significant in the case of transpiration ($P = 0.05$) and conductance ($P = 0.0007$).

Light intensity varied greatly between the upper and lower parts of the plant canopy (Fig. 8). At low light intensity under cloudy conditions, light in the lower part of the canopy of the unbrowsed treatment was similar to, or higher than in the upper part of the canopy. This pattern was not found in plants of the browsed treatment, probably due to the fact that the canopies of these plants were smaller and closed. Reductions to 1/10th of the light that reached the upper canopy were measured in the lower canopy in the range of 1000 to 2000 μmol m^{-2} s^{-1}, for both treatments. However, light reductions to less than 1/2 of upper canopy levels were not uncommon. Less heterogeneity was exhibited by the other variables measured (Fig. 8). Temperature tended to be similar, or lower, in the lower part of the canopy, with differences as high as 2 °C, and CO_2 concentration tend to be higher in the lower canopy. Changes in environmental conditions affected gas exchange variables, with photosynthesis and transpiration consistently higher in the upper canopy (Fig. 8). Photosynthesis rate in the lower canopy was often half of that in the upper canopy. WUE tended to be higher in the upper canopy but some erratic values were found for low light intensity, as occurred in the second set of measurements. Changes in photosynthesis rate as a function of light intensity in this set of measurement followed the pattern described previously. However at light intensities higher than 1000 μmol m^{-2} s^{-1}, photosynthesis rates of the lower canopy tended to be lower than in the upper canopy.

Plant nitrogen. Similar dynamics in nitrogen concentration were found in leaves, and in 1997 and 1996 shoots of both treatments (Fig. 9). However significant differences between treatments and watersheds were found on some dates. The percentage nitrogen in 1996 shoots was high at the beginning of the season and decreased until the end of the growing season, when values increased again probably due to translocation of nitrogen from leaves. Plants in Horseshoe Park had a higher nitrogen concentration in 1996 shoots at the end of August, but on the other sample dates values were not different between watersheds and treatments. Leaves had highest nitrogen concentrations at the beginning of the season when they were not fully developed, with concentrations decreasing thereafter. During the growing season, browsed plants had higher nitrogen concentrations than unbrowsed plants, but this difference disappeared during the last part of the growing season (end of August). A significant amount of nitrogen was retranslocated at the time of leaf senescence, producing a decrease in the nitrogen concentration of the leaves prior to litterfall. At this time leaves from browsed plants had higher nitrogen concentration than unbrowsed plants. Shoots produced during the 1997 growing season contained more nitrogen than the previous year's shoots. Nitrogen concentrations in these shoots decreased with increasing shoot length until the end of August, when increases in nitrogen concentration occurred. It is interesting to note that this increase in nitrogen concentration did not correspond with the translocation of nitrogen from the leaves that occurred in the following month. In general, willows growing in Horseshoe Park tended to have higher nitrogen concentrations than willows in Moraine Park, but this difference was not always significant.

One-year-old shoots are the part of the woody biomass that exhibited the highest percentage of nitrogen (Fig. 10). Shoot cohorts older than 2 years presented similar nitrogen content, although the oldest shoot cohort appears to have lower nitrogen percentage. The estimated total aboveground plant nitrogen content was not different between treatments (Fig. 11a). Leaves were the most important sinks of nitrogen in the plant (Fig. 11a). The amount of nitrogen allocated to leaves was similar to or higher than the nitrogen in shoots older than 2 years (old shoots), which represented a high proportion of the total plant biomass (Fig. 4a). A high proportion of the total aboveground nitrogen was allocated to the new shoots. All of the described variables were not different between treatments, but differences were found when the nitrogen content of plant components was expressed relative to the total plant nitrogen. A higher proportion of the total plant nitrogen was allocated into new shoots in browsed than in unbrowsed plants, (0.11 and 0.19 g, P=0.003). Elk browsing reduced 1996 shoot nitrogen proportion to lower values than in unbrowsed plants (0.08 and 0.047 g, P = 0.001). The amount of nitrogen allocated to leaves relative to total plant nitrogen was similar between treatments (P = 0.40). However, browsed plants retained a greater amount of the nitrogen invested in leaves compared to unbrowsed plants (Fig. 11b).

DISCUSSION

Willow growth primarily occurred during times of a shallow water table. Accordingly, groundwater is the most important source of water for these willows (Alstad et al. 1999). Even though snowpack accumulation and melting dynamics varied between years, affecting ground water depths and causing river level fluctuations (Zeigenfuss et al. 2000), It is expected that willows growing close to the active river channel will never experience growth limitation due to restrictions in water availability. This describes the growing conditions of plants measured in this experiment, which were growing in conditions of high water availability. However, this situation does not represent the growing conditions found in some other areas of the watershed where willows are growing, or once grew in the past (see chapter 3).

The reconstruction of the trend in plant biomass formation by the identification of the age of the shoots allowed us to obtain information about the response of the plant to browsing on a time scale longer than the extent of the period of measurements. However, this analysis assumes that plant biomass losses due to other factors besides elk browsing are not important (see chapter 2). During the growing season of 1994, prior to the building of exclosures, plants of the unbrowsed and browsed treatments would have produced a similar amount of shoot biomass. During the winter of 1994/1995, when the long-term exclosures were built, the removal of tissue by browsing produced a significant difference between browsed and unbrowsed willows in the amount of 1994 shoot that remain on the plant. A similar difference between treatments in shoot biomass was found in the case of the shoots formed in 1995 after the exclosures were in place. However, it was not possible to make inferences about the shoot biomass produced that year in either treatment. Total and relative shoot biomass produced in 1996 were not different between treatments at the time of harvest. Total shoot biomass produced in 1997 was not statistically different in terms of total biomass per plant however it was higher in the browsed treatment relative to biomass present at the start of the year. No browsing had occurred on these shoots, since I protected the browsed plants to prevent offtake by elk during the 1997 growing season. The continuous offtake by elk of an important part of the annual woody productivity probably keeps the plant in a more juvenile stage of development, inducing a vegetative growth pattern similar to that of young plants. Consequently, it is probable that browsed plants produce a similar amount of biomass each year. On the contrary, plants in the unbrowsed treatment tended to produce lower relative amounts of biomass as the plants increased in size (Fig. 4a). As a consequence, the total biomass remaining on the plant after browsing occurred would probably have been similar between browsed and unbrowsed treatments some years after treatments began (see chapter 2, table 2 and 3). In this way, the trend in biomass formation through plant development (see chapter 2) interacts with changes in biomass formation induced by elk.

The removal of part of the axis of the shoot by elk causes a reduction in the number of meristems, which constrains the number of buds available for new tissue development. Different compensatory mechanisms were found in browsed plants to overcome this constraint. Despite developing 1/3 of the number of shoots of unbrowsed plants, plants in the browsed treatment produced the same amount of shoot biomass. Browsed plants compensated for tissue removal by producing longer shoots and by developing shoots from axilary meristems of shoots older than one year. The development of old buds into shoots was a characteristic pattern of browsed plants but not of unbrowsed plants. Reduction in the length of shoots axes also constrained leaf and flower production. Since leaves are produced only on new shoots, and there was a significant reduction in the total number of new shoots under browsing, the production of bigger leaves was also a compensatory response. A similar constraint occurred in the production of flowers, but flowers developed from buds of the previous years shoots at the time new shoots start to differentiate. Winter browsing by elk reduced the number of buds that could differentiate into flowers at the beginning of the growing season causing inhibition of flowering. A reduction of flower production could have important effects on plant population ecology (Paige and Whitham 1987).

A browsing-induced reduction in the number of buds available to produce new shoots has important consequences for plant morphology. Browsed plants maintain woody primary productivity by developing buds from old shoots, but these shoots will not produce a significant increase in plant height. In young willows, growth is limited to a few large shoots, which produce a large increase in the overall height of the plant since they develop in the upper part of the canopy. However in older plants, large shoots developing from the lower part of the plant will not contribute significantly to overall plant height. Few shoots will be produced in the upper canopy, and elk will browse preferentially on these shoots during the winter, thus suppressing plant height. In addition, shoots developed from old buds, inside the canopy, will make the canopy more compact, which could have consequences for photosynthetic carbon input.

Although no differences in photosynthesis rate were found between treatments on leaves in the upper part of the canopy, and plants in both treatments developed similar leaf areas, changes in plant canopy architecture induced by elk could still have reduced whole plant carbon input. Photosynthesis rate measured in the upper canopy is not an accurate measure of canopy-level photosynthesis. Reductions to ½ of the maximum photosynthesis rate in the lower canopy were not uncommon in both browsed and unbrowsed plants. Thus, more compact canopies of browsed plants will produce a high proportion of leaf overlap, which could reduce canopy-level photosynthesis.

The higher shoot production per unit of leaf biomass observed on browsed plants was apparently the result of a reduction in the amount of carbon allocated belowground. Browsed willows produced more shoots per unit of leaf biomass, yet browsed and unbrowsed plants had comparable photosynthesis rates and specific leaf area. Additionally, considering differences in canopy structure, as discussed above, it is possible that carbon input per unit of total leaf area was lower in the browsed plants. Together, these results indicate that there will be a lower allocation belowground in browsed compared to unbrowsed plants. In addition, browsed plants will probably have lower shoot/root ratio than unbrowsed plants, because elk reduce aboveground biomass. Lower shoot/root ratios improve the water status of grazed plants (Welker and Menke 1990). Higher water potentials were found in browsed *S. monticola* compared to unbrowsed controls (Alstad et al. 1999). In general elk browsing should increase in the short term, the ability of willows to withstand drier conditions (Alstad et al. 1999). However willows rely on the water table as their main source of water (Alstad et al. 1999). A reduction in belowground allocation of carbon in browsed plants will reduce root development, and browsed willows will be unable to obtain water from a deeper water table. Thus, in a long term, elk browsing will probably reduce willow survival in areas of the watershed with deeper water tables.

Aboveground nitrogen concentrations in grazed plants are often higher than in ungrazed plants (Detling 1988). This was also found in the current study, but as in previous work on these willows (Alstad et al. 1999), differences were not always found through the entire growing season. It is important to consider that nitrogen concentration in leaves as well as in young shoots is continuously changing through the growing season due to growth and translocation, while nitrogen concentration of old shoots is probably more stable. At the end of the growing season some part of the nitrogen recovered through retranslocation, before leaf senescence, was probably moved to previous year's shoots, which recover some of the nitrogen previously in the growing shoots. However, most of this nitrogen was moved to other parts of the plant, most probably the belowground component. Younger shoots were not the sinks for this nitrogen, but nitrogen concentration markedly increased in these shoots by the end of the growing season, before leaf nitrogen retranslocation. This increase in shoot nitrogen probably occurred because growth was almost finished at this time but the shoot was still acting as a sink for nitrogen. Nitrogen concentration increased because there was no dilution effect due to shoot growth. Younger shoots constituted the most nitrogen rich tissues of the aboveground part of the plant after the growing season ended. The nitrogen stored in younger shoots, as well as the nitrogen translocated from leaves during leaf shedding probably constituted the most important sources of nitrogen to support growth initiation in the subsequent growing season. This pool of nitrogen was largely reduced in browsed plants because the amount of nitrogen retranslocated from leaves was lower and an important portion of the nitrogen in younger shoots was removed by elk. Results here indicated that at the beginning of the growing season the total pool of nitrogen in the plant was lower in browsed willows. If this is the case, browsed plants need to take up a higher proportion of nitrogen from the soil to start leaf area development. A lower amount of nitrogen stored in browsed plants could be one of the reasons for later growth initiation. Beside this possible limitation in nitrogen availability in browsed plants, nitrogen concentrations in the most active aboveground biomass (leaves and younger shoots), were similar between treatments, as was biomass production. However, browsed plants could mobilize more nitrogen from the soil if soil nitrogen availability were increased by grazing. Ungulates could increase nitrogen availability through feces and urine deposition or by changing chemical secondary composition in plant tissue, which in turn will affect nitrogen mineralization rate (Frank et al. 1994, Menezes 1999).

CONCLUSIONS.

Willow plants support high levels of elk browsing without incurring a reduction in aboveground productivity. Tissue removal by elk reduces the number of axilary meristems, which are required for further plant size increases and development, but browsed plants compensate for this constraint by developing old buds and producing larger shoots and leaves. However, the reduction in the length of shoot axes prevents flower production, which could affect willow population dynamics. Total carbon input was similar or lower in browsed than unbrowsed plants but browsed plants produced a higher shoot biomass per unit of leaf biomass. This indicates that more carbon is allocated aboveground in browsed plants, which in turn will reduce root development. Tissue removal by elk apparently reduces the pool of nitrogen available for growth initiation. Similar nitrogen concentrations were found in both treatments during the growing season, which could be the result of higher soil nitrogen availability on grazed areas. Most of the short-term effects induced by elk involved morphological rather than physiological changes. However, long-term plant morphological changes induced by elk such as changes in canopy architecture, will in turn affect plant physiological processes. Reduced root development could reduce competitive ability and survivorship of willow under drier growing conditions and deeper water table levels.

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Table 1. Regression models of leaf area on shoot and leaf morphological variables, and leaf area on leaf dry weight of grazed and ungrazed treatments.

Dependent variable	Predictors	Model	P value	R2
Log of the leaf area/shoot - Ungrazed treatment (cm^2) (LAUG)	-log of the longest leaf per shoot (cm) (LL) -log of the number of leaf per shoot (LN) -log of the shoot length (cm) (SL)	LAG = - 0.12 + 0.98 * LL + 0.62 * LN + 0.35 * SL	<0.0001	0.89
Log of the leaf area/shoot - Grazed treatment (cm^2) (LAG)	-log of the longest leaf per shoot (cm) (LL) -log of the number of leaf per shoot (LN) -log of the shoot length (cm) (SL)	LAG = -0.22 + 0.96 * LL + 0.67 * LN + 0.32 * SL	<0.0001	0.93
Leaf area (cm^2) - Ungrazed treatment (LAUG)	Leaf dry weight (g) (LDW)	LAUG = 6.64 + 129.22 * LDW	< 0.0001	0.98
Leaf area (cm^2) - Grazed treatment (LAG)	Leaf dry weight (g) (LDW)	LAG = 31.78 + 126.42 * LDW	<0.0001	0.98

Table 2. Pearson correlation coefficients for the unbrowsed (lower left), and browsed (upper rigth) treatments of different components of plant biomass.

	Total dry Weight	**Leaves dry weight**	**1997 shoots dry weight**	**1996 shoots dry weight**
Total dry weight	1	0.85 (0.007)	0.74 (0.03)	0.91 (0.001)
Leaves dry weight	0.74 (0.03)*	1	0.96 0.0001	0.96 (0.0001)
1997 shoots dry weight	0.79 (0.02)	0.97 (0.0001)	1	0.92 (0.001)
1996 shoots dry weight	0.86 (0.006)	0.93 (0.0009)	0.94 (0.0004)	1

* P-values in parentheses

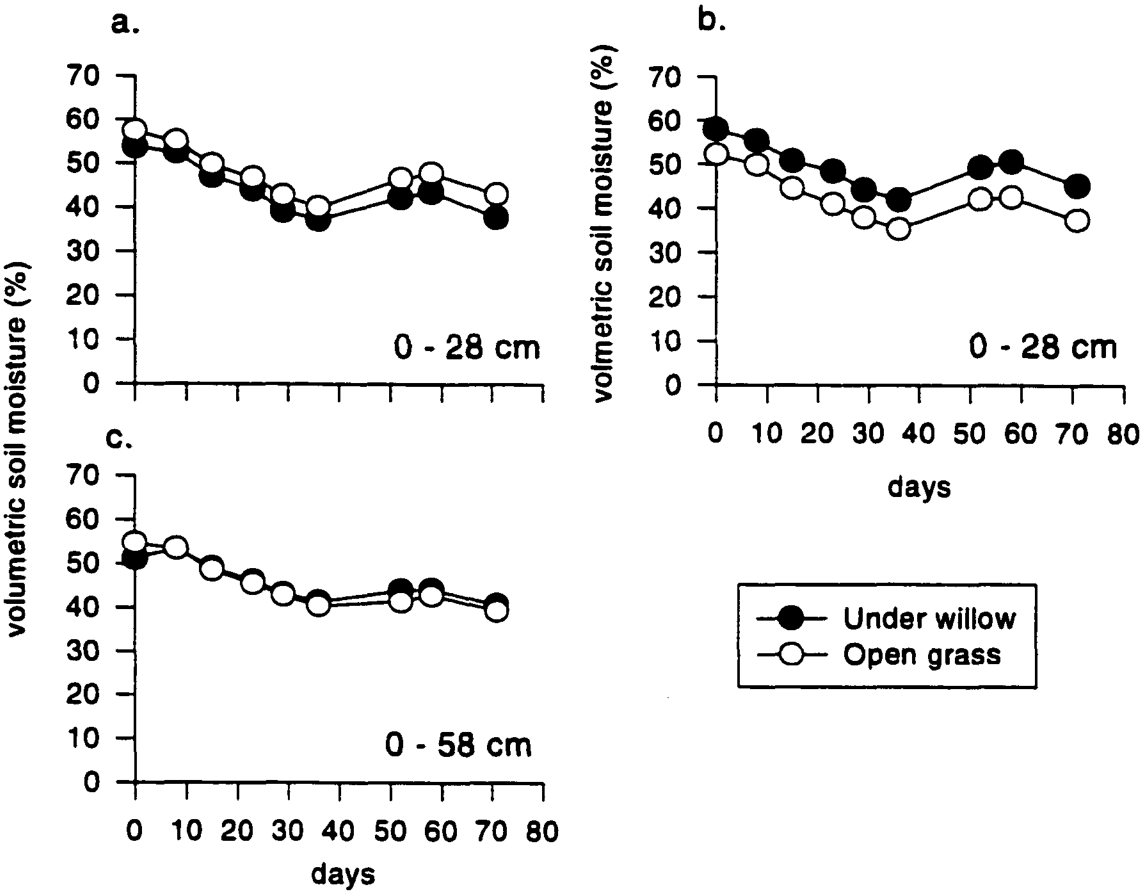

Figure 1. Volumetric soil moisture in open grass and under willow trees of Horseshoe Park (a and c) and Moraine Park (b) from July 16 to August 26

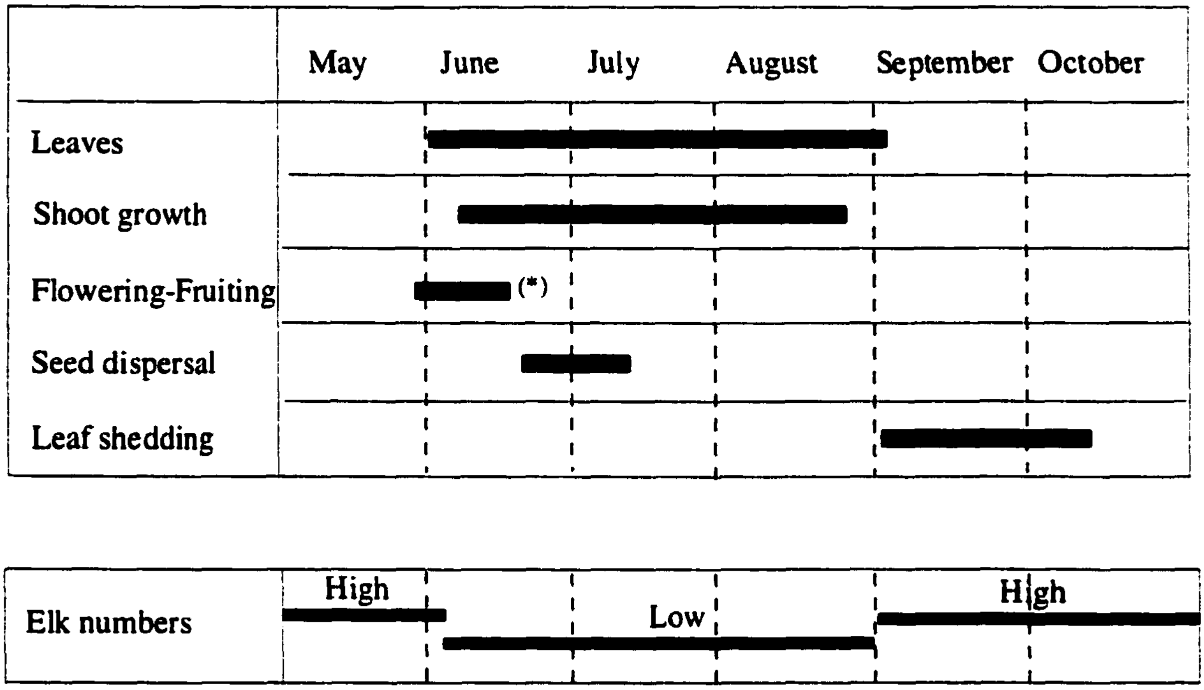

Figure 2. Phenological phases of Salix monticola and relative number of elk on the study areas (*) no flowers were found in browsed plants.

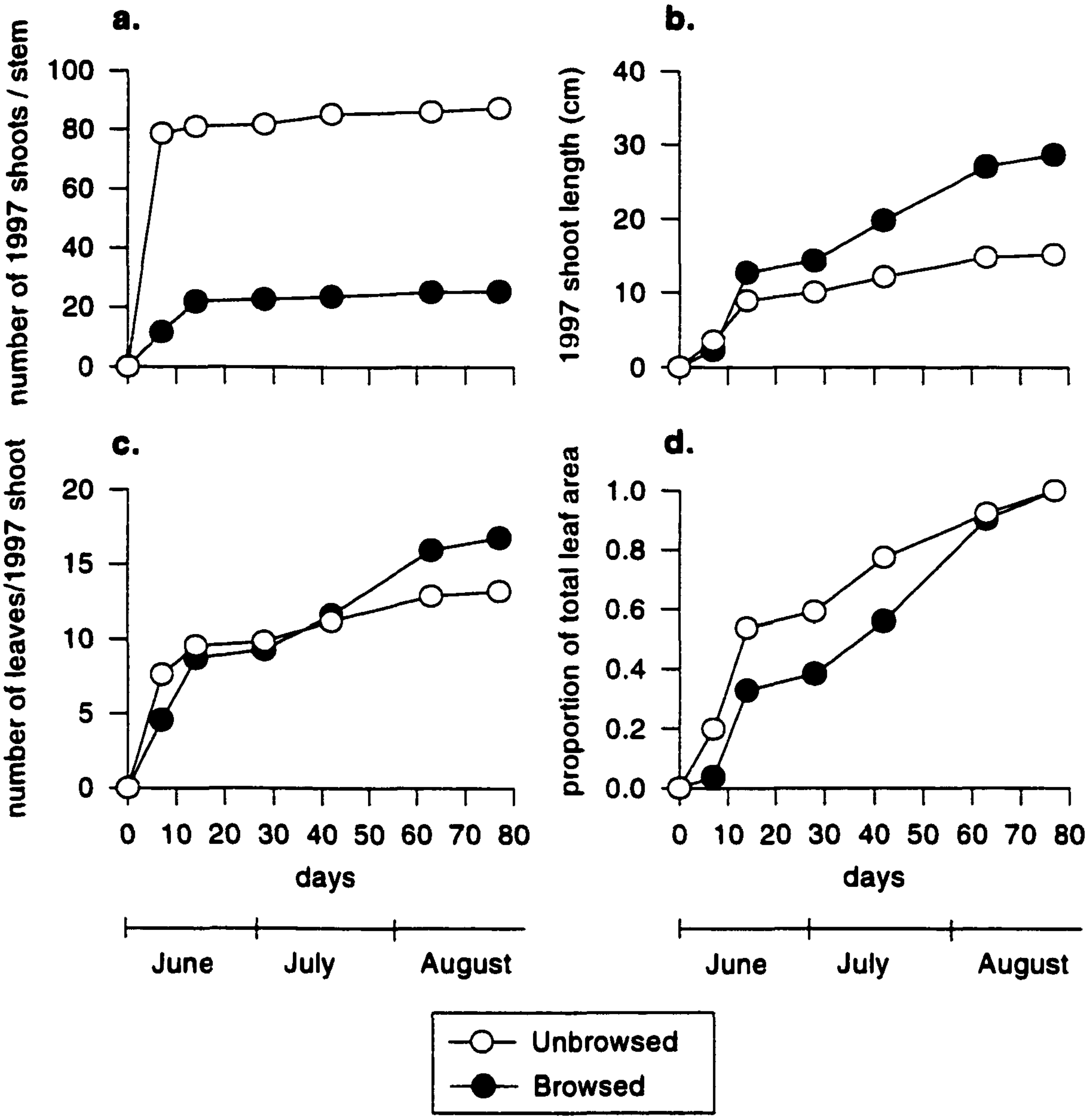

Figure 3. Number of 1997 shoots per stem (a), 1997 shoot length (b), number of leaves per 1997 shoot (c), and proportion of total leaf area (d) through the growing season, begining June 2. Values indicate means of the unbrowsed and browsed treatments.

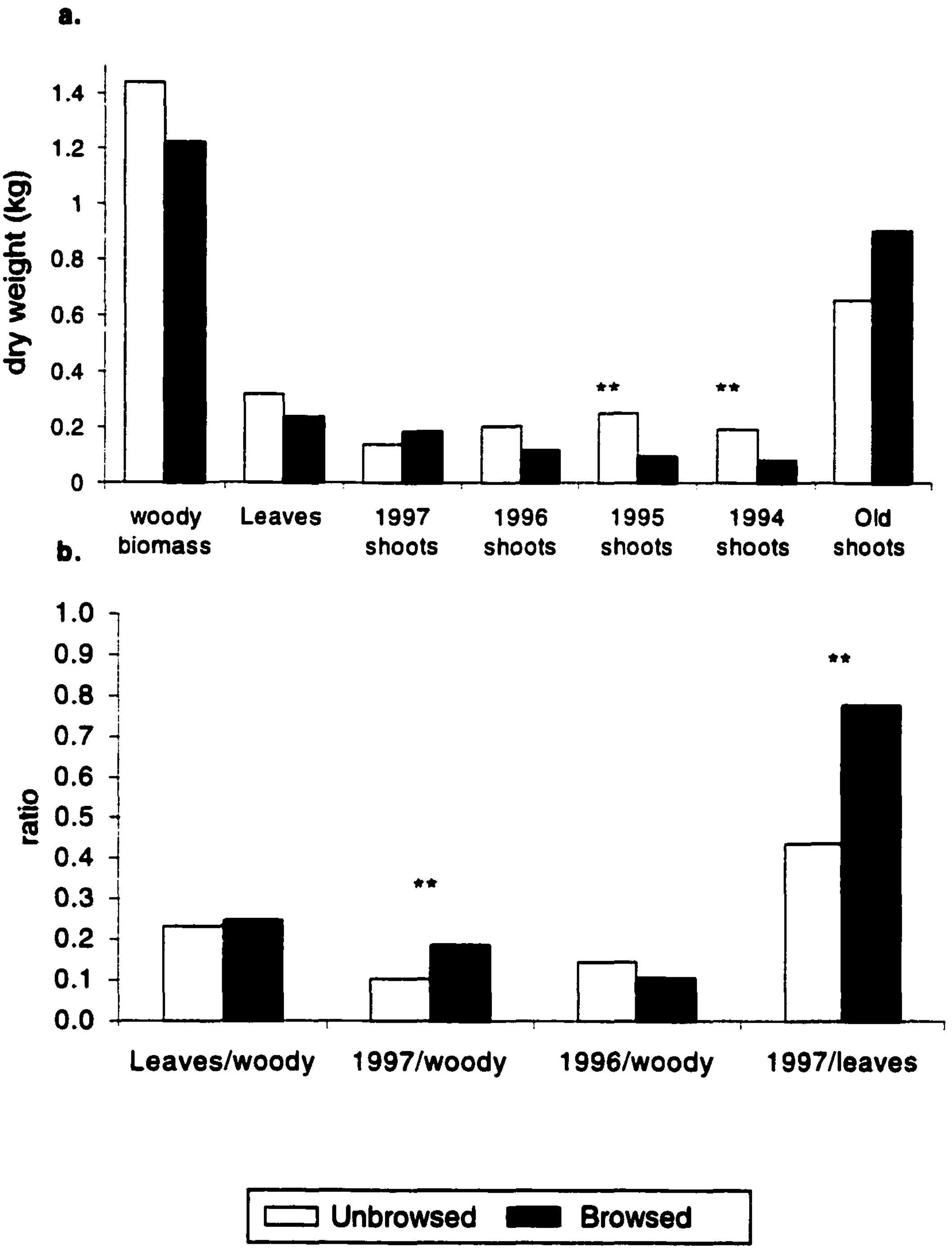

Figure 4. Dry weight of different plant components (a), and ratio of leaves, 1997 shoot, and 1996 shoot biomass to total woody biomass, and ratio of 1997 shoot to leaf biomass (b) for the unbrowsed and browsed treatments.
** indicates that means are statistically different ($P < 0.01$).

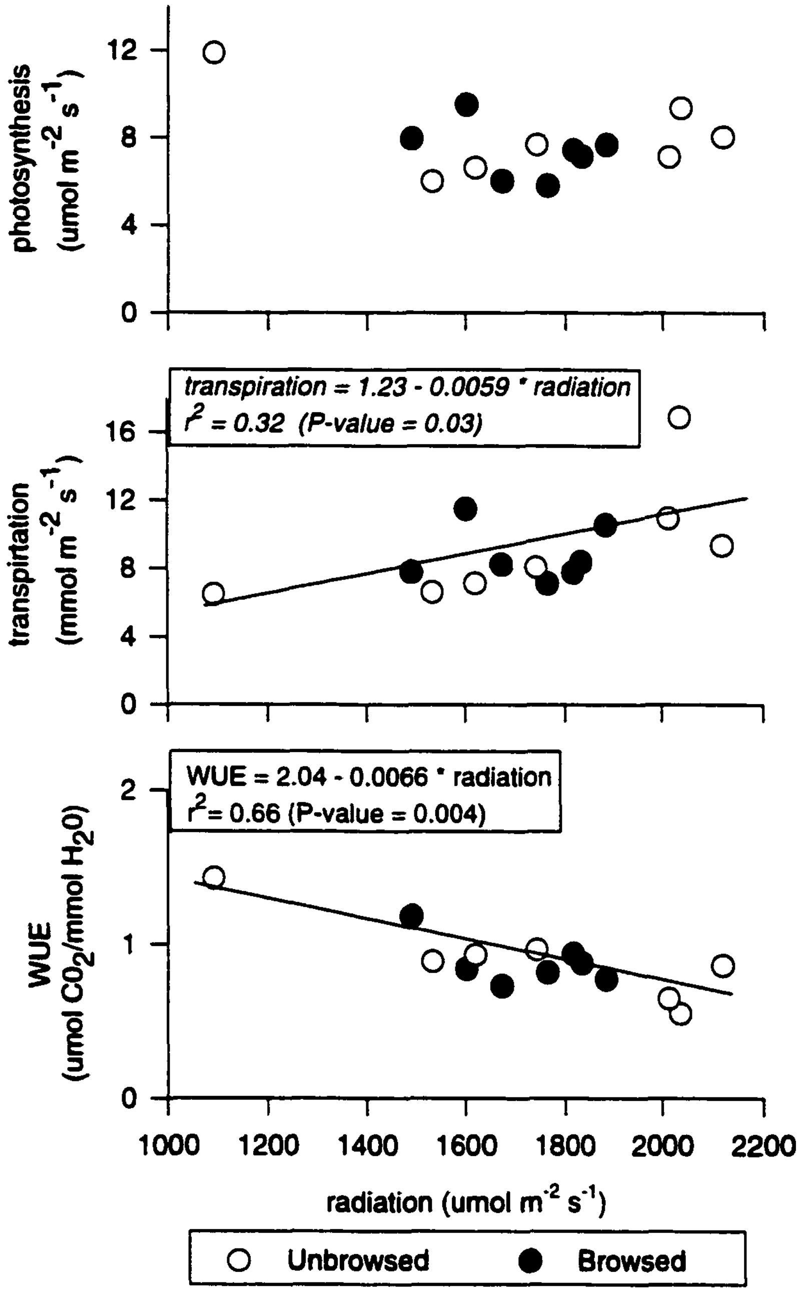

Figure 5. Gas exchange variables as a function of light intensity on plants of unbrowsed and browsed treatments. Each point represents a mean of 2 plants. Regression models were created based on the represented points.WUE : water use efficiency.

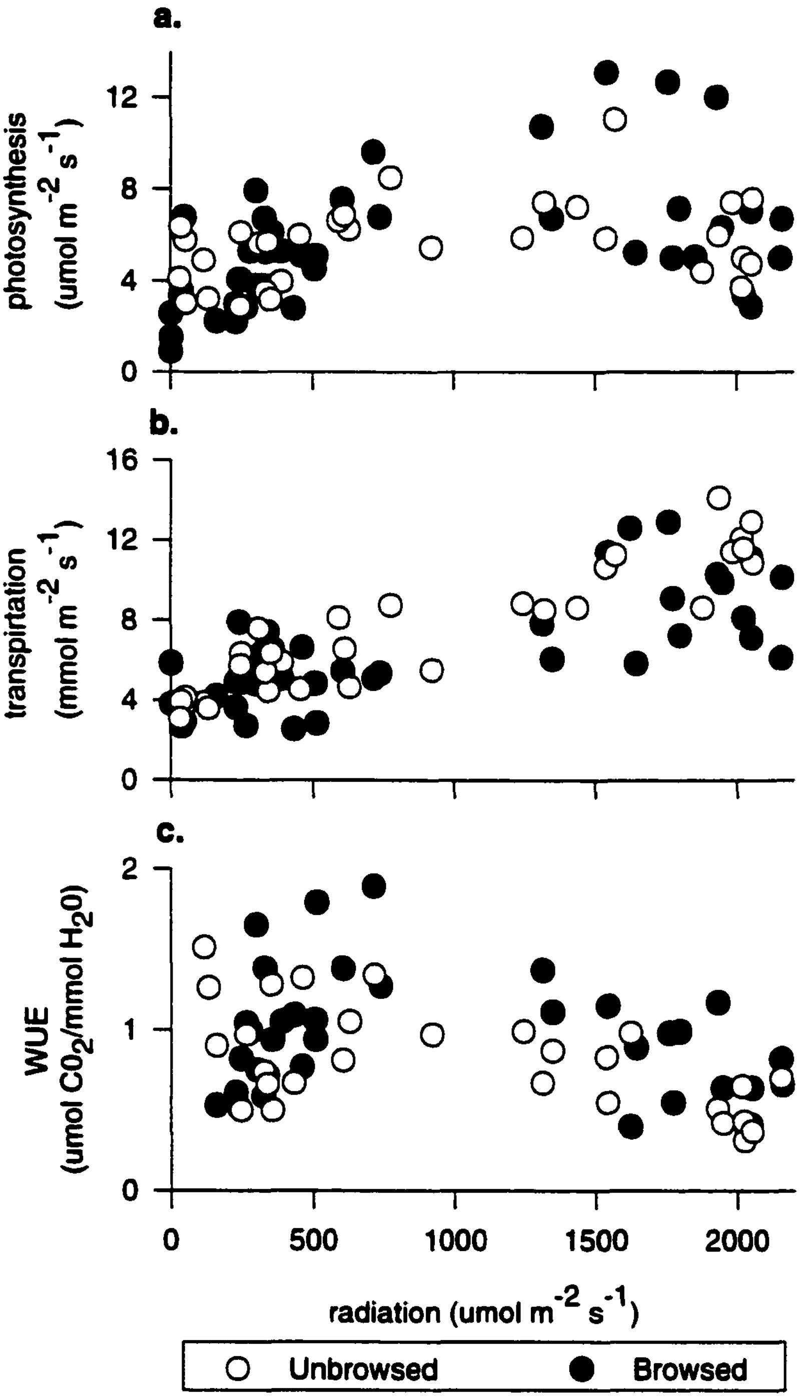

Figure 6. Photosynthesis (a), transpiration (b) and water use efficiency (WUE) (c) as a function of light intensity in the grazed and ungrazed treatments. WUE values at a light intensity lower than 100 umol m-2 s-1 are not shown.

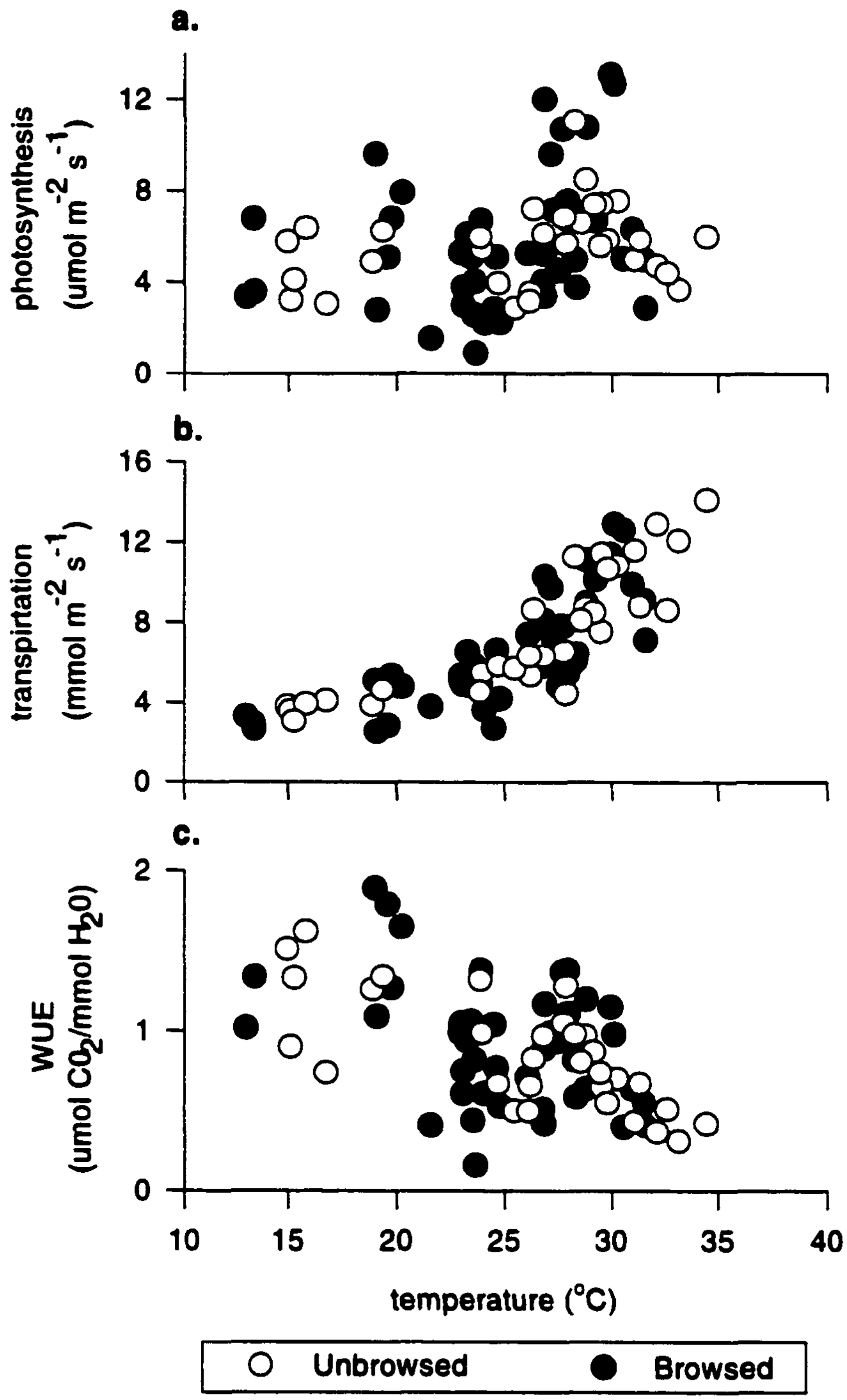

Figure 7. Photosynthesis (a), transpiration (b) and water use efficiency (WUE) (c) as a function of temperature in the unbrowsed and browsed treatments.

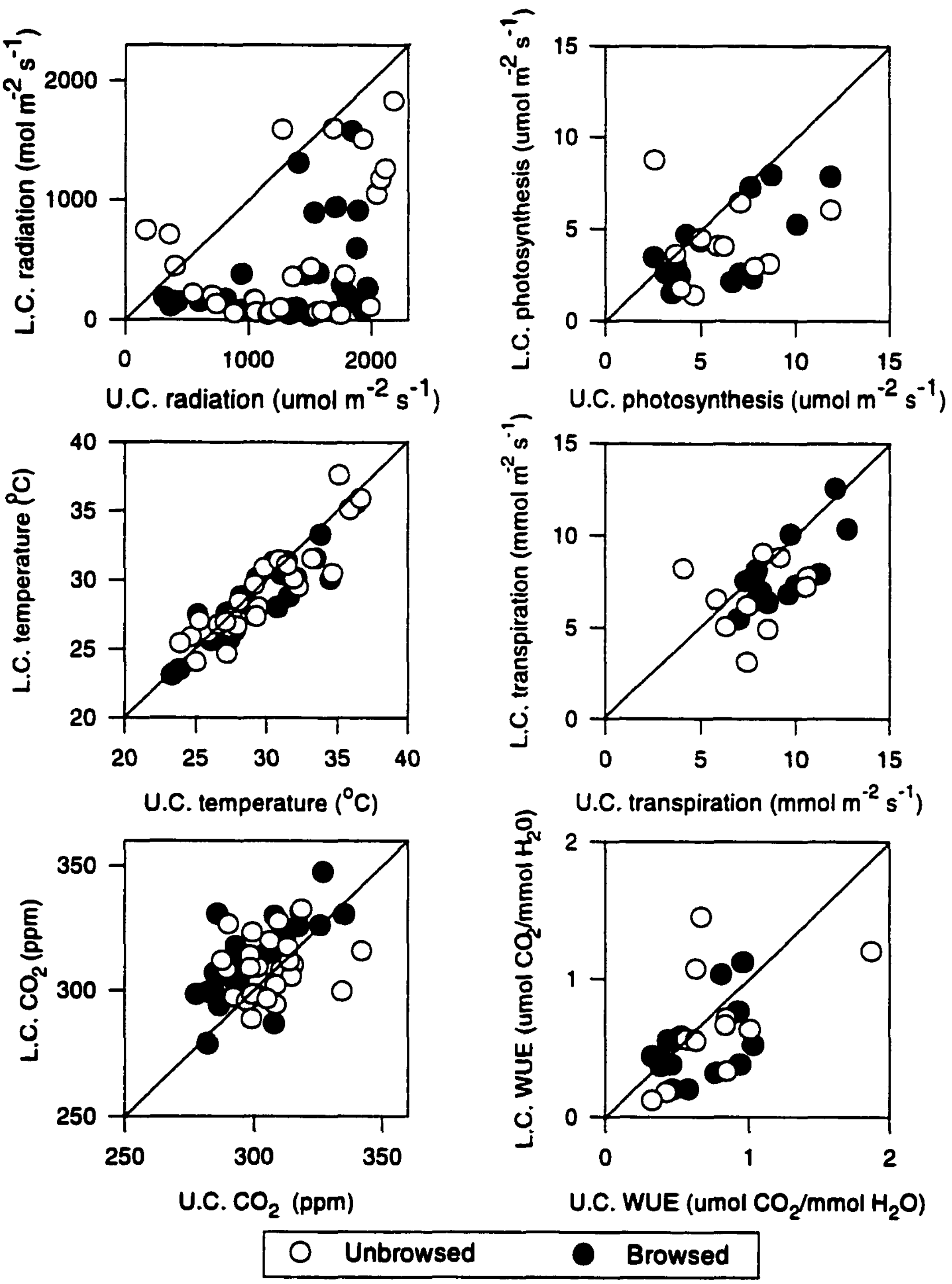

Figure 8. Environmemtal conditions and gas exchange variables in the upper and lower parts of the canopy of unbrowsed and browsed plants. References: U.C. : upper canopy, L.C. lower canopy, WUE: water use efficiency.

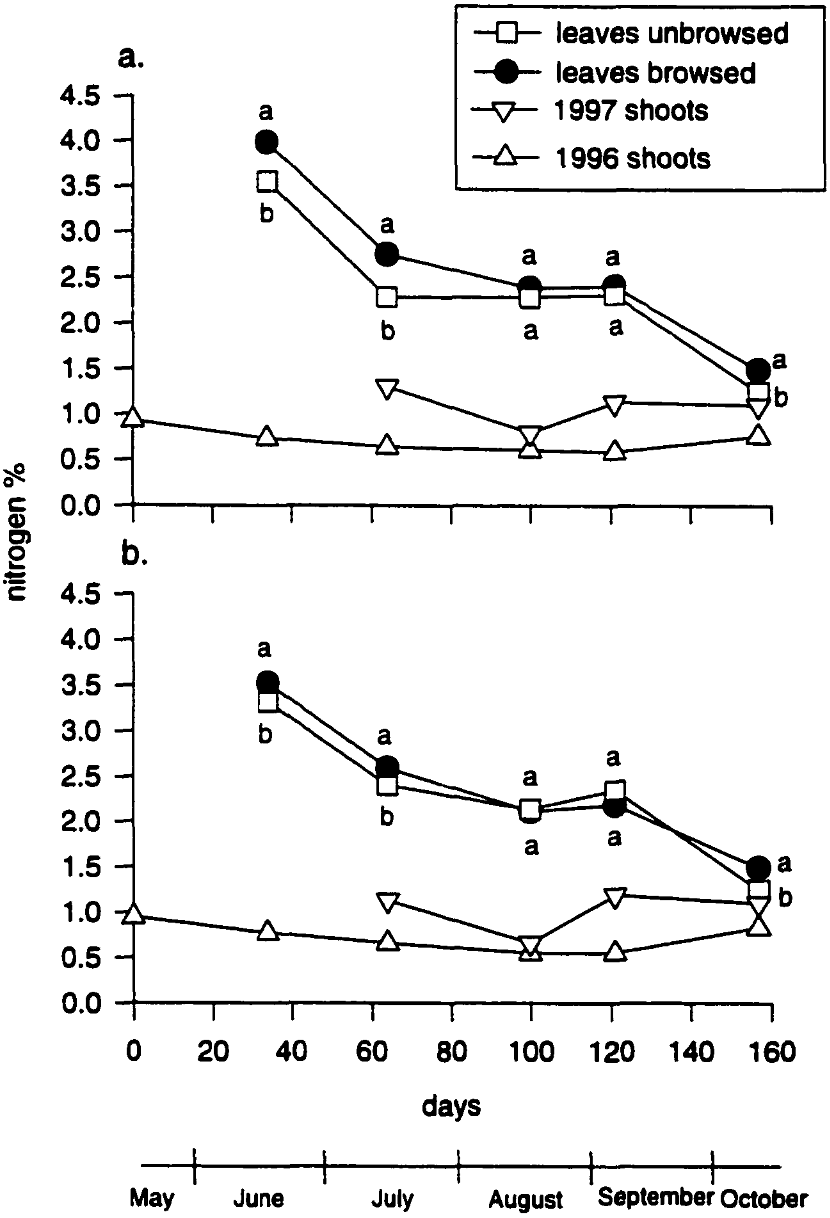

Figure 9. Percentage of nitrogen in leaves, 1997 shoots, and 1996 shoots in Moraine Park (a) and Horseshoe Park (b). Unbrowsed and browsed treatment mean are represented in case of leaves. Letters indicate significant differences between points at the same date ($P<0.05$).

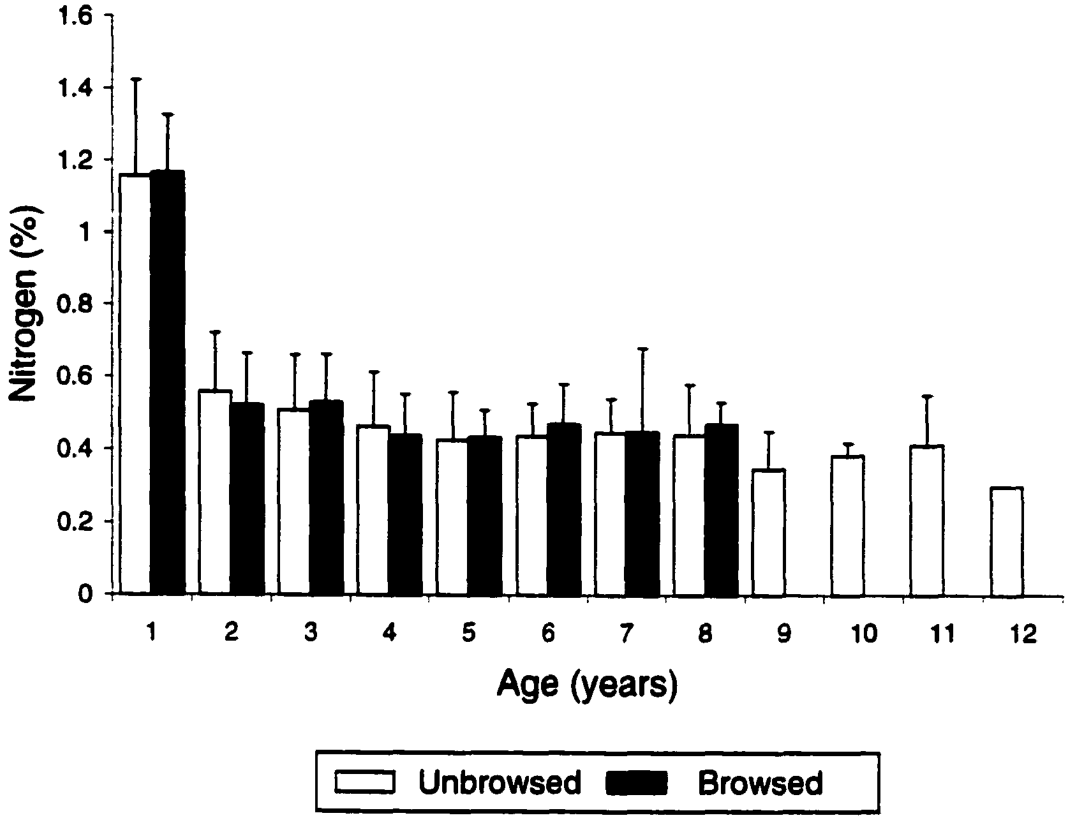

Figure 10. Percentage of nitrogen of shoots of different age of plants of unbrowsed and browsed treatments. Bars represent standard deviations.

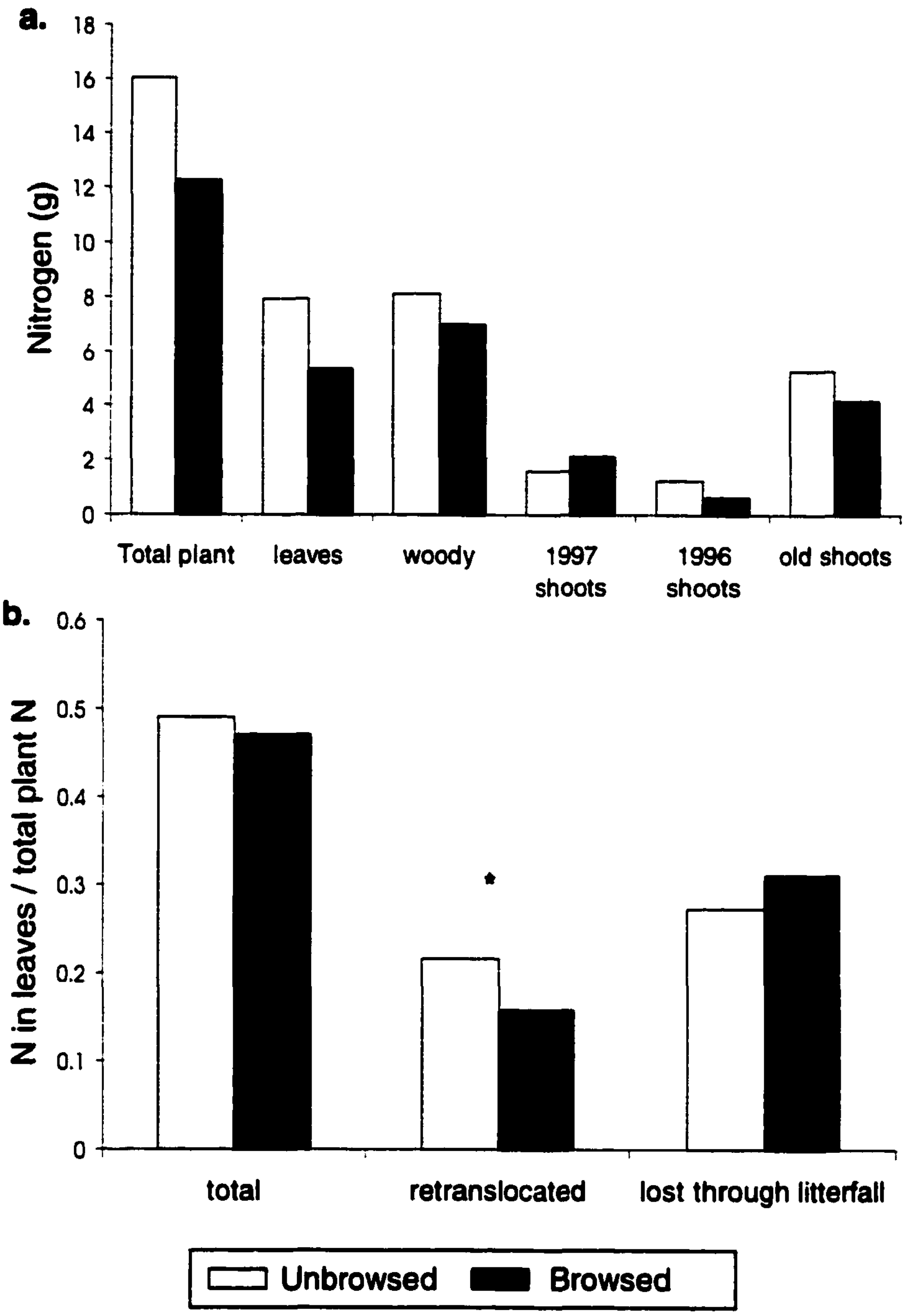

Figure 11. Total nitrogen per plant in different plant components (a), and ratio of leaf nitrogen to total plant nitrogen (b). Bars correspond to mean values of unbrowsed and browsed treatments. References: (*) indicates that means are statistically different at $P<0.05$.

CHAPTER 2

Plant metameric units as a record of past growing conditions to assess the effect of elk browsing on willow growth.

Abstract. I evaluate the hypothesis that elk (*Cervus elaphus*) browsing on willow (*Salix spp.*) induces suppressed short morphotypes. Elk herbivory visually appeared to be responsible for height suppression, but both short and tall willow could be found in the same watershed. Willows exhibit a sympodial branching pattern in which the abortion of apical buds is genetically programmed, and the extension growth of the metamer (shoot thereafter) is restricted to the growing season in which it was formed. Willow response to elk browsing was studied by comparing shoot morphology and biomass of plants with different elk browsing histories. This information was integrated with a population level study to infer the long-term response of willow to elk browsing.

The study was conducted using samples from 3 populations growing in the same watershed namely; short willow protected from browsing by 4 exclosures built during the fall of 1994 (short protected); short willow around each exclosure in areas open to elk browsing (short browsed) and tall willow from 4 spatially separated sites of the upper watershed (tall). In each stem, shoots were aged and separated by cohorts, and the number, length, and total biomass was measured. I also compared height growth of stems of *S. monticola* plants, which had 5 years of protection from elk browsing (1994-1998), with tall willow stems. Finally, I surveyed 3 willow populations growing in different areas of the watershed, which included one of the exclosures built in 1994, the associated short willow area, and a tall willow area.

The number of shoots in the 1998 cohort was 2 to 4 times that of the 1997 cohort. A lower number of 1998 shoots and a higher frequency of shoots in the longest category was observed in browsed stems, while stems of tall and short protected willow were similar. The effect of protection from elk browsing was evident in the length and biomass of shoot cohorts produced after 1994 in the short fenced treatment. Stems from exclosed short willow showed higher relative biomass accumulation rate (RGR) in the shoot cohort produced in 1994. As time progressed, RGR on this treatment become similar to that of tall willow plants. Short exclosed willow tended to have lower values of RGR, however short willows showed the highest RGR on the 1998 cohort (different form other shoots, these shoots were not browsed). Shoot biomass accumulation on the stem was higher in the older cohort and decreased progressively to the youngest cohort in tall and short browsed treatments. This pattern was similar to the pattern of tree ring growth. Protected willow showed a disruption in this pattern with a peak of biomass accumulation in the year the exclosures were built. The same pattern was observed in all three species studied. Plant protection favored plant height increase, but 4 years of protection was not enough for a short willow to reach the height of tall willow. Stems of protected willow showed a similar rate of height increase to young stems of tall willow in the period 1994-1998 (36 and 31 cm/year, respectively), and a higher rate than old stems of tall willow (17 cm/year, P=0.003). A similar pattern was found in the population level study in which fenced willows showed a clear shift from short to tall population characteristics in terms of percent cover and height frequency distribution of individuals in the population.

INTRODUCTION

In modular organisms, growth is ultimately a result of the increase in the number of metameric units (Harper and Bell 1979). Early botanists developed this concept, but different criteria have been used to define metameric units in plants (White 1979). In woody plants, one important metamer is the part of the plant determined by the annual extension growth of the apical or axillary meristems (hereafter shoots). The dynamics and characteristics of these units will determine the increase in plant height and canopy volume, and therefore most of the overall increases in aboveground plant biomass. These metameric units have been used in plant morphology to understand branching pattern and to model plant canopy structure (Honda 1971; Hallé et al. 1978), but few studies have considered the use of these units to study woody plant ecology. Shoot cohorts can be used as a reference to date individuals. Then, the age of the plant can be determined by counting shoot cohorts (Alliende and Harper 1989, Hibbs 1979). Shoot cohorts also can be used to reconstruct the temporal dynamics of aboveground growth of individual plants. Shoot of the same age can be cut and grouped to determine shoot cohort biomass. Records of annual aboveground biomass accumulation of individual plants created based on shoot cohort biomass, can be used to infer long-term characteristics of plant growth. Similarly, shoot cohorts morphology instead of biomass can be used. This approach was used in this study to gather historic information of individual willow plants (*Salix spp.*), under different elk (*Cervus elaphus*) browsing intensities. This information was integrated with a population level study to infer long-term responses of willows to elk browsing.

Suppressed (> 1.5m) and tall (< 2 m) willow morphotypes grow in the same watersheds of the eastern slope of Rocky Mountain National Park (RMNP), Colorado. It is not clear whether these two willow morphotypes are the result of differences in site conditions, elk browsing pressure, or genetic differences between the two populations (Singer et al. 1994). In this paper I evaluate the hypothesis that short morphotypes are primarily the result of the removal of current annual shoots by elk, which inhibits subsequent willow height increase. A 3-fold increase in elk population that has occurred in RMNP could have favored an increase in the proportion of short willow (Singer et al. 1998). Consequently, if the current browsing pressure is what determines the suppressed morphology, plants should shift to a tall morphotype when elk browsing is prevented. To test this hypothesis, short willows that had been protected from browsing for 4 years were compared with browsed short and tall willow morphotypes. The hypothesis was evaluated at both the individual and population levels.

MATERIALS AND METHODS

Sampling sites and characteristics.

The winter range for elk in Rocky Mountain National Park (RMNP) encompasses about 10,000 ha, which includes land within the eastern side of the park and private and national forest lands outside the park in the town of Estes Park and the Estes Valley, Colorado (Singer et al. 1998). Sampling was conducted in two riparian ecosystems on the northeastern quarter of RMNP: Horseshoe Park (Fall River watershed, elevation 2,598 m), and Moraine Park (Big Thompson River watershed, elevation 2,481 m).

Different sampled units were used in this study. The study willows exhibit a shrub morphology, in which the individual plant is composed of several stems that arose from the crown placed at the ground level. The stem was the sampled unit in the individual level study. In the population level study, the sampled unit was the individual plant, which was determined based on stems clump that indicate the position of the crown.

Individual level study.

Identification of shoot age. In plants with a sympodial growth pattern such as willows, abortion of the shoot tip is genetically programmed (Raven 1992), and extension growth of the shoot is restricted to the growing season in which the shoot was formed. Thus, at the start of the growing season, terminal shoots are one year old. Shoots that support one-year old shoots are 2 years old. By continuing this sequence, most of the shoots of the plants could be dated.

This sequential order is that of the proleptic shoot, in which the shoot develops from a bud that is one year old. Shoots also develop from buds older than one year (epicormic shoots) (Tomlinson 1983, Remphrey and Davidson 1992). Although epicormic growth should make the aging of shoots more complicated, the method could still be used. Epicormic shoots do not follow the spatial-temporal sequential order described above, however other shoots of the same age as the epicormic shoots did follow the sequential order and they can be considered as a reference for ageing the stem. Since shoot cohorts were removed sequentially starting from the youngest cohort, any epicormic shoot on the removed cohort was easily identified as those shoots that were placed on shoot older than one year of difference with the removed cohort.

Because the main axis of the stem is composed of more than one shoot, the scars left from dormant overwintering buds were used to distinguish individual shoots (Alliende and Harper 1989). The accuracy of the methods was checked in some samples by counting annual rings at the base of the shoots. In all cases the predicted age by the morphological method gave the same result as the ring count.

Shoot morphology and biomass. Stems from different willow species and morphotypes were sampled in Horseshoe Park at the end of the 1998-growing season, before leaf shedding started (end of August). Short willow patches occurred mostly in the lower part of the valley while tall morphotypes were predominantly in the upper areas of the valley (see chapter 3). This spatial distribution constrained the sample design because samples from different morphotypes had to be taken from spatially separated sites on the watershed. Short willow samples were taken in the lower part of the watershed from 4 exclosures (30 m x 46 m) built during the fall of 1994 (short protected), and from short willow around the each exclosure in areas open to elk browsing (short browsed). Tall willow samples were taken from 4 spatially separated sites in the upper part of the watershed (tall). In each case I randomly chose one plant each of *S. geyeriana*, *S. monticola*, and *S. planifolia* within the tallest strata of the willow stand. Nine treatments were defined, that corresponded to the combination of 3 willow populations (short protected, short browsed, and tall) and 3 species.

In each plant I cut one of the tallest stems at the base of the plant. The height of the cut stem was measured and all dead ramifications of the stems were removed and discarded. Shoots produced during the 1998 season were cut and grouped. Since all leaves were situated on the current annual shoots, leaves were collected together with the 1998 shoots. All shoots of the rest of the stem were identified following the morphological methods described previously, cut and grouped by cohort. Leaves were separated from the 1998 shoots and leaf area and biomass (dry weight) were measured. Leaf area was measured with a LI-3000 LI-COR leaf area meter. In each cohort I measured the number and total dry weight of shoots, and the length of each shoot longer than approximately 5 cm.

Elk browsing on willow occurs mainly during the winter, and most of the elk population was on the summer range at the time samples were taken. Nevertheless, I checked every sampled stem to ensure that 1998 shoots were not affected by browsing removal. Elk offtake was prevented inside the exclosures since the fall of 1994. However, elk browsing could have occurred on some 1994 shoots of the protected plants during the time the exclosures were being built because at this time elk were just coming on to the winter range. Nevertheless, any such offtake would have been much lower than that in the browsed treatment.

Height increase of stems. A second sample was taken on tall and short protected *S. monticola* plants to determine the dynamics of height increase. The goal of this study was to determine if willows growing under protection from elk browsing are able to increase height at a rate similar to tall willow plants. Consequently, samples were taking only from the short protected and tall populations. Sampling was conducted during the first week of September of 1998 and included Horseshoe and Moraine Parks. Short willow stems were taken from plants growing inside 4 exclosures built in 1994 in each watershed. In each exclosure I randomly chose one *S. monticola* plant and I cut one of the tallest stems at the base of the plant. A total of 16 stems from tall willow plants were sampled (8 plants in each watershed). Samples of old and young stems were taken. In half of the selected plants, I cut one of the tallest stems with a small stem diameter (young tall stem), and in the other half I cut one of the tallest stems with a large stem diameter (old tall stem). In this way, I compared the rate of height increase of stems of protected plants with that of stems of plants having a range of height rate increases. The height of the cut stem was measured, and later shoots were removed sequentially starting with the youngest. Once a shoot cohort was cut, the height of the remaining stem was recorded. I continued this procedure until all of the shoots of the stem were removed.

Data analysis. Morphology and biomass variables of shoots and stems were analyzed using a two-way ANOVA, and the rates of stem height increase were compared using one-way ANOVA. In both cases, a complete randomized design was assumed. A logarithmic transformation was used in some variables to meet the homoscedasticity assumption. Analyses were restricted to shoots younger than 1994, the year the exclosures were built. Analyses of older shoot biomass or morphology were not performed due to differences between treatments in the age of the stems. Since shoot length exhibited a skewed distribution, particularly in younger shoot cohorts, shoots were classified into four length classes within each treatment and age cohort. Shoot frequency within each length category and cohort was compared. The smallest class was defined as shorter than 5 cm. The limits of the other 3 classes were defined as 5-15 cm, 15-45 cm, and > 45cm. Additionally, in the case of short protected willows, a correspondence analysis (Greenacre 1984) was used to characterize changes induced by the exclosures in the frequency distribution of shoot cohorts on the stems. In the case of shoot biomass, a relative biomass accumulation rate variable (RGR) was defined to account for differences in the heterogeneity in total biomass of the sampled stems. The relative growth rate for a shoot cohort of age n was calculated as

$$RGR_n = \frac{DWT_n}{\sum_{i=1}^{n} DWT} \qquad \text{Eq. 1}$$

where DWT_n is dry weight of shoots in cohort n and where 1 is the oldest cohort.

Population level study.

Short and tall willow populations were surveyed in Horseshoe Park during summer, 1998. Surveys included a short willow population located inside an exclosure built during the fall of 1994 (short willow, protected), a population of short willows growing in an associated browsed area (short willows, browsed), and a tall willow population growing in the upper areas of the valley. A quadrat was randomly located in each survey population, and all of the individuals inside the quadrant were counted and measured. Quadrat size was 50m x 50m in the case of short browsed and tall willow populations, and 25m x 30m in the case of short willow protected. A smaller quadrant was used inside the exclosure due to the size of the exclosure (30m x 46m). Plant canopy diameter was estimated as the average of the widest and narrowest canopy diameters. Canopy area was calculated for each plant assuming a circular shape. The response of short willows to protection from elk browsing was evaluated by comparing the height frequency distributions of short and tall browsed willow with the protected willow population.

RESULTS

Individual level study.

Stem characteristics. The ages of the stems in the entire sample ranged from 6 to 25 years (Table 1). Tall willow stems were generally older than short willow stems, and short browsed stems tended to be older than the stems of short protected willow plants. Stem age varied among species within the same sample population. The highest heterogeneity occurred in the tall willow population where *S. planifolia stems* were much younger than the stems of the other 2 species. Stem heights were consistently different among populations, but they were not significant differences among species (Table 1). Tall stems were taller than 3 m, and protected short willow stems were significantly taller than browsed short willow stems. Leaf area, leaf biomass and woody biomass per stem were similar in exclosed and browsed willows. These variables had smaller values in short than in tall morphotypes. However, leaf:woody biomass ratios were higher in protected short willows than in tall willows ($P<0.05$). Although leaf and woody biomass of *S. planifolia* tended to be lower than in other species in protected and browsed willows, and higher tall willows, no significant differences between species were found.

Shoot morphology and biomass. Few shoots of the sampled stems were epicormic in tall and protected willows. Epicormic shoots were more frequent in stems of short fenced willows. The different populations differed in the total number of shoots developed in the last growing season, and in the number of shoots remaining on the stem from previous growing seasons, but no significant differences were found between species. There was no shoot cohort older than 15 years that was represented by more than 1 shoot. Tall willows had a higher number of shoots from 1994-1997 shoot cohorts compared to the other treatments (Fig 1 a-e). Short protected and browsed willows had similar numbers of shoots in 1994 and 1995 cohorts, but the 1996 and 1997 shoot cohorts were more numerous in short protected willows. Number of shoots produced in 1998 was lower in short browsed compared with tall and short protected willows (P = 0.001) (Fig 1a).The numbers of shoots formed during the 1998 growing season were between 2.4- to 4.3-fold higher than the number remaining from the 1997 growing season in all treatments (Fig. 1a, b). Most of the shoots produced in 1998 were classified in the shortest category (< 5 cm), particularly in the case of tall and short exclosed willow. Thus, differences in the number of 1998 shoot among different willow populations were mainly due to differences in the number of short shoots. Browsed willows had higher frequencies of shoots in the longest size classes compared with tall and short browsed willow, indicating that browsed plants allocate more resources to the production of long shoots. The skewed distribution to short shoots that was observed in the 1998 cohort was also characteristic of the other cohorts analyzed in tall and short browsed willow. Short exclosed stems showed a different pattern. The 1994,1995 and 1996 shoot cohorts showed bell-shaped size class distribution and the other cohorts showed a change to the skewed size class distribution found in the other populations.

Correspondence analysis of the frequency distribution of shoot cohorts of exclosed willow showed that responses of protection from browsing, beginning in 1994, were similar in the three species studied (Fig 2). Shoot length classes from the different species were arranged from shorter to larger scores along the first axis. Changes in the lengths of the shoots that occurred after plant protection were evidenced by the relative positions of shoot cohorts younger and older than 1994. The oldest shoot cohort (1988) had a similar axis 1 value as that of the longest shoot length classes (> 45cm). Browsing reduced the lengths of the shoots produced between 1988 and 1993, and the frequencies of these shoots were within a cluster similar to medium (15-45 cm) and small (6-15 cm) size classes. A disruption in the relative position of the cohorts occurred in the year the exclosures were built. The 1994 cohort had a distribution similar to the longest shoot classes, and the following cohorts were arranged from long to short length classes indicating an increase in the proportion of short shoots since the time elk browsing protection was initiated.

Total stem biomass was unevenly distributed among shoots of different cohorts. Old shoot cohorts tend to have higher biomass than young cohort in the case of tall and short browsed stems (Fig 3a and c). A deviation from this pattern was observed in stems of short protected willow (Fig 3b). Each short protected willow stem showed two peaks of biomass accumulation, that correspond to the oldest shoot cohorts, and the shoot cohort produced the year the fences were built. However, the mean age trend of biomass accumulation presented a displacement of the second peak of biomass accumulation in some treatments

(Fig 3b), which was produced by the combination of stems of different ages. The pattern of biomass accumulation of stems of short browsed willow was similar to that of tall willow, but the heterogeneity between old and younger cohort was greater (Fig 3c). Shoot biomass sizes of 1994 to 1998 cohorts were different among treatments, but interaction between species and populations was significant only in 1994 to 1997 shoot cohort ($p<0.05$) (Table 2). Higher shoot biomass amounts were generally found on tall and protected short willow stems within the same species, in 1994 to 1997 cohorts, compared with short browsed stems. The 1998 shoot cohort biomass was similar between short protected and browsed willow stems, and both short willow stems were lower than tall willow stems. Shoot biomass of *S. planifolia* tended to be higher than the other species in the case of tall willow stems, and lower in the case of short protected and browsed willow stems. However, these differences were probably the result of the original sizes of the stems (Table 1). Shoot biomass production in different treatments was better represented by the relative biomass accumulation rate (RGR) (Table 3). Protected willow showed higher RGR than tall willow stems from 1994 through 1997 shoot cohorts. However, RGR in protected plants seemed to decrease since 1994, and RGR's of 1998 cohort were not different from tall treatments. RGR's of shoot cohorts of browsed plants were similar to those of tall plants from 1994 to 1997 and lower than those of short protected plants during the first two years after protection. The highest 1998 shoot RGR was found in short browsed plants, which showed a similar type of response to that observed in the 1994 shoot cohort of short protected willow plants.

Height increase of the stems. Young tall willow stems showed a high elongation rate and reached the top of the canopy between 8 to 10 years, while the elongation rate of old tall willow stems decreased with the age of the stem (Fig 4a). The age of the old tall willow stems ranged from 11 to 20 years. Protected willow stems were in general younger than in other treatments, with ages ranging from 6 to 9 years. Old stems of short protected willow showed evidence of height suppression before being protected, but height suppression are not evident in younger stems (Fig 4b). Height increase of short protected willow stems seems to follow a lineal model of height increased during the period of protection. Consequently, similar values of mean annual rate of height increase were observed during this period in stems of this treatment (Table 4). Protected willows showed an annual rate of height increase similar to that of younger tall stems and a higher annual rate of height increase than older tall stems during the 5-year period of protection (Table 4). The annual rate of height increase in the last year (1998-1999) was greater in the short protected than in the tall young willow probably because tall willow stems reached the top of the canopy and after that, the elongation rate was reduced.

Population level study.

Browsed short willows had higher densities (0.44 plants m^{-2}) than the other treatments (0.35, 0.32 for tall, short protected, respectively), however most of the plants in the short browsed population were shorter than 30 cm (74 %). A high frequency of small plants resulted in a low canopy cover (25%) compared to the other treatments. An Increase in size of short protected willows produced increased canopy cover (46%), but cover was lower than that observed in the tall willow population (65%). As expected, browsed short willows and tall willows showed contrasting height frequency distributions (Fig. 5 a and c). Browsed short willow showed a skewed distribution, with high numbers in the range of 30 to 120 cm. On the contrary tall willows showed a more even distribution with a bell-shaped curve, and a long tail in the tallest height classes. The bell part of the curve is centered around 120 cm, and a high relative frequency of plants was found in the range of 200 to 380 cm. The height frequency distribution of short willows protected from browsing had a high fraction of plants in 60 to 220 cm, with some plants in the tallest classes being similar in form to tall willow, but with lower frequency.

DISCUSSION

Protection from browsing favored overall plant height increases among short willow, but 5 years of protection were not enough to increase plant heights to the level of tall willow plants. Plant protection also appeared to favor a shift to a younger age structure of the stems in the plant. This may have occurred because suppressed plants maintained old stems at the same height as young stems, and when plants were protected in 1994 young stems could have had a competitive advantage to overtop old stems. As the stems became older the proportion of photosynthate allocated to maintain old structures increased (Fitter

1986). As expected in sympodial growth, the main axis of the older stems was formed by several shoots of different ages (Aliende and Harper 1989).This indicates that a significant number of shoots must be shed from the plant each year even when unbrowsed. Stems of all treatments produced high numbers of short shoots (0-5 cm), which resulted in skewed distributions of shoot lengths. Shoot length distributions of cohorts older than one year were also skewed in tall and short browsed willow stems. In short protected willow stems, the 1994-shoot cohort displayed a bell-shaped frequency distribution of length, which was progressively changed to the skewed distribution observed in 1998-shoot cohort. It is important to consider that the original frequency distribution of shoot length is changing with time due to shoot shedding and reduction of shoot length due to death or, in the case of short browsed stems, elk tissue removal. The original length distribution of the 1994 shoot cohort of protected willow stems was probably skewed, and similar to the 1998 shoot cohort of the short browsed stems. Due to a proportionally higher shedding of short shoots, the original frequency distribution was progressively changed to the bell shape distribution observed four years latter.

High shedding of short shoots seemed to be a characteristic of stems of all treatments. Thus, short shoots are temporary, most of them only live for one growing season. Shoot abscission in *Salix spp.* is determined in part by the anatomical characteristics of its basal region (Raven 1992). In addition, as the stems became longer there was a tendency for an increase in the proportion of short shoots produced. It is probable that short shoots are important for reducing leaf overlap in the canopy, and they could be considered analogous to the rachises of compound leaves. Rachises in compound leaves have been interpreted as inexpensive temporary lateral branches that a plant produces with little investment of energy. This gives an advantage to the plant, which does not need to invest a lot of energy in structure that will be shaded by its own growth, and the saved energy can be used to increase plant height (Givnish 1978). Additionally, the shedding of rachises and leaves during dry periods such as north temperate winters minimizes water loss during dormancy (Givnish 1978, Stowe and Brown1981). Thus net stem biomass accumulation will depend on total biomass production as well as the proportion to the total production that is allocated to long vs. short shoots. Short willows protected from browsing will, compared to tall morphotypes, increase biomass accumulation by increasing the proportion of long shoots. This growth pattern seems to gradually change to the growth pattern observed in tall willow stems, characterized by the production of a large number of short shoots. After four years of protection, the frequency distribution of shoot lengths of short protected willow stems was more similar to that of tall rather than short browsed willows. A similar type of pattern was observed in the relative biomass accumulation rate. An elevated RGR of short protected willow stems was observed during the first years after protection, but later, it become similar to the RGR values of tall willow stems.

Annual shoot biomass production of a woody plant is not only determined by growing conditions but also by the developmental patterns of the plant (Fritts 1976, Cook and Kairiukstis 1990). In order to differentiate between these two factors, knowledge of the trend in ages of aboveground biomass is required. The change in biomass production with age is normally inferred from tree ring widths, assuming that tree ring growth correlates with the overall aboveground growth of the plant (Fritts 1976). The age trend in biomass production can also be inferred by analyzing the biomass of shoot cohorts. However this analyzes provides information of the net biomass productivity only. Different from tree rings, the age structure of shoot biomass is affected by shoot death and shedding, and shoot diameter increase. It is assumed that under good growing conditions plants will show a characteristic pattern of biomass accumulation. For a given species, the age structure of annual shoot biomass can be inferred by analyzing shoot cohorts of individuals growing under favorable environmental conditions. The age structure of shoot biomass can be used as a baseline to compare other individuals or populations. A deviation from the expected trend would indicate that plants grew under different environmental conditions, or that material was removed due to herbivory or disturbance. The age structure of shoot biomass of tall stems was used in this case as a baseline to compare to the other treatments, since these stems have the lowest historic browsing pressure. The temporal trend in annual biomass accumulation of shoots of tall and short browsed treatments showed a remarkably similar pattern to that expected for the age trend of tree ring width (Schweingruber 1987.) (Fig. 3). The peak of biomass accumulation occurred in the old shoot cohorts and biomass accumulation decreased in younger shoot cohorts. However, browsed willow stems showed a high accumulation in the oldest shoot cohorts, and a sharp decrease in younger cohorts, compared to tall stems. Biomass accumulation in the oldest shoots probably is not affected by browsing since these shoots normally grow inside the canopy of the plant, which is difficult for elk to reach. Once the stem reaches the top of the canopy, shoots become accessible to elk. Elk will remove a portion of shoots, probably reducing shoot size heterogeneity, which will determine a more even distribution of shoot biomass of these cohorts. The age structure of shoot biomass distribution is disrupted by protection from elk herbivory. The exact year this disruption occurs could be determined by looking at the date of the second peak of biomass accumulation in each stem.

Adaptations for plant regrowth and/or reproduction following herbivory can be considered as herbivory defenses (Strauss and Agrawal 1999). Regrowth in herbaceous plants has been interpreted as a mechanism to compensate for the amount of material that has been removed by herbivores in order to reestablish whole-plant photosynthetic capacity (Briske and Richards 1995). In woody plants, such responses could be interpreted as strategies to avoid browsing by growing apical meristems tall enough to be inaccessible to browsers (Rohner and Ward 1997).Thus, plant height is an important morphological variable because it determines the likelihood of avoiding or reducing browsing as well as the space captured by the plant to obtain more resources (Harper 1985, Hutchings 1988). Reduction of shoot length by elk will maintain the plant in a suppressed morphology, which will positively feedback to elk browsing offtake (Romme et al. 1995). Increase in shoot length and biomass of short willow under protection was also correlated with height increase. Assuming that the height increase of protected willow will continue at similar rates to those observed during this 5-year period of protection, plants will converge to the tall morphotype height after three or four more years of protection. The importance of elk suppression of willow height growth could be inferred from the height frequency distribution of different willow populations. Assuming that the height frequency distribution of fenced willows at the time exclosures were built was similar to the distribution observed in the short browsed population, there was a tendency for the protected population to acquire the morphological characteristic of tall willow during the protection period (1994-1998).

Individuals shorter than 30 cm dominated the population of short browsed willow. The small basal diameter of larger stems in these plants seemed to indicate that they were young, however they could be resprouts of old individuals. The tall willow population maintained a high proportion of individuals with heights less than 1.5 m, which could potentially be suppressed by elk as occurred in the short willow populations where plants were mostly less than 1.5 m tall. Although my results indicated that elk browsing was the main factor determining short willow morphotypes, it is not clear how the short willow populations developed from an original tall willow population. And, why did elk not suppress tall willow communities to produce a uniform short willow community throughout the entire valley? I hypothesize that elk could have induced the change from tall to short willow communities by two nonexclusive processes. High levels of elk browsing could suppress young willows growing in the understory of tall willow stands, as well as young stems of tall willow plants. Turnover of plants, or stems within the plants, could then gradually cause a shift from a tall to a short willow community, as tall willow plants and stems die. Turnover of stems or individuals in a population could be accelerated by disturbances like flooding, changes in river course, or dry periods. After a disturbance, elk would more likely suppress new individuals or stems, and the shift in the size class composition of willow community would occur in a shorter amount of time. Thus, under high elk density, it is expected that short willow will eventually be the only morphotype occurring in these watersheds. However, tall willow populations still cover an important part of the watersheds and there is no evidence that they are changing to a short willow population. It is likely that this is because tall willow communities are spatially distributed in the upper areas of the watersheds, where there is more snow accumulation that restricts elk movement. Elk density is in fact less in the upper areas of the valley compared with lower areas where the short willows are (F. Singer unpublished result). Elk offtake in tall willow communities has apparently not been high enough to cause a shift to short willow.

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Table 1. Characteristics of the stems from different willow species and populations that were sampled in Horseshoe Park at the end of the 1998-growing season (end of August).

Population	Species (*)	Age-range years	Height (m)	Leaf area (m^2)	Woody biomass (g)	Leaf biomass (g)	Leaf /woody
Short protected	***Sg***	7 to 10	2.3 a(**)	5.0 a	241 a	37 a	0.15 a
	Sm	9 to 11	2.1 a	4.7 a	205 a	41 a	0.20 a
	Sp	6 to 12	2.1 a	3.9 a	130 a	27 a	0.21 a
Short browsed	***Sg***	10 to 14	1.4 b	3.5 a	132 a	21 a	0.16 ab
	Sm	8 to 12	1.3 b	4.5 a	153 a	25 a	0.17 ab
	Sp	12 to 15	1.3 b	2.2 a	93 a	15 a	0.17 ab
Tall	***Sg***	16 to 21	3.2 c	8.3 b	667 b	60 b	0.09 b
	Sm	13 to 25	3.3 c	10.4 b	587 b	63 b	0.11 b
	Sp	14 to 15	3.2 c	13.4 b	824 b	98 b	0.12 b

(*) *Sg: Salix geyeriana; Sm : Salix monticola; Sp ; Salix planifolia*

(**) Different letters within the column indicate that means are significantly different ($P<0.05$)

Table 2. Dry weight (g/stem) of shoot cohorts of different willow populations and species.

	Tall			**Short protected**			**Short Browsed**		
	Sg(*)	***Sm***	***Sp***	***Sg***	***Sm***	***Sp***	***Sg***	***Sm***	***Sp***
1994	13 bc(**)	23 ab	39 a	34 ab	31 ab	16 ab	5 c	5 c	3 d
1995	13 b	22 ab	33 a	38 a	24 ab	16 b	5 c	6 c	5 c
1996	14 abc	19 abc	31 a	29 a	24 ab	14 abc	8 cd	13 bc	3 d
1997	20 ab	19 ab	35 a	21 ab	14 ab	9 bc	6 c	11 bc	3 c
1998	17 a	19 a	34 a	12 b	13 b	9 b	12 b	16 b	8 b

(*) *Sg*: *Salix geyeriana*; *Sm* : *Salix monticola*; *Sp* ; *Salix planifolia*

(**) Different letters within a row indicate that means are different ($P< 0.01$)

Table 3. Relative biomass accumulation rate (mg g^{-1} yr^{-1})(RGR, see text) of shoot cohorts of different willow populations and species.

	Tall			**Short protected**			**Short Browsed**		
	***Sg*(*)**	***Sm***	***Sp***	***Sg***	***Sm***	***Sp***	***Sg***	***Sm***	***Sp***
1994	24	32	58	214	260	203	35	46	33
	b(**)	b	b	a	a	a	b	b	b
1995	24	20	41	228	160	143	59	49	92
	b	b	b	a	a	a	b	b	b
1996	26	23	37	119	114	60	78	100	37
	b	b	b	a	a	a	ab	ab	ab
1997	33	27	33	72	76	45	35	78	39
	b	b	b	a	a	a	ab	ab	ab
1998	32	28	36	51	64	33	120	85	81
	b	b	b	b	b	b	a	a	a

(*) *Sg*: *Salix geyeriana*; *Sm* : *Salix monticola*; *Sp* ; *Salix planifolia*

(**) Different letters within a row indicate that means are different ($P< 0.01$)

Table 4. Annual rate of height increase (cm yr^{-1}) since 1994, and total rate of height increase in this period of willow stems in different treatments.

Period	**Tall old**	**Tall young**	**Short protected**	**P-value**
1994 to 1995	12 (7)(**) a(*)	26 (18) b	30 (11) b	0.021
1995 to 1996	10 (11) a	28 (16) b	30 (20) b	0.045
1996 to 1997	19 (22) a	22 (13) a	32 (16) a	0.30
1997 to 1998	10 (5) a	33 (34) a	27 (15) a	0.11
1998 to 1999	16 (4) ab	13 (9) b	25 (9) a	0.027
1994 to 1999	17 (8) a	31 (14) b	36 (6) b	0.003

(*) **Values in parentheses correspond to standard deviation of the mean.**

(**) **Different letters indicate that means within a row are different.**

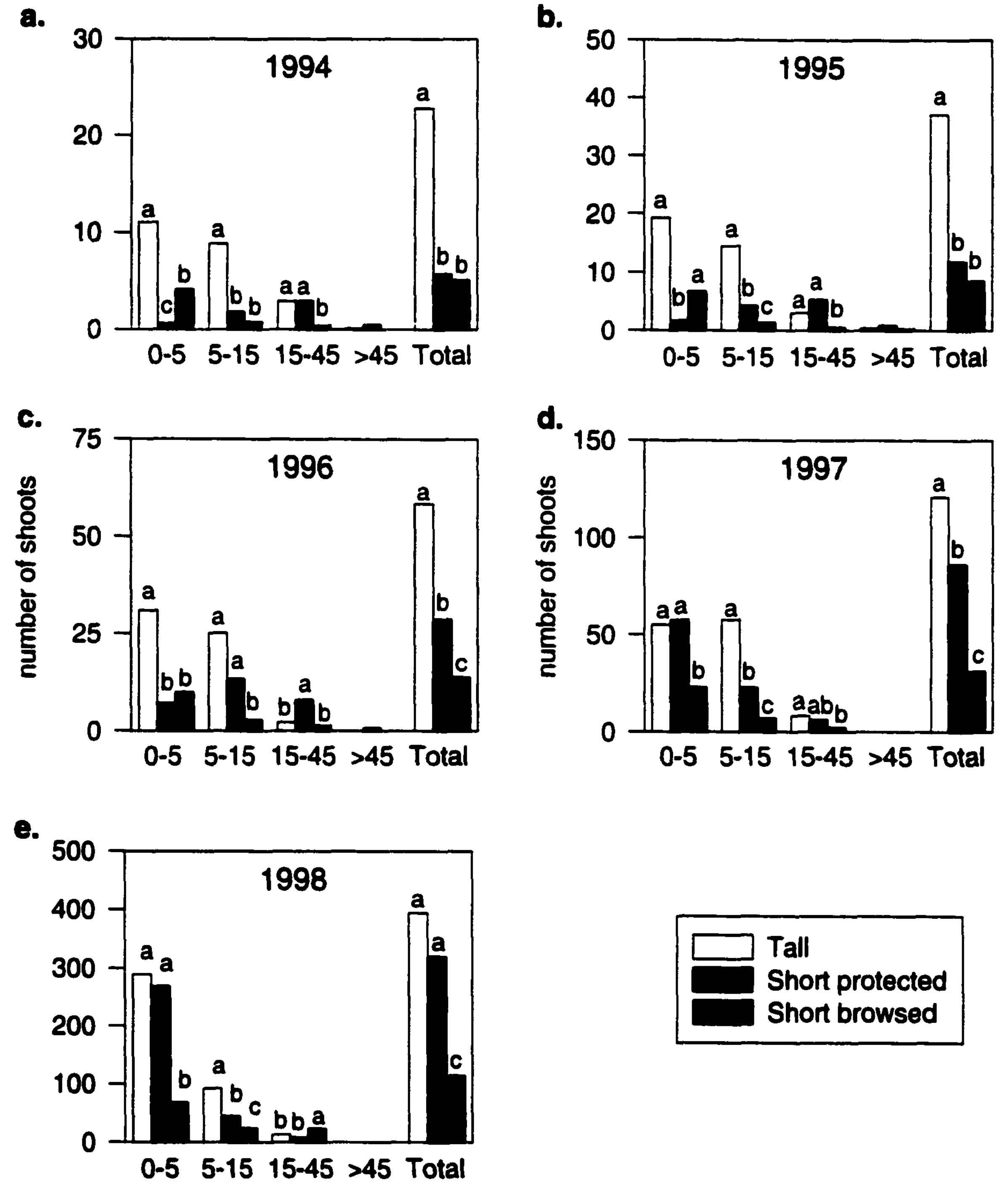

Figure 1. Frequency distribution of shoot length classes averaged across species in 1994 (a), 1995 (b),1996 (c),1997 (d) and 1998 (e) cohort of different willow populations. Bars represent mean values of the three studied species. Different letters indicate significant differences between means within each length class or total. Each graph presents different y axis scale.

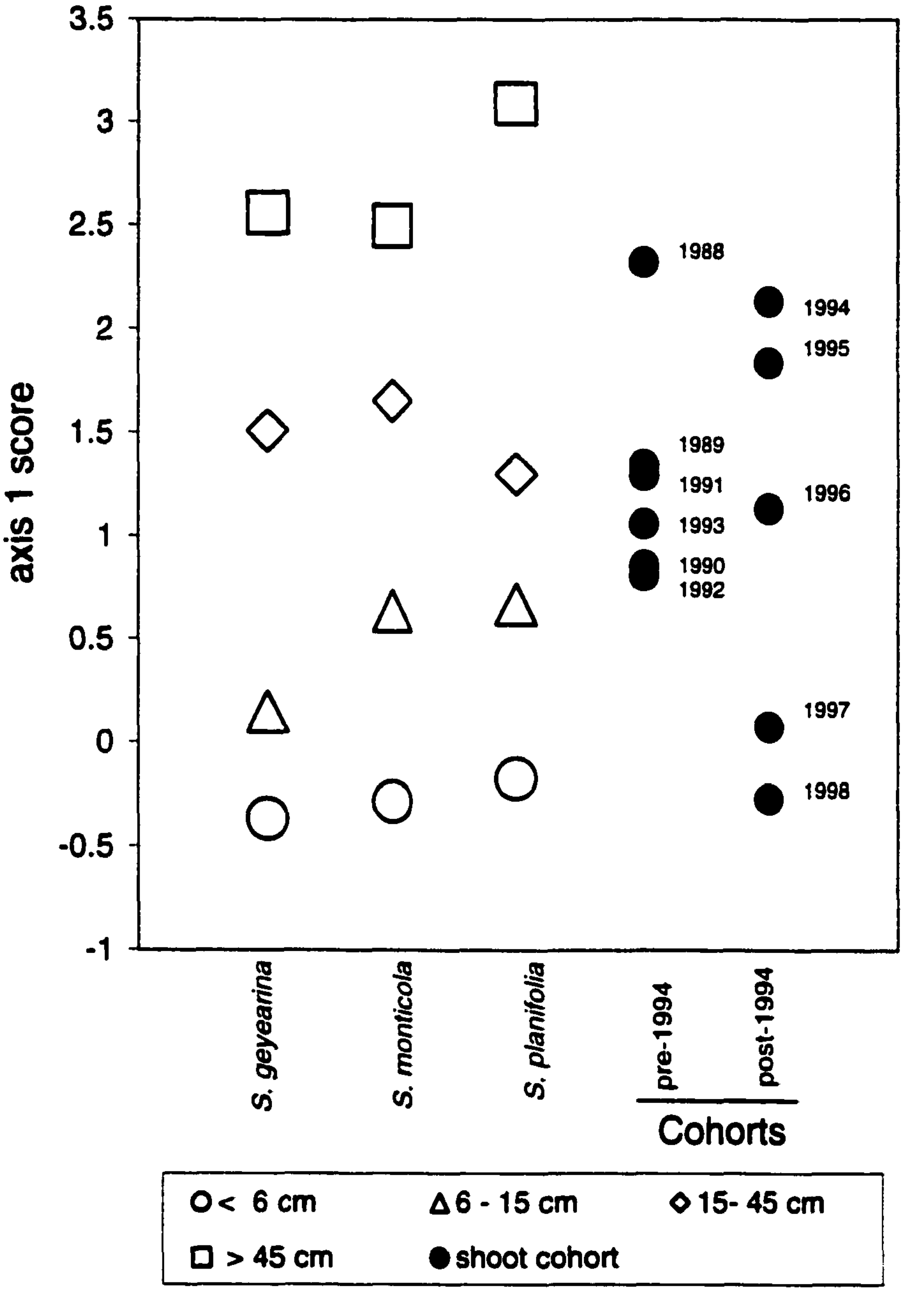

Figure 2. Correspondence analysis of frequency distributions of pre or post grazing exclosure shoot length classes of size classes and species, and shoot cohort. Only axis one is shown, and it accounted for over 70 % of the variation.

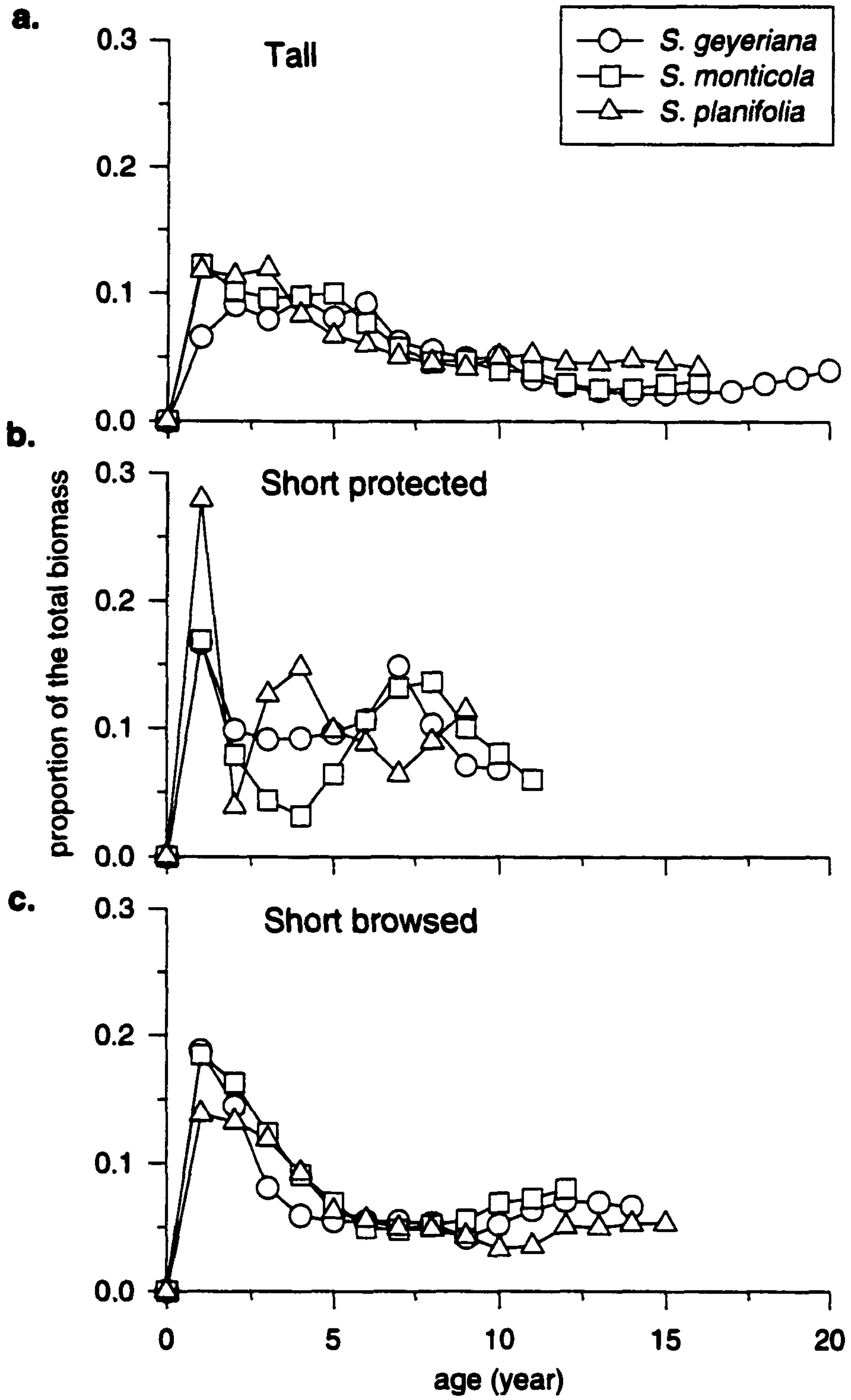

Figure 3. Distribution of total stem woody biomass among shoots cohorts in tall (a), short protected (b) and short browsed (c) willow. *S. geyeriana*, *S. monticola* and *S. planifolia* species are represented in each plot. Values represent a moving window of 3 years.

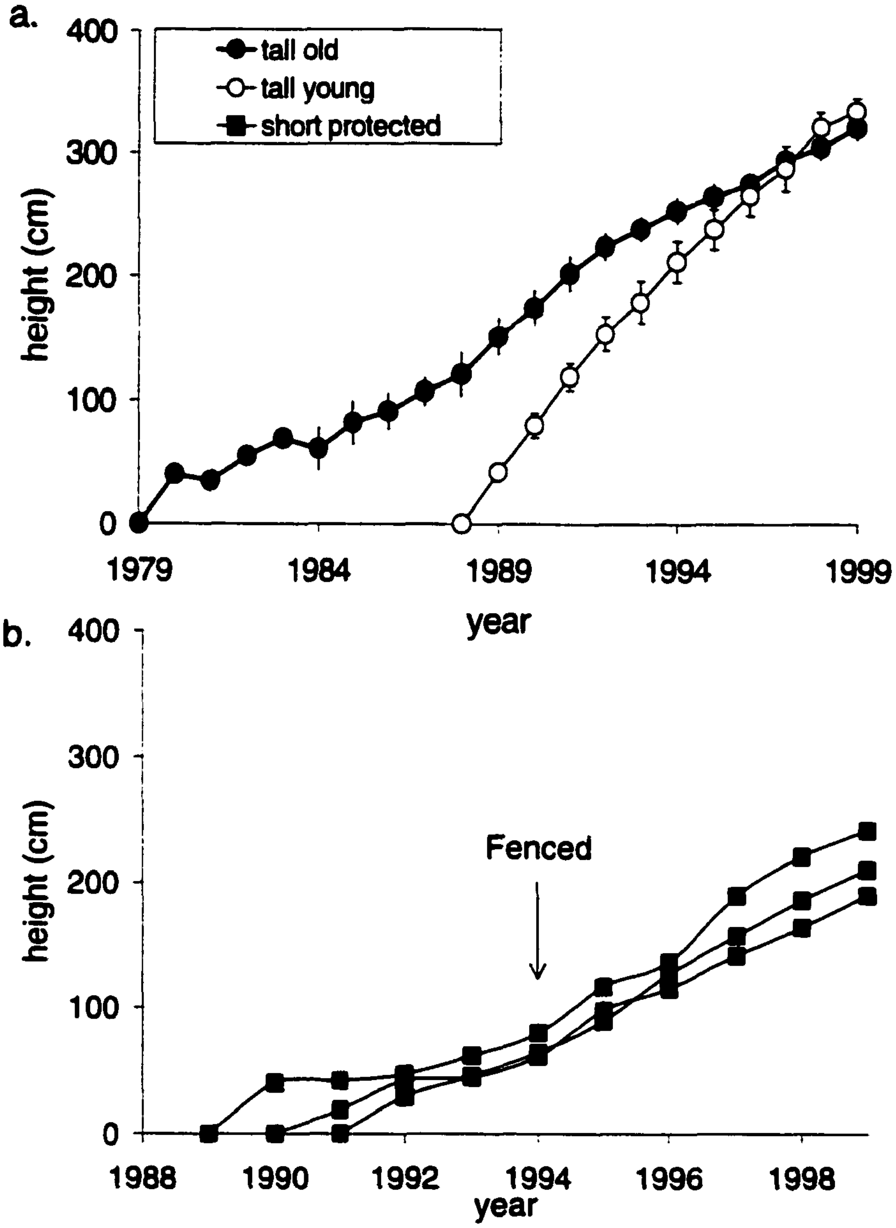

Figure 4. Dynamic of height increases of stems of *S. monticola* of tall old and tall young (a), and short protected (b) willows. Lines of tall old and tall young treatments represent a mean of 8 stems, and vertical bars represent the standard error of the mean. Lines in short protected willows represent a mean of stems with no more than one year of difference in age. Arrow indicates the year exclosures were built.

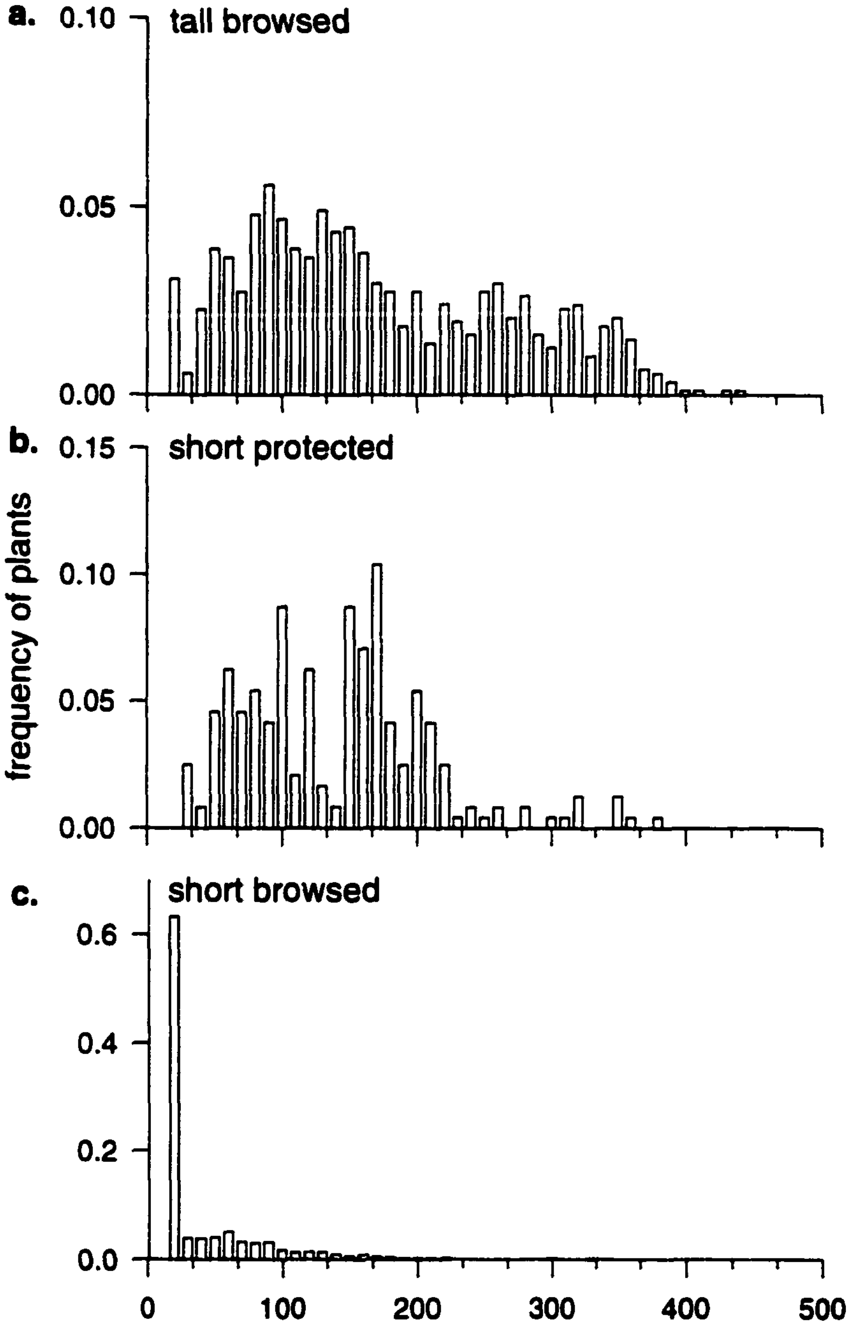

Figure 5. Height frenquency distribution of three willow populations. (a) tall willow browsed (b) short willow protected (c) short willow browsed. Height class intervals are equal to 10 cm. The scale of the y axis is different in each plot.

CHAPTER 3

Long-term changes in willow spatial distribution on the elk winter range of Rocky Mountain National Park.

Abstract. I determined the extent and the spatial pattern of changes in willow (*Salix spp.*) cover in the riparian areas of the eastern slope of Rocky Mountain National Park (RMNP), Colorado, between 1937 or 1946 and 1996, and relate these changes to suspected causative factors. The study was conducted in two watersheds of the northeastern side of RMNP, which includes the Moraine Park (MP) area of the Big Thompson River watershed (2481 m of altitude), and the Horseshoe Park (HP) area of Fall River watershed (2598 m of altitude). Changes in vegetation were inferred from digital map generated from aerial photointerpretation and field surveys conducted with a global positioning system (GPS) (low-resolution and GPS-based digital maps). Low-resolution digital maps were created based on old (1937 or 1946) and new (1996) aerial photos to determine the extent of willow decline. GPS-based digital maps of vegetation cover were created from a field survey conducted in the summer of 1998. In these maps, willow cover was described in terms of morphotypes (sapling, young short, old short, intermediate, and tall), density, and percentage of dead plants. Maps were produced by combining digital and attribute information.

The decrease in riparian shrub cover in MP was 21 ha (21%) and in HP it was 17 ha (19%) over the 50 or 59 year-period. Reductions in the total length and surface water of the main river were 56% and 69% in MP and 44% and 47% in HP, respectively. Tall willow cover was found mainly in the upper areas of both valleys. Short old willow morphotypes were spatially distributed preferentially in areas affected by flooding in HP, and in areas where major river reductions were observed in MP. Both valleys had sites that were being colonized by willows, in

wet meadows, and in the case of HP, open areas created by flood disturbance. The decline in tall willow cover corresponded to 54 and 65% in MP and HP, respectively, over 50-59 years.

Willow decline in MP was apparently the result of a reduction in water availability for growth. Over the last 50 years there has been a trend toward simplification of river spatial pattern, i.e. less complex branching and channelization, and a decrease in total water surface area in MP. The same trend in river morphology was documented in HP but here willow decline occurred mainly because of a large flood disturbance in 1982. In both valleys, surveys indicated a decline in beaver in excess of 90% since 1940. This has generated unfavorable conditions for willow growth. The causes of these fluvial changes were not determined, but are likely related to a decline in beaver populations and an increase in elk population (from approximately 700 to about 3300, and form 500 to 1000 within the Park, during the study period). The elk increase has also placed increased browsing pressure on willow, which has led to a reduction in plant heights. Persistence of these riparian willow communities may depend on the reestablishment of beaver.

INTRODUCTION.

Riparian vegetation comprises a small area of the landscape along river courses, in which the river has a major control on physical conditions (Gregory et al 1991). These areas are subject to periodic fluvial disturbances occurring because of flooding and /or migration of the active channel and meanders of the river (Gregory et al 1991, Bradley and Smith 1986, Miller et al. 1995). Disturbance produces irregular patches of riparian vegetation types, arranged in a mosaic along the area of river influence (Miller et al. 1995). Non-fluvial disturbances are also common. These include fire, wind, plant disease, insect outbreaks (Gregory et al 1991), herbivory by large mammals (Collins and Helm 1997, Naiman 1988 Johnston and Naiman 1990b), and beaver dams (Johnston and Naiman 1990a). Riparian areas have been extensively modified by human activities resulting in habitat degradation, which has affected both terrestrial and aquatic species composition (Décampus et al 1988, Roth et al 1996). Trends in cover and characteristics of riparian vegetation are often difficult to distinguish from the normal recurrent disturbance effects, so long term analyses are required (Miller et al 1995, Johnston and Naiman 1990c).

Documentation of temporal and spatial dynamics of landscape pattern has been greatly stimulated by the availability of new technological tools, in particular geographic information system (GIS) and remote sensing technology (Ustin et al 1993, Johnson and Gage 1997). The comparison of historic and recent aerial photos at a medium level of resolution is a reliable, quantitative method for evaluating long term vegetation changes, particularly when combined with GIS (Johnston and Naiman 1990c, Clemmer, 1994). This approach was used here to analyze the temporal change of riparian shrub cover in two watersheds in Rocky Mountain National Park, Colorado, and to make inferences about the factors that could drive vegetation change.

Willow (*Salix sp.)* dominates the riparian landscapes of the eastern slope of Rocky Mountain National Park (RMNP), Colorado, forming a complex mosaic of patches of willow plants of different heights. A decline in willow abundance, distribution and stature apparently has occurred on these areas. Three main hypotheses have been proposed for willow declines (Singer et al 1998a): 1) higher grazing pressures on willow, caused by increases in the elk (*Cevus elaphus*) population 2) warmer and drier climatic trends occurring during this last century, and 3) a reduction in riparian habitats with shallow water tables caused by a decline in beaver (*Castor canadensis*) population. Since humans extensively used this study area and drained some areas in the Park, human impact should also be considered among the probable causative factors.

In this paper GIS maps of riparian vegetation and hydrology of two closed watersheds of RMNP were generated at two scales of resolution. The analysis procedure was designed to answer the following set of questions: Has the spatial distribution of willow vegetation been reduced at the landscape scale? If so, what is the spatial pattern of willow decline, and what factors could be associated with this pattern? Since vegetation changes are normally controlled by a complex interaction of factors, I hypothesized that multiple causative factors might explain the overall changes in vegetation cover. However factors could be hierarchical, with some of them primary and others secondary. Primary factors might override the effects of secondary factors. Some of the proposed factors that could produce changes in willow cover, for example drier climatic trend determined by a reduction in precipitation was probably similar in both study valleys, since they are only 5 km apart and they have a similar altitude. Consequently this primary factor will produce similar changes in the patterns of willow cover in both watersheds. However, any differences between watersheds would indicate that more localized primary factors are driving these changes.

METHODS.

Study sites.

The study was conducted in two watersheds of the northeastern side of RMNP which includes: the Moraine Park area of the Big Thompson River watershed (elevation 2481 m), and the Horseshoe Park area of Fall River watershed (elevation 2598 m). Vegetation in these valleys is composed of communities of riparian shrubs dominated by willow (*Salix monticola*, *S. geyeriana*, and *S. planifolia*), and in some areas by birch (*Betula spp.*). Meadows occur in several parts of the valley farther from the river course. Wet meadows are dominated by *Poa spp.*, and dry meadows by *Carex spp.* and *Artemisia spp.*. Vegetation communities dominated by trees represent a minor proportion of the total cover, and include conifers (*Pinus contorta* and *Pinus ponderosa*) and aspen (*Populus tremuloides*) communities. The two watersheds are within 5 km of each other and have perennial alpine snowfields at their headwaters (Baron 1992). Mean annual precipitation for the sites is 41 cm (Estes Park weather station) (Singer et al. 1998a) and peak stream flow usually occurs in early to mid-June.

Historical changes in land use, Elk and Beaver.

Native people camped and hunted in the valleys, mountains and tundra of what is now known as RMNP since as long ago as 3850 BC (Hess 1993). Trappers and explorers occasionally visited this area but it was not until after 1860 that permanent settlement began (Buchholtz 1983, Hess 1993). Moraine and Horseshoe Parks were not within the National Park boundary when it was created in 1915. Horseshoe Park was incorporated in 1932 and Moraine Park in 1962. These valleys were occupied by ranches and resorts from the 1870's until the 1930's (Buchholtz 1983). An official Park Service report [1930] described the conditions of the herbaceous vegetation in these valleys as heavily overgrazed by livestock, but shrubs and trees as less affected (Stevens, 1980, Unpublished report). It is clear that drainage and irrigation ditches were built on Moraine Park, and remnants are still evident today. Ditches could have been used to drain overly wet areas and to irrigate hay fields and the golf course. The golf course was irrigated through at least 1961. One of the main disturbances on riparian vegetation in Horseshoe Park was the flood produced by the failure of the Lawn Lake Dam in 1982, which released a huge amount of water into the Fall River (Jarret and Costa 1993). The sediments carried by the flood were deposited as an alluvial fan covering part of a willow community (Keigley 1993).

The two study valleys are in the winter range for elk, which encompasses about 10,000 ha (Singer et al. 1998a). The elk had been hunted to extinction by 1900, but in 1913 and 1914, 49 elk from Yellowstone were transplanted to the park (Hess 1993). Elk increased rapidly to approximately 1,500 individuals in

1942, but population control by park managers and reduce the population to around 400 individuals until 1964 (Hess 1993). At this time the natural regulation policy was implemented and the elk population increased to 3,300 individuals in 1997 (Singer et al 1998a, Singer et al 1998b), 1,000 of which winter in RMNP.

Beavers were abundant in areas of RMNP prior to European settlement, but they started to be intensively trapped in the mid 1800's (Buchholtz 1983, Hess 1993). Pressure on beaver did not decrease after demand for beaver pelts declined (Hess 1993). In 1890 beaver was virtually eliminated from the adjacent valley of Estes Park but beaver were abundant when the National Park was created (Hess 1993). A decrease of more than 90% of the beaver population can be inferred from the surveys of beaver conducted since 1939 (Zeigenfuss et al. 2000). On the Big Thompson River the estimated number of beavers were 315, 102, 18 and 12 in 1939, 1964, 1980 and 1994/98, respectively. Most of these beavers were in Moraine Park. Values reported for the Fall River in Horseshoe Park were 96, 24 and 6 in 1939, 1980 and 1994/98, respectively.

Digital map generation.

Low resolution digital maps. Digital maps of Moraine and Horseshoe Park were created from interpreted aerial photos obtained for different years (Table 1). Aerial photos were scanned, geo-registered, and interpreted, rectified and digitized on a high-resolution computer screen. Photos were scanned with a 600-dpi resolution and the generated image files were geo- registered based on x-y UTM coordinate points. UTM coordinates of prominent features such as trees or road intersections were registered with a global positioning system (GPS) (Trimbal Pathfinder Proffesional) with an error lower than 2 m. For image geo-registration, 18 and 30 GPS points were used in Moraine and Horseshoe Park, respectively. GPS locations were uniformly distributed throughout the area of interest. A 2-degree polynomial geometric correction procedure, available in ERDAS-IMAGINE Software (Version 8.3), was used to geo-register the 1996 image files based on GPS locations. Aerial photos older than 1996 were registered using the corrected 1996 images as a reference. Vegetation and hydrological features were digitized using ARC/EDIT module of ARC/INFO Software (version 7, ESRI, 1994) program, employing the digital photos as a background image. This procedure greatly increases the possibility of identifying features, allowing both margins of river channels to be digitized.

Vegetation was classified in four classes: open, meadow, riparian shrub, aspen (*Populus tremuloides*), and forest (*Pinus spp.*). Areas with a high percentage of bare soil were included in the open class, and areas dominated by grasses were considered meadows. Since willow and birch, the two shrubs that grow in these riparian areas, could not be separated in the photo-interpretation, they were included in the riparian shrub class. Hydrological features were also delineated form the aerial photos. Main river, temporary and old river channels, and ponds were digitized. All channels that contained water were considered main river. Branches or meanders of the river that did not contain water were classified as temporary or old if they were wet or dry, respectively.

GPS-based digital maps. During the summer of 1998, I surveyed the same areas covered in the low-resolution maps in Moraine and Horseshoe Park. Aerial photos of these valleys taken in 1996 (Table 1) were used as a guide to organize the survey. Homogeneous vegetation patches were identified in the field by visual observation, and a GPS unit was used to delimit its boundaries. The number as well as the size and shape of the patches were determined according to the vegetation characteristics to minimize within patch heterogeneity. Hydrological features such as main river, lakes, or ponds were mapped following the same methods. I walked along the boundaries of every vegetation patch or hydrological feature with a GPS unit set to digitize lines. Since the focus of the studies was on willow cover the boundaries of the survey area were defined by the extent of willow distribution. However some patches without willow plants occurring between the extent of the willow distribution were also delimited. GPS digital data and the associated attribute information were incorporated in ARC-INFO Software (version 7, ESRI, 1994), to generate polygon coverages. The final error of the GPS-generated lines was lower than 2 m after correcting the data for the distortions that are purposefully introduced by the satellite system.

As in the case of the low-resolution maps, vegetation patches where primarily classified according to the general characteristic of the vegetation. A more detailed classification system was created to identify vegetation classes and subclasses. Further, in those patches were willow were present, additional attributes were registered. Four groups of species were recognized in the woody strata, namely; willow (*Salix spp.*), birch (*Betula spp.*), conifers (*Pinus spp.*) and aspen (*Populus tremuloides*) (Fig. 1). Patches without woody strata or with few sparse woody individuals were included in the meadow class. Woody vegetation classes were distinguished based on the dominant and co-dominant species. The group that presented the highest density in a patch was considered dominant, without regard to the overall woody strata density. Other groups occurring in a patch were co-dominant. Groups comprised of isolated individuals in an overall high-density patch were not considered in the classification. Since visual observation was used to delimit and classify vegetation patches, there was no quantitative value for the minimum number of plants determining if a group should be classified as co-dominant, or not included. Nevertheless, ambiguous cases were rare, because no more than 2 groups occurred in most patches. Since the survey was targeted on willow areas some vegetation class such as meadow were only partially surveyed (particularly one large meadow in Horseshoe Park, and several meadow areas in Moraine Park). Forest and aspen vegetation classes were separated from the riparian vegetation, and consequently they were seldom included in the survey. Only willow and birch were completely surveyed.

Additional attributes were used to describe the heterogeneity in willow cover in more detail. Four categories were defined to characterize the morphological characteristics of: a) dominant and b) co-dominant willow morphotypes, c) density, and d) percentage plants dead (Table 2). As previously, classification was based on visual estimations. A zero value was assigned in all of the four categories in the case of patches without willow plants. Density was estimated considering both live and dead willow plants. The morphotype that presented the highest density in a patch was considered dominant and the second most common morphotype was considered co-dominant. Only one morphotype was included in the co-dominant categories to make the classification simpler.

Height difference was the primary attribute used to discriminate willow morphotypes, but more detailed observations were made to differentiate between saplings and young short willow, and between young and old short willow. I considered saplings to be individuals that were recently established (4-5 years) from seeds or vegetative reproduction, but not from resprouting of old individuals. Areas with high density of willow saplings, and without woody strata, were classified in the meadow-willow vegetation subclass (Fig 1). I identified willow saplings using several morphological characteristics such as height shorter than approximately 50 cm, basal diameter of the largest stem approximately equal to 5 cm, brownish stem without sign of lignification, and small crown size relative to the size of the plant. These later characteristics indicated that plants were not sprouts from old individuals. Additionally, some of the largest stems were dated based on the ramification pattern (see chapter 2), and they were between 4 and 5 years old. The young willow category included plants that were similar in height to short willow morphotypes (approximately 1.5 m. in the case of tallest plants). Mature plants were composed of several large stems and consequently had crowns several times larger than plants considered as saplings. The largest stem diameters in short young willows were on the order of 1.5 to 2.0 cm. These plants looked younger than other short willows, as indicated by the brownish color of the stem that contrasted with a white color typical of old stems of old willow plants. Additionally, no dead stems, in particular old dead stems, were found inside or between the canopies of young plants, as were commonly found in older short willow stands. This distinction was made to infer dynamics occurring within the short morphotypes.

Patches comprised of saplings or young short willows were interpreted differently if other morphotypes were or were not present in the patch. If patches with a high density of saplings and/or young short willow occurred together with other willow morphotypes, they were interpreted as areas originally covered by willow with high recruitment. Areas dominated by saplings or young short willow in which no other dead or live willow morphotypes were present were considered to be areas recently colonized by willows. These patches were classified as "new colonization" if only saplings were present and they were interpreted to be areas that had been colonized less than or equal to 4 or 5 years ago. Similarly, patches that contained young short willows and saplings, but not other morphotypes were interpreted as an older colonization (older than 5 years), and designated in the maps as "colonized several years ago".

Data analysis. Changes in willow vegetation were interpreted relative to hydrological changes and historic events. GIS data from the low-resolution maps were used to examine the transitions in riparian shrub cover. Willow was the most common shrub in these watersheds so I assumed that the riparian shrub class was mostly composed of willows. GIS data were derived from 1998 field survey by aggregation of detailed vegetation attributes. Willow cover was estimated based on 3 criteria resulting from a combination of different attributes used to classify willow patches (Table 3). The first criterion considered willow cover to be patches in which willow plants were present. Since this was the least strict criterion, it gave the highest values of total willow cover and was used to calculate percent cover of the different willow types. The second criterion classified willow cover as areas where willow is the dominant vegetation type. A third and more strict criterion classified willow cover as woody areas dominated by willow with a high density of living individuals.

Cover areas of riparian shrub classes from maps created by the interpretation of old and new aerial photos were compared. The minimum resolution of the photo-interpretation was inferred by overlaying low-resolution and GPS-based maps. This procedure allowed us to determine characteristics of the low-resolution polygons based on the attributes recorded in the high resolution maps generated with the GPS. In this way, the minimum map resolution in the photo-interpretation was defined based on the characteristic of the vegetation in the GPS-based maps, namely dominant group, density and percentage of dead plants.

RESULTS.

Low resolution digital maps. Important hydrological changes, including reductions in the complexity of the river pattern and in the total surface water, were found in both watersheds. Changes were more dramatic in Moraine Park, where the length and water surface area of the main channel were reduced by 56% and 69%, respectively (Table 4). Most changes in the river course occurred in the south main branch of the river (Fig. 2). By 1996 the river channel had almost no branching and most of the temporary river courses had disappeared. The complex pattern of the river observed in 1937 was most likely the result of beaver activities, but it was difficult to identify beaver ponds. Not all ponds that were identified in the 1937 and 1996 maps (Fig 2) were a result of beaver activities. Beaver created several dams that produced small impoundment areas, but the main impact of beaver appeared to be an increase in river ramification and meanders. Most of the 1937 river channels that had disappeared by 1996 could not be identified in the photos. Flooded areas on wet meadows were evident in the central part of the Moraine Park valley in both years, but were more extensive in 1996 (Table 4). In Horseshoe Park the length and surface water of the main channel of the river in 1996 were reduced to 44% and 47%, respectively, of the values observed in 1937/46 (Table 4). The main reduction in river complexity occurred in the upper reaches of the valley (Fig 3). Several ponds created by beaver could be clearly identified on the old photos. These ponds disappeared by 1996. A 1982 flood event produce important hydrological changes like the creation of a lake and the modification of the river course. Changes in the lower part of the valley did not appear to be as important as in the upper areas but the river pattern become less meandering by 1996.

Changes in spatial patterns and decline in the total area covered by riparian shrubs were determined in both watersheds. The reduction was 21 ha (21%) in Moraine Park during the span of 50 years, and 17 ha (19%) in Horseshoe Park during the time spans of 50 and 59 years (1946 and 1937 aerial photos, Table 1). In Moraine Park, riparian shrubs covered 101 ha in 1937 and 80 ha in 1996. Changes in shrub cover occurred mostly in the wider part of the valley (Fig. 4). The two narrow valleys in the upper areas of Moraine Park (west) did not show any important change. Compared to the spatial pattern of willow cover delimited in the 1946 photos, willow in the northwest part of Moraine Park slightly increased over meadows, and the forest area also become larger. It is important to consider that in these two narrow valleys there is an ecotonal zone in which riparian areas dominated by willow are replaced by birch and forest. These transitions were difficult to delimit from the photos. Wider areas of the watershed in Moraine Park showed major changes in willow cover. Decreases in willow cover were spatially associated with reductions in river meanders and small impoundments. Some meadow areas identified in the 1996 map were previously covered by willow.

In Horseshoe Park willow cover was reduced from 90 ha in 1937/1946 to 73 ha in 1996. The 1982 flood caused a remarkable change in vegetation cover in the middle of the watershed (Fig.3). In the upper area of the watershed, where the flood had less effect, willow vegetation cover did not change noticeably, but there was an important reduction in the total impoundment areas. Unlike Moraine Park, the reduction in surface water was not associated with a willow cover decline. Changes in willow cover in the lower part of the valley were not as spatially localized as in Moraine Park. Some willow stands were replaced by meadows, and a minor proportion was replaced by forest.

GPS-based digital maps. Vegetation maps of Moraine and Horseshoe Park produced by the ground-based GPS survey (Fig. 5) were similar to the 1996 low-resolution air photo maps (Fig 3 and 4). However, some meadow and forest patches were not delineated in the GPS based maps, and the shrub vegetation class was separated into areas dominated by birch and willow. The birch cover class was greater in Moraine Park than in Horseshoe Park (18 and 0.7 ha, respectively). Birch cover was mostly restricted to the south part of Moraine Park in the area where major changes in river channel were documented. The three different methods used to classify willow cover produced markedly different estimates of willow in Moraine Park but not in Horseshoe Park (Table 3). This indicated that the spatial pattern of willow cover was more complex in Moraine Park than in Horseshoe Park.

Willow cover was very heterogeneous. Observed combinations of area types and willow categories ranged from areas in which willow were decreasing and had a high percentage of dead individuals to meadows or open areas that had been colonized by willow during the last few years (Table 5). Dead willow areas were more extensive in Moraine Park than in Horseshoe Park (Table 5, and Fig. 6). In Moraine Park, these areas were dominated by tall willow as evidenced by the high number of dead willow with large crowns, and several tall stems that remained on the plant. Some of the live willow were also tall, but with several dead stems indicating stressful conditions for willow growth. Many old river channels and old signs of beaver activity were found in the two largest dead willow polygons. On the contrary, only a few patches dominated by dead willow were found in Horseshoe Park (Fig. 6). New and old willow colonization was found in both parks. These areas were more extensive in Horseshoe Park (34 % and 12 %, respectively), but some of them had a low density (Table 5). In Moraine Park, the major areas colonized by willow where on a meadow that received water diverted from the northeast branch of the river by beaver disturbances (yellow area of Moraine Park map in Fig 6). These areas corresponded in part to some of the flooded areas identified in the low resolution maps (Table 4). Flooding was produced by beaver activity. Beaver dams apparently reduced water flux in the main channel, resulting in a ramification of the river into several small channels. Although, there was evidence of new beaver cuts on willows, beaver did not seem to maintain the dams. Under high water flow resulting from snowmelt (June and July), water moved out of the channel and into the meadow. This water was ultimately routed to the southern main branch of the river. Water flow through the meadow was gone by August in the summer of 1998. Several willow saplings were established in this area under conditions of soil water saturation. In Horseshoe Park, new willow colonization was found on the alluvial fan created by the 1982 flood (Fig. 6). Willows were also colonizing several meadows in the upper areas of the valley. Evidence of old colonization was also found in meadows of both the upper and lower parts of Horseshoe Park. Several small patches with high willow recruitment were found in areas flooded temporarily by the river in both watersheds.

Differences in willow morphotypes were the other source of heterogeneity in willow cover. Short old morphotypes were abundant in Horseshoe Park (Table 5), but most of the short willows in Moraine Park occurred at low density in the south-central part of the watershed. These areas were classified as areas covered by low willow density (Table 5). If low density area type is included, the total cover of the short old morphotype increases considerably in Moraine Park but not in Horseshoe Park (Table 5). Short morphotypes were on the areas where major reductions in river channels were documented indicating that these morphotypes occur in areas of unfavorable growing conditions (Fig. 7).

Tall willow was more abundant in the upper areas of the valley in both watersheds. Changes in river course were probably less important in these upper areas because the river is constrained to a narrow valley. The tall willow polygon in the southwest part of the valley in Moraine Park has many ponds (not shown in the GPS maps) and saturated soils which create favorable conditions for willow growth. Even though major changes in surface water were documented in the upper part of the valley in Horseshoe Park with the low resolution maps, no shift to lower willow cover or larger cover of short old morphotypes had occurred. In the lower valley of Horseshoe Park, tall morphotypes tended to be more abundant in areas farther from the river course. Intermediate morphotypes were found in the wider areas of both valleys more spatially associated with short old willow morphotypes.

A more complicated pattern of river channels could be inferred from the extensive evidence of abandoned branches of the river and old meanders in Moraine Park. Old meanders were also found in Horseshoe Park but they seemed to be less frequent than in Moraine Park. Much evidence of old beaver activities was found in Moraine Park, but little was found in Horseshoe Park. Few signs of new beaver activities were observed in either watershed, only one small beaver pond was found in the tall willow area of Horseshoe Park.

Comparison between low resoultion and GPS-based maps. In both valleys willow cover based on criterion 2 (Table 3) was similar to the riparian shrub cover of low resolution maps. In the case of Horseshoe Park riparian shrub cover corresponded almost exactly to the value of willow cover estimated by using criterion 2 (723,676 and 727,389 m2, respectively). In Moraine Park, riparian shrub cover overestimated willow cover obtained with criterion 2 by 83 ha (716,012 and 799,471 m2 respectively). The riparian shrub class included areas dominated by birch, but excluded most of the dead willow areas. Since birch and dead willow covered a small portion of Horseshoe Park, cover values obtained from the different resolution maps were nearly the same. On the contrary, in Moraine Park riparian cover was larger in the low resolution map because dead willow areas could not be excluded, and cover of some of the shrub patches was overestimated.

DISCUSSION

Geomorphological characteristics of drainage segments (reaches) have important effects on the development of riparian vegetation (Gregory et al 1991). The upper areas of both watersheds occurred in narrow valleys and had constrained reaches. Consequently, the position of the stream channel was relatively fixed. Riparian vegetation in the upper areas of both watersheds was dominated by tall willow and no important changes in riparian cover occurred in these areas. Lower areas of both study watersheds had unconstrained reaches, characterized by lack of significant lateral constraint and low streamflow gradient. This allowed the stream to form braided channels. Importantly, short willow morphotypes were mostly restricted to these lower, more unstable reaches, where there were major changes in hydrology between 1946 and 1996.

Decreases in willow cover as estimated from the change analysis only took into account areas where willows disappeared. Other changes in willow community characteristics, such as the proportion covered by different morphotypes, were not included. On the 1937/1946 aerial photos it was difficult to identify whether areas covered by riparian shrubs corresponded to tall willow, or a combination of different willow morphotypes and birches. In contrast, the

GPS survey provided accurate estimates of the proportion of the areas covered by different morphotypes and birches, but only for 1996. The combination of information from the historical and recent cover maps allowed me to make two inferences about trends in willow cover over the study period. The first requires an assumption that in the old photos all of the areas classified as riparian shrubs were dominated by tall willows. From this I inferred that the declines in tall willow equaled 54 and 65% for Moraine and Horseshoe Park, respectively. If, in addition to the previous assumption, areas currently classified as birch are also considered to have been formerly dominated by tall willows, then the declines in tall willow become 72 and 66% on Moraine and Horseshoe Park respectively. Changes in willow cover, such as reductions in willow density or shifts from tall to short morphotypes could not be determined with these data. However, it is safe to say that the analysis of willow decline based only on areas where willow disappeared, underestimated the total changes that actually occurred.

A comparison of estimates of willow decline using the two different methods (low-resolution and GPS-based maps) provides additional insight about the effects of disturbance. From the low-resolution maps, declines were determined based on the difference between old and recent air photos, assuming that willows were the dominant shrub species. From the GPS survey, declines were inferred based on the amount of area dominated by old dead willow plants. By comparing the two results, I found that the declines based on the extent of dead willow were 20 and 80 % less than the estimates based on disappearance in Moraine and Horseshoe Park, respectively. This indicated that most dead willow plants remained in Moraine Park, but dead willows were removed in Horseshoe Park, probably by the 1982 flood event.

Even though changes to drier and warmer climatic conditions (Singer et al 1998a), could have affected willow growth and productivity, climatic change did not seem to be the primary causative factor producing the observed willow decline. The two valleys both experienced a drier climatic trend but they showed different willow cover dynamics. Water used for willow growth comes mainly from groundwater rather than current precipitation (Alstad et al 1999), and in mountain valleys the level of the water table is mainly regulated by the hydrological characteristics of the river (Patten, 1998). Willows growing in areas where the water table remains high would not be affected by decreased precipitation, as long as the water table level remains high. In this way, willow would be buffered from a slightly drier climate. However, it is also possible that under lower precipitation water table will be deeper, or/and, the duration of the period of the growing season with shallow water tables will be shorter.

As expected, changes in hydrology were a critical factor in determining willow colonization and population persistence in both parks; however, hydrological changes were different between parks. In Moraine Park, willow disappeared from areas where major reductions in river complexity were documented. Although this could have been the result of reduced water flow, high river complexity and impoundment areas were clearly the results of beaver activities. Well-defined beaver dams surrounded by riparian shrubs were found in the upper Horseshoe Park valley in 1937/1946. Almost all of these ponds disappeared by 1996 but no noticeable changes in riparian shrub vegetation were documented as was observed in Moraine Park.

These contrasting responses of the riparian shrub community to decline in beaver could have resulted from differences in interactions between basin geomorphology and beaver activities. Johnston and Naiman (1987) distinguished the characteristics of beaver dams in upland V-shaped valleys from wetlands with extensive floodplains. Beaver dams in upland streams, produced small ponds with well-defined contours. In these ponds there is little change in surface water level when stream water level fluctuates. In wetland floodplains, small beaver dams often inundate a large surface with shallower water depth and the pond boundary is diffuse. Beaver alterations seem to have less impact on ecosystem level processes in wetlands than on uplands because soils in wetlands are saturated (Johnston and Naiman 1987). Well-defined beaver dams were found in the upper areas of Horseshoe Park, in the V-shaped part of the valley. There, the water table was probably not reduced by the decrease in beaver and their ponds, because the water table is controlled by geomorphology more than by beaver ponding. If this was the case, then hydrological conditions for shrub growth were little affected by the beaver decline.

Floodplains of both watersheds represented conditions that were intermediate between the two contrasting situations just described. On floodplains, geomorphic characteristics are similar to a valley with a low elevation gradient, but soil water saturation can occur only during a short period of time, in a restricted area close to the river. Water table, in areas close to the river fluctuated between 0 and 20 cm during the annual peak in steam flow (June) but it become deeper than 50 cm after that (Zeigenfuss et al. 2000). In this situation, beaver dams noticeably changed the hydrological conditions for vegetation growing around edges of ponds. Although ponds did not have a defined boundary as in the case of wetlands, they were not large. The gradient of the floodplain in Moraine Park was large enough to limit the size of the pond because further increases in pond surface area were limited by the formation of a new drainage channel. In this valley, well-defined beaver ponds were difficult to identify in 1946, but there were several small impoundment areas and many branches of the river.

This hydrological process ultimately increases the branching pattern of the river, and probably resulted in a larger area of water subsidization than would occur with a few large beaver ponds. Thus, decreases in beaver abundance caused a simplification of the river course and a reduction in the area of land surface influenced by the river and associated water tables. In areas where water tables diminished, drier conditions prevailed, and riparian shrub communities were replaced by meadows.

Willow decreases in Horseshoe Park seemed to be, in large part, caused by the flood disturbance following a collapse of an earthen dam in 1982. Most of the reduction in riparian shrub cover occurred on downstream areas that were directly affected by the flood. In 1996, areas with bare soils created by the flooding were being colonized by willow. Periodic large flood disturbances that destroy vegetation and generate open patches for plant establishment have been considered to be important in models of riparian landscape structure (Miller et al. 1995). Some riparian species depend on these recurrent disturbance events for establishment. Thus, alterations of the flood regime have negatively affected many riparian ecosystems (Bradley and Smith 1986).

The flood event in Horseshoe Park produced a larger disturbance than normally expected in a recurrent flood regime in mountain valleys (Patten 1998). The hydrological characteristics of the river were not only altered downstream but also upstream, through a large mass of rocks and boulders that slid into the valley (Jarret and Costa 1993). Restriction of river flow in the area of the alluvial fan could have risen water tables in the upper areas of the valley. This is the area where major reductions in beaver ponds were found.

In addition, water table levels in the meadows that were being colonized by willow in the upper areas of the valley (Fig 3 and 6) could have risen since the flooding, producing favorable conditions for willow establishment. Willow seedlings rapidly colonized the sediments deposited in the alluvial fan in the summer of 1983 (Keigley 1993.). Even though some patches contained a high density of seedlings, few of them survived to the following years (Keigley 1993.). Most of the willow observed on the alluvial fan in 1988 came from the original establishment of 1983 (Keigley 1993). This area was classified in the GPS survey as being colonized several years ago because it was dominated by young short willows (Fig 6). These willows were no older than 15 years old.

Willow produces wind-dispersed seeds that have a limited viability and no willow seed bank ever develops (Raven 1992). In RMNP tall willow normally produce a large number of seeds and seed availability does not limit willow establishment (Cottrel 1995). Willow saplings (younger than 4 -5 years) were observed in meadows with high soil water content indicating that recruitment is not restricted to bare soil as occurs with other riparian species (Bradley and Smith 1986). However wet sandbars are suitable sites for willow establishment, as indicated by high recruitment observed in areas affected by flooding.

The study areas were intensively affected by human activities since the late 1800's. Important changes could have occurred in riparian communities before the area became part of the National Park. Nevertheless, during the period covered by this study, the impacts of human activities on riparian communities decreased because the area become protected under National Park policy. However, in the last 50 years both watersheds have shown signs of deterioration in the riparian plant communities. These changes do not seem to have been caused by direct impacts on the ecosystem. However, humans may have generated conditions for an increase in elk population size, which could have affected the riparian ecosystem.

The large proportion of willows with short morphotypes in 1996 could be a result of increased elk browsing. Elk browse on willow mainly during the winter, on the new shoots developed during the previous growing season. An increase in elk browsing on willow leaders could produce suppressed willow morphotypes (see chapter 2). In a similar way, high elk browsing pressure inhibits height elongation on young aspen stems, and suppressed plants are preferentially browsed by elk (Romme et al. 1995). Tall plants are protected from browsing because new meristems are beyond the reach of the elk, and also because younger stems developing inside the canopy are difficult to reach by elk, and then, they could scape height suppression. By killing tall stems, disturbance open up willow canopy stimulating stems turnover. However, in a more open canopy, young stems will be browsed by elk and suppressed. Disturbances such as flooding or beaver activities facilitate elk access to willow shoots. Interestingly, in Horseshoe Park, short and intermediate willow morphotypes were primarily located in the downstream flooded area. Then, the combined effect of disturbance and high elk density could ultimately lead to the change from a tall to a short willow community. Additionally, new established willow plants growing under heavy browsing levels will develop into a short morphotype. It is expected that under heavy browsing, areas newly colonized by willow will be primarily comprised of short morphotypes, thus increasing the total area of short willow.

Browsing pressure on willow increased following elk reintroduction and cessation of artificial controls, but it is not clear how this could have affected the extent of willow cover. I hypothesize that increased elk browsing did not directly cause a long-term decrease in riparian shrub cover but may have indirectly contributed to the decline. All of the areas where willow disappeared suffered important hydrological changes. A willow cover decline was also found in Yellowstone National Park (Engstrom et al. 1991), where a similar interaction between elk and drier conditions has occurred (Singer et al 1998a). During the

1988 drought in Yellowstone, willow in two stands located on dry marginal sites died. Willows in one stand were heavily browsed but willows in the other were not (Singer et al. 1994). Under a long term trend of reduced water availability, riparian shrubs will be replaced by other vegetation types, since they are not adapted to withstand water stress (Patten 1998). Under this scenario, differences in the level of elk browsing on willow would make little difference in the long term vegetation trend. Thus, elk could have reduced willow canopy cover within a willow patch by suppressing plant growth, but the total area covered by willow in the valley will be primary controlled by the amount of wet habitats suitable for riparian vegetation growth. However, elk could indirectly affect beaver by reducing the extent of tall willow morphotypes. Beaver decreases have induced the reduction in river length and water subsidized surface area, causing drier conditions for willow growth. It is not clear why beavers have almost disappeared from these RMNP watersheds, but it is possible that the elk increase could contributed to the beaver decline by reducing willow biomass availability for beaver.

Direct species interactions (physical interaction) have been most commonly studied, but recently, indirect effects have been shown to be important in many studies (Wooton 1994, Schmitz et al 1997, Olff and Richie 1998). Beaver have a direct effect on riparian shrubs by cutting stems that are used for food or to build dams and lodges (Nolet et al 1994). But additionally, beaver impoundment creates favorable physical conditions for riparian vegetation growth (Naiman 1988, Johnston and Naiman 1990a). Shrub re-invasion has been observed in abandoned beaver ponds (Remillard et al. 1987), and fragmentation of willow plants and the movement of the cut stems by beaver could be an important factor in the asexual propagation of the species (Cottrell 1995). At the same time, a direct interaction occurs between elk and willow. Changes in willow communities induced by elk, such as increases in cover of suppressed morphotypes, will have indirect negative effects on beaver. One of the major challenges in ecology is the identification of the strength of species interactions (Wooton 1994, Bertness and Leonard 1997). The signs and intensities of the interactions are dynamic. Here they depend on the size of the beaver and elk population, as well as the characteristics of the riparian vegetation and environmental conditions. Responses of plant biomass production to different levels of browsing (Bergstrom and Dannel. 1987), beaver cutting (Kindschy 1989), and biogeochemical changes induced by elk or beaver also need to be considered (Pastor and Naiman 1992, Naiman and Melillo 1984, Hobbs 1996). Species interactions, particularly between beaver and willow, seem to be an important source of stability in these riparian ecosystems, which are subject to continuous disturbance events These ecosystems are largely dependent on beaver, which act as a keystone species (Heywood 1995, Bond 1994) generating favorable conditions for willow growth. Thus, persistence of these riparian communities will depend on the reestablishment of the biotic and abiotic conditions which support beaver populations.

CONCLUSION

Trends in willow cover were similar in both parks, but the characteristic of the decline and the conditions of the current vegetation were different. In Moraine Park riparian shrub declines were spatially associated with major reductions in river complexity. In Horseshoe Park declines were mainly spatially associated with areas that were directly affected by the 1982 flood disturbance. Willow vegetation in Moraine Park was more heterogeneous than in Horseshoe Park. This heterogeneity was caused by a high proportion of short willow morphotypes that grew in low density in areas dominated by birch and dead willow cover. Willow colonization was found in both parks on wet meadows, and also in areas affected by flooding in Horseshoe Park.

The potential causes of willow decline are many, but it is clear that beaver played a role in increasing riparian habitat cover, by increasing stream channel complexity, creating impoundments of water, and thus increasing the area of land surface where there is an elevated water table. The decline in beaver between 1939 and 1969 is not well quantified, and the available data indicate that there were still many beaver present in 1969. It would be useful therefore to conduct an additional willow survey using 1969 aerial photography, to try to determine how much of the willow decline occurred before or after 1969.

Humans may have played a role in decreasing riparian habitat, through their activities between 1875-1961, including substantial alterations of the hydrology through ditching in Moraine Park. Despite these alterations, however, beaver were still present in abundance in 1939 and to a lesser extent in 1969.

Horseshoe Park was not affected this way, yet there was still a decline in willow cover, and a shift to shorter morphotypes. There is a need to try to reconstruct human activities and their effects more precisely.

Elk wintering in RMNP increased in number from 0 in 1914, to at least 800 in 1943, were kept at 600 or below 1944-1968, and then increased to over 1,000 in the late 1980's. Yet, studies indicate that willows are well adapted to tolerate herbivory. Willow were still abundant in 1939-1946, when there were also abundant elk. There may also have been abundant elk prior to their extirpation through market hunting. Climate data suggest a slight warming and drying, but the impacts of such a climate shift on hydrology and riparian habitats have not been determined. In our opinion, decreases in the area of riparian, water-subsidized habitat resulting from beaver decline, have probably been much more significant than either changes arising from elk herbivory alone, or from slightly decreased stream flows under a warmer and drier climate. The cause(s) of the beaver decline are still unknown, and there is a need to evaluate alternative explanations which might include disease outbreak, beaver overabundance and resultant crash due to loss of forage, competition with elk, and loss of habitat and forage due to human land use and hydrologic alterations.

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Table 1. Aerial photography used to map willow cover and river in the two study watersheds.

Year	Site	Map type	Scale	Film type	Commissioning agency
1937	MP(*) HPl(**)	River Vegetation-River	1:22,000 1:20,000	Black & White	U.S. Forest Service
1946	MP HPu(***)	Vegetation Vegetation-River	1:20,000 1:20,000	Black & White	U. S. Forest Service
1996	Both watershed	Vegetation River	1:28,000	Color	RMNP(****)

(*) *Moraine Park*
(**) *Horseshoe Park, lower area of the valley*
(***) *Horseshoe Park, upper area of the valley.*
(****) *Rocky Mountain National Park*

Table 2. Description of categories used to classify patches that contain willow.

Category	Values	Description
Dominant willow	0. No willow	
Co-dominant willow	1. Sapling	Lower than 0.5 m. tall
	2. Short young	Between 0.5 to 1.5 m tall young stems
	3. Short old	Between 0.5 to 1.5 m tall old stems
	4. Intermediate	Between 1.5 to 2.0 m tall
	5. Tall	Higher than 2.0 m tall
Willow density	0. no willow	
	1. Few willows	Sparse willows
	2. Low density	Distance between plants around 5 m
	3. Moderate density	Distance between plants around 3 m
	4. High density	Distance between plants less than 2 m.
Dead willow	0. no willow	
	1. Less than 10 %	
	2. Between 10 - 30 %	
	3. Between 30 to 50 %	
	4. Between 50 - 80 %	
	5. More than 80 %	

Table 3. Total area (ha) covered by willows in the surveyed watersheds according to three different criteria. Values in parenthesis indicate percent covered using criteria 1.

Criteria	**Classification**			**Moraine Park**	**Horseshoe Park**
	Vegetation class	***Vegetation Subclasses***	***Willow category***		
1. Willows present	No specified	No specified	Dominat willow > 0	104.5 (100)	88.3 (100)
2. Dominant vegetation	Willow	No specified	No specified	71.6 (68)	72.4 (82)
3. High density-Low dead percentage	Willow	No specified	Willow Density = 3 or 4, and Dead Willows = 1 or 2	50.0 (48)	65.3 (74)

Table 4. Length (km) and surface area (ha) of hydrological features in Moraine Park in 1937 and 1996 and Horseshoe Park in the combined years of 1937/46 and 1996.

	MORAINE PARK				**HORSESHOE PARK**			
	Length		**Surface area**		**Length**		**Surface area**	
	1937	**1996**	**1937**	**1996**	**1937/46**	**1996**	**1937/46**	**1996**
Main river	30.2	13.3	23.8	7.5	16.8	9.4	9.7	5.1
Current meanders	12.1	6.9	10.1	2.6	0.5	1.8	0.2	1.0
Old meanders	3.0	0.3	2.5	0.1	2.2	2.3	0.8	1.6
Ponds	-	-	1.4	1.0	-	-	10.9	47.6
Flooded areas	-	-	4.6	21.4	-	-	-	-

Table 5. Total area covered by willow (ha) according to criterion 1 in table 3, divided into different area types and willow categories.

	Area Type	**Willow Categories**				**Moraine Park**	**Horseshoe Park**
		Dominant	***Co-dominat***	***Dead*** (*)	***Density*** (**)		
Colonization new	**Saplings**	young	none	low	any	8.4 (8) (***)	3.0 (3)
Colonization Old	**Short young**	short young	young or none	low	low	0.02 (0)	12.2 (14)
					high	4.2 (4)	14.8 (17)
Areas originally cover by willow	**Short old**	short old	any	low	high	10.1 (10)	18.7 (21)
	Intermediate	intermediate	any	low	high	7.6 (7)	4.1 (5)
	Tall	tall	any	low	high	28.3 (27)	30.4 (34)
	Dead Willow	any	any	high	high	17.6 (17)	2.1 (2)
	Low density	any	any	any	low	28.3 (27)	3.2 (3)
					TOTAL	104.6 (100)	88.3 (100)

(*) low: dead percentage values = 1 or 2; high: dead percentage values = 3, 4 or 5 (Table 2)

(**) low: density values = 1 or 2; high: density values = 3 or 4 (Table 2)

(***) values in parenthesis correspond to percentage of total cover estimated with criteria 1 (Table 3)

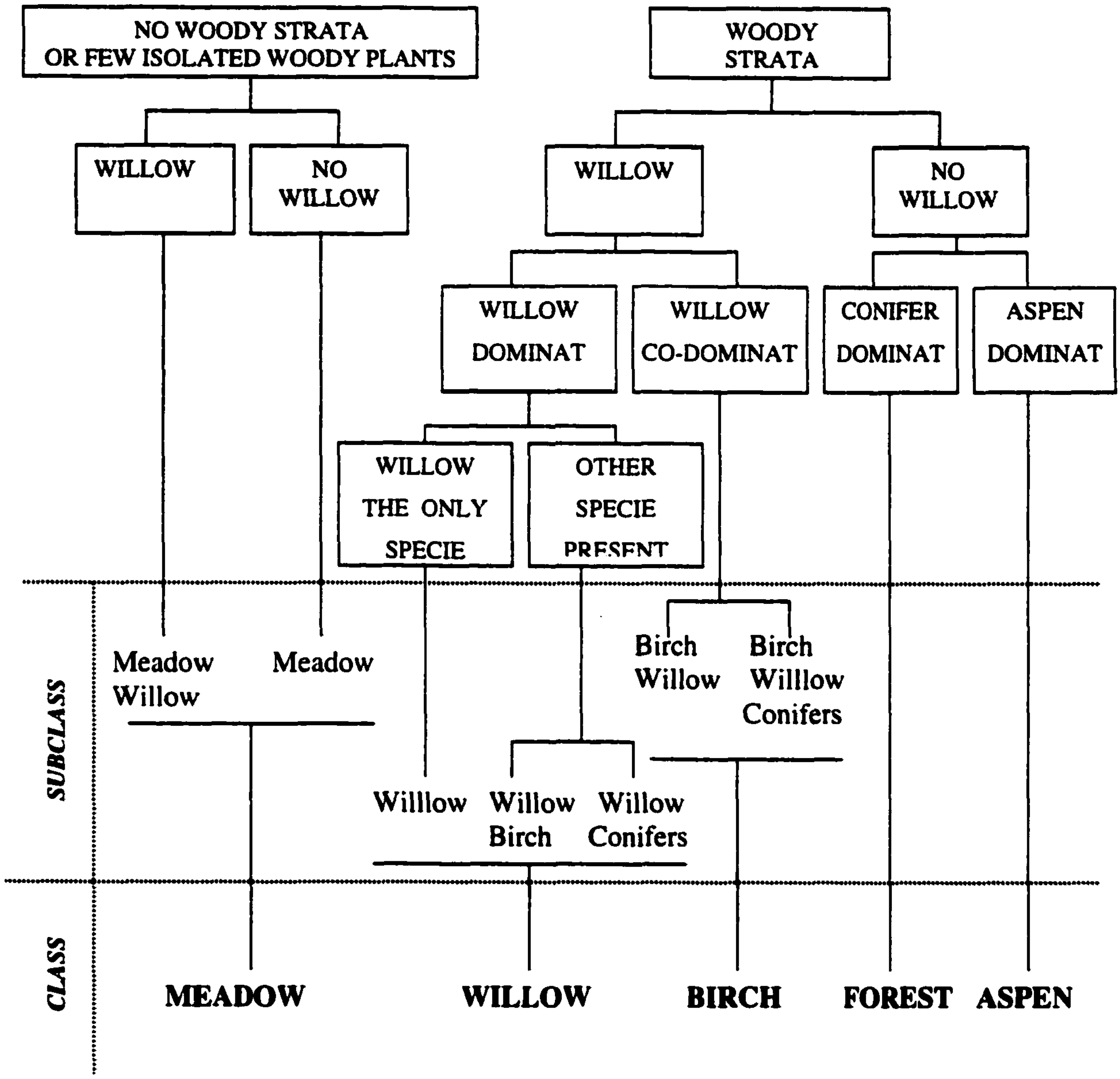

Figure 1. Schematic of vegetation class and subclass classification.

Figure 2. Hydrological maps of Moraine Park in 1937 (upper map) and 1996 (lower map) determed using low resolution digital maps based on aerial photo interpretation.

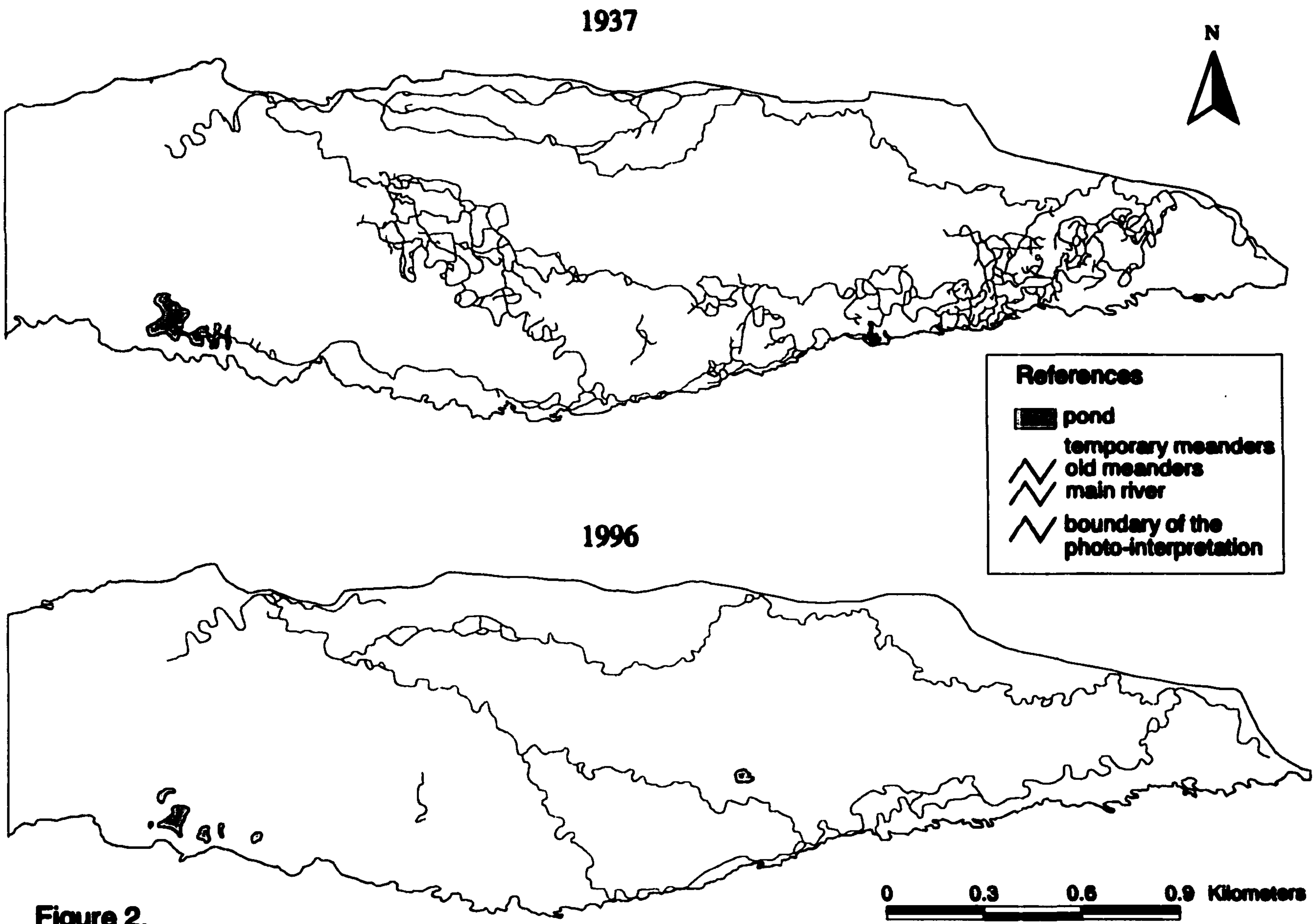
1937
N
References
▨ pond
temporary meanders
old meanders
main river
boundary of the photo-interpretation
1996
0
0.3
0.6
0.9 Kilometers

Figure 2.

Figure 3. Spatial distribution of vegetation classes and hydrology in Horseshoe Park in 1946, in the upper part of the valley and in 1937 in the lower part of the valley (upper maps, and the same area in 1996 (lower map). Maps were created using low-resolution digital maps based on aerial photo interpretation.

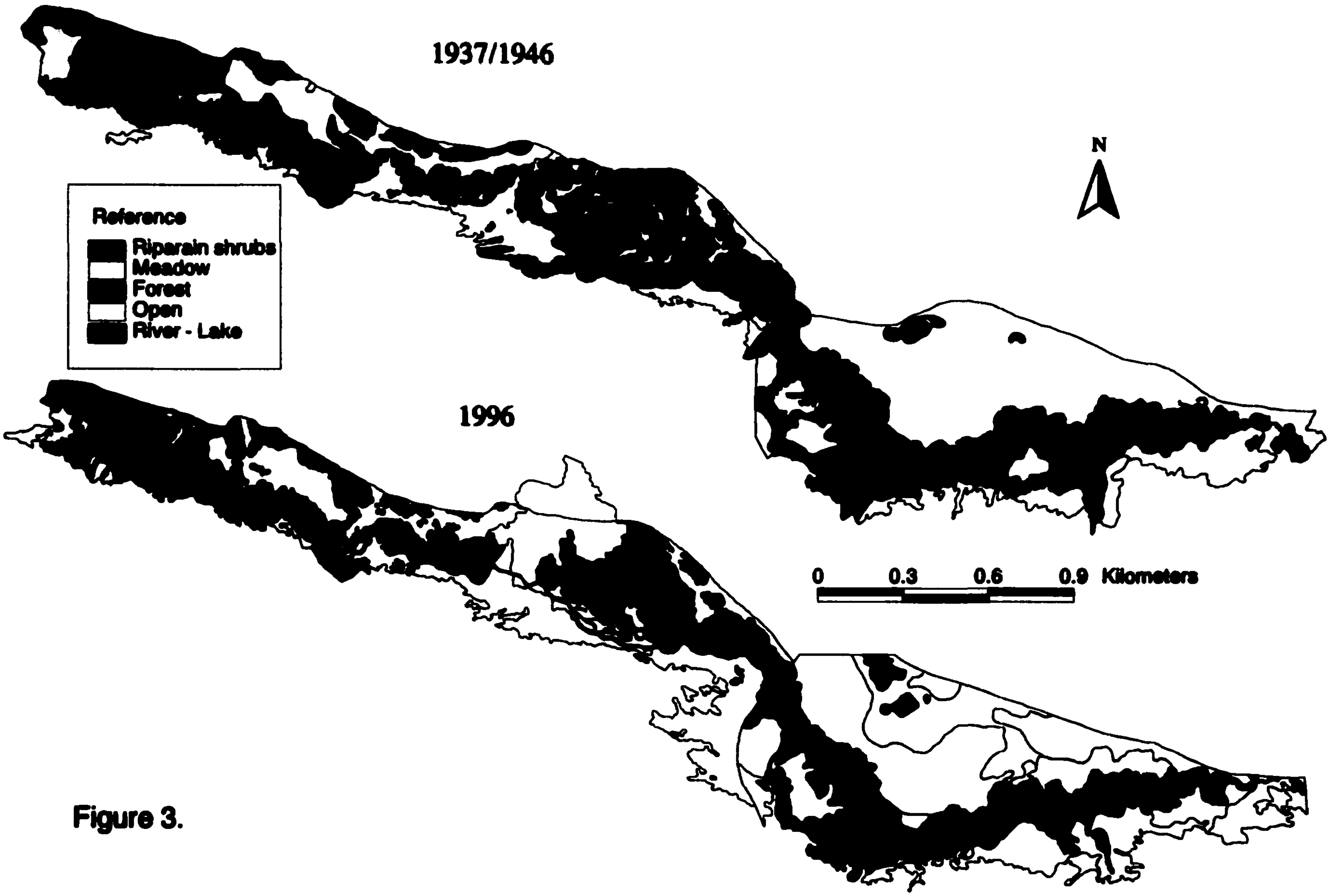
1937/1946
1996
N
Reference
Riparain shrubs
Meadow
Forest
Open
River - Lake
0
0.3
0.6
0.9
Kilometers

Figure 3.

Figure 4. Spatial distribution of vegetation classes and hydrology in Moraine Park in 1946 (upper map) and 1996 (lower map), determined using low resolution digital maps based on aerial photo interpretation.

Figure 5. Spatial distribution of vegetation class in Horseshoe Park (upper map) and Moraine Park (lower map), determined using GPS-based digital maps.

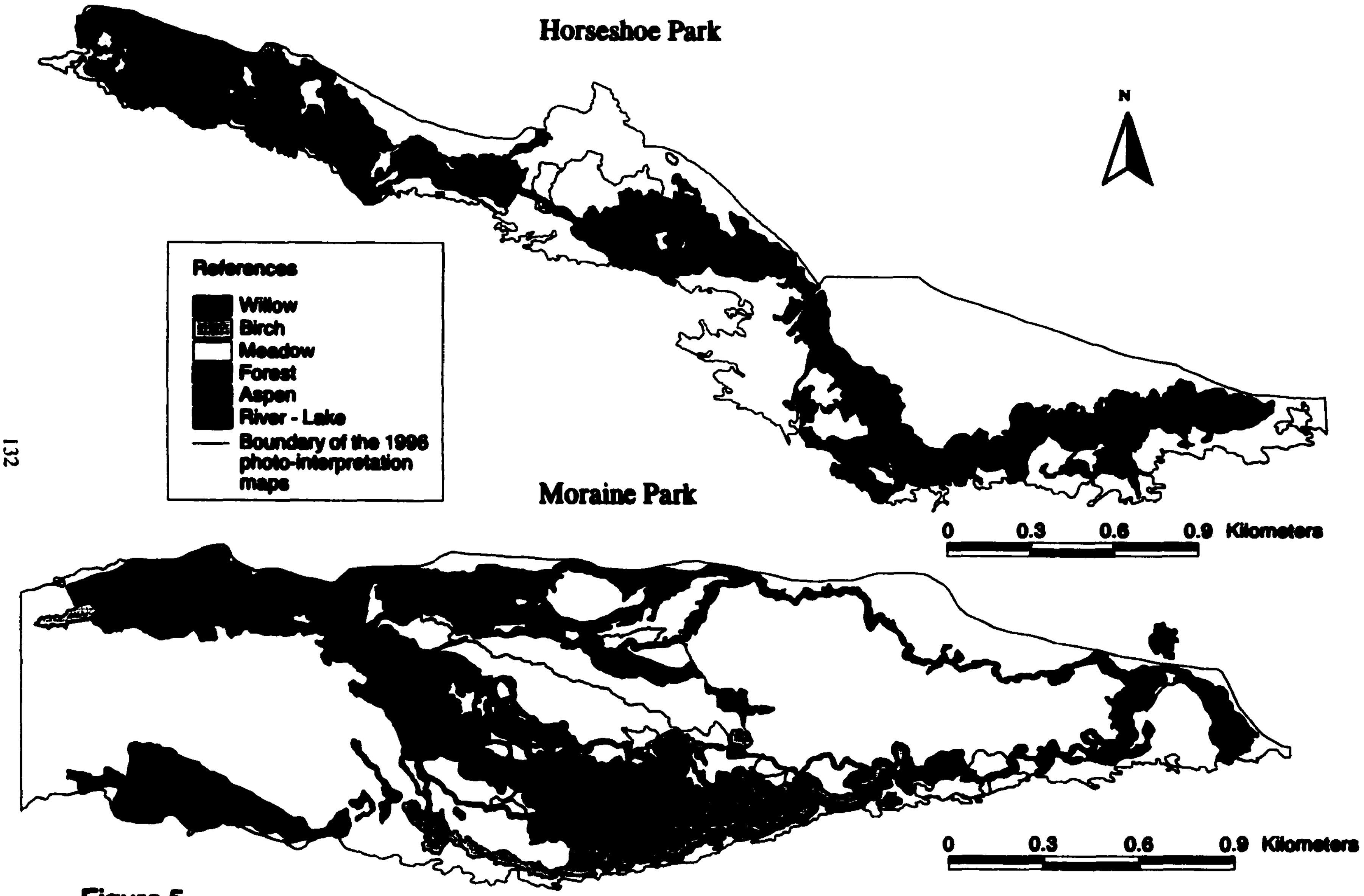
Horseshoe Park
N
References
Willow
Birch
Meadow
Forest
Aspen
River - Lake
Boundary of the 1996 photo-interpretation maps
0 0.3 0.6 0.9 Kilometers
Moraine Park
0 0.3 0.6 0.9 Kilometers

Figure 5.

Figure 6. Spatial distribution of areas dominated by dead willows and areas colonized by willows in Horseshoe Park (upper map) and Moraine Park (lower map), determined using GPS-based.

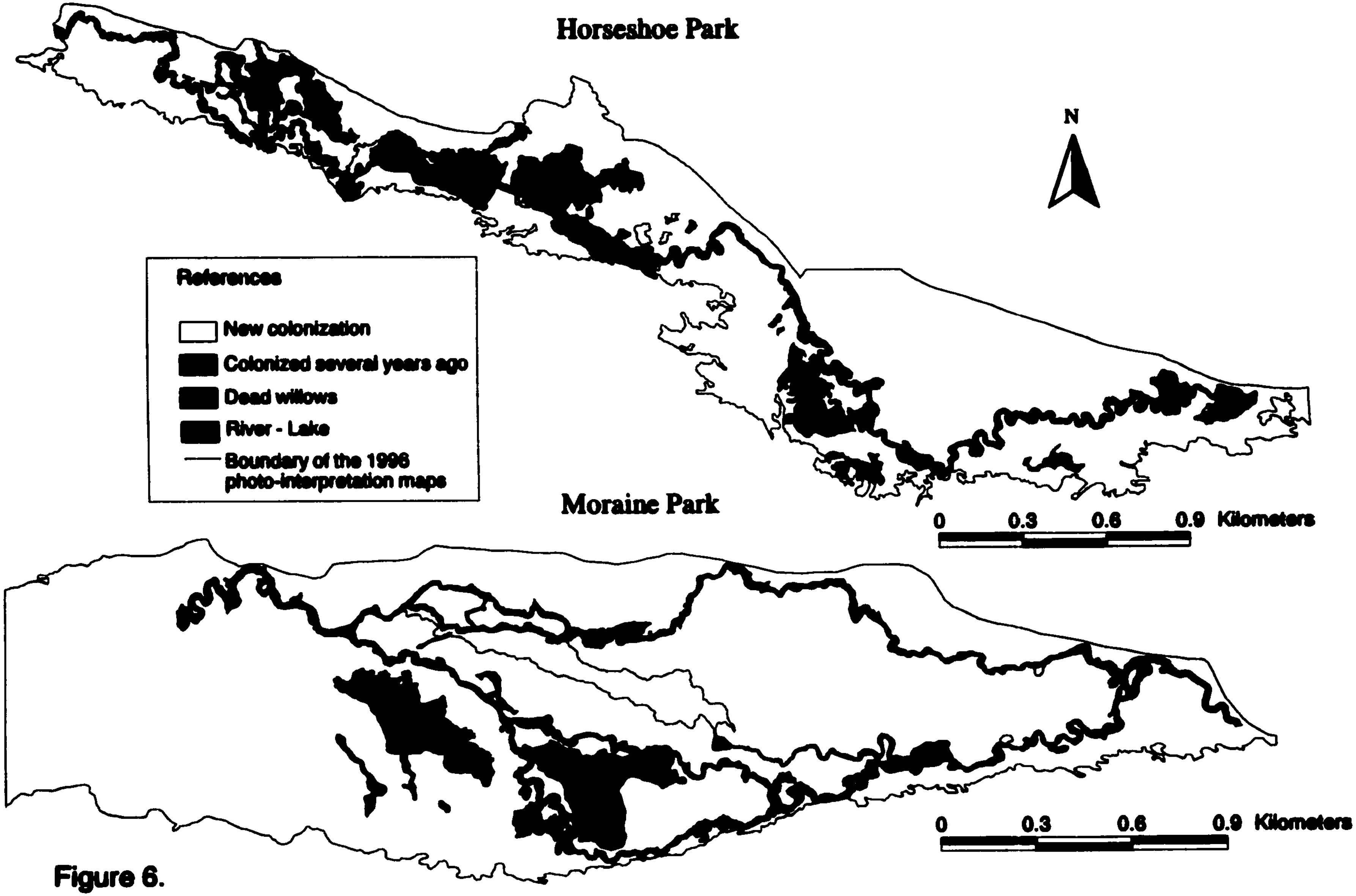
Horseshoe Park
N
References
☐ New colonization
■ Colonized several years ago
■ Dead willows
■ River - Lake
— Boundary of the 1996 photo-interpretation maps
0 0.3 0.6 0.9 Kilometers
Moraine Park
0 0.3 0.6 0.9 Kilometers

Figure 6.

Figure 7. Spatial distribution of willow morphotypes distribution in Horseshoe Park (upper map) and Moraine Park (lower map), determined using GPS-based digital maps.

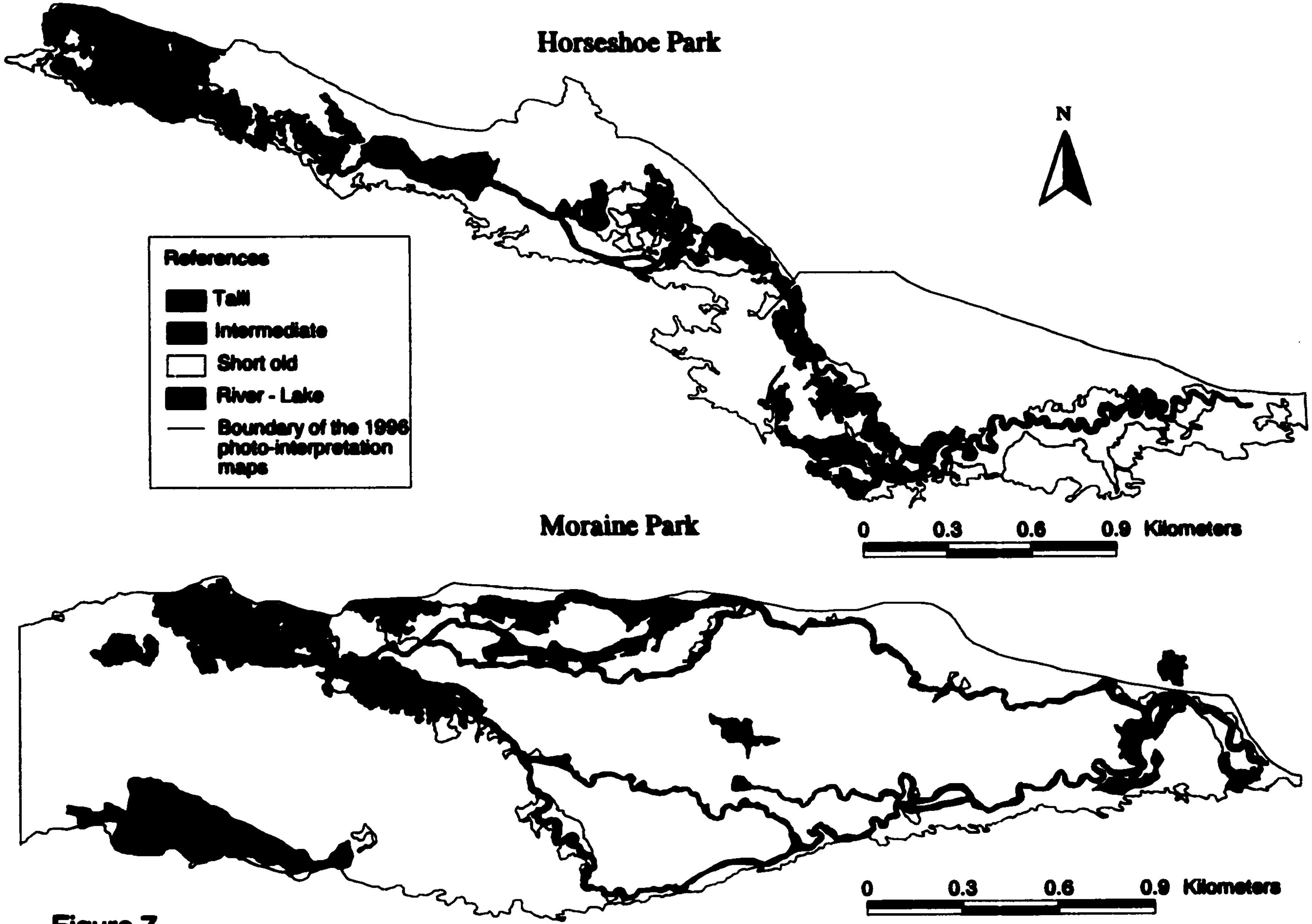
Horseshoe Park
N
References
■ Talll
■ Intermediate
□ Short old
■ River - Lake
— Boundary of the 1996 photo-interpretation maps
0 0.3 0.6 0.9 Kilometers
Moraine Park
0 0.3 0.6 0.9 Kilometers

Figure 7.

CHAPTER 4

Willow population dynamics on the elk winter range of Rocky Mountain National Park: a simulation model-based assessment.

Abstract. Willow (*Salix spp.*) population dynamics under different combinations of elk density and hydrological conditions were evaluated using a simulation model (SAVANNA). SAVANNA is a process-oriented, spatially explicit model that simulates water balance, nitrogen cycling, vegetation dynamics and herbivory. The study area included one valley of the elk winter range of Rocky Mountain National Park, in which during the last 50-year period, willow cover has decreased approximately 20%, and where the proportion of short (<1.5 m) vs. tall willow (> 2.0 m) might have increased by more than 50%. The willow decline occurred over the same period of time that the elk population increased (approximately 3-fold), beaver declined to a very low abundance, stream channel density decreased and climatic conditions became drier. Compared with grass, willow productivity was more dependent on water table depth than on precipitation. Water table depths deeper than 1 m greatly decreased willow productivity. Highest willow productivity was predicted under the combination of shallow water table and low precipitation at the beginning of the growing season, and high precipitation during the late season when the water table was deeper. Elk browsing on willow will cause a decrease in willow productivity. However, densities as high as 50 elk km^{-2} did not reduce productivity over the short-term (3 years) when willows were growing under conditions of high water availability. The model predicted that water stress will interact with herbivory, producing a greater than proportional decrease of willow productivity under increasing elk densities. Elk will increase the proportion of total nitrogen in the system found in herbaceous plants but it will slightly stimulate N-mineralization rate after a 10

year period. Elk will also suppress height growth of willow, affecting the transition from short to tall willow. Under good growing conditions and no herbivory, this transition could occur in approximately 10 years. Densities of 75 elk km^{-2} will prevent this transition, but lower densities (50 elk km^{-2}) could produce more than 50% reduction of height growth. Willow productivity of past and recent times was estimated with the model using maps generated by interpretation of old aerial photos (1946) and field surveys (1998). The estimate of total willow aboveground productivity in 1998 was 48% lower compared with 1946 (132 and 63 tons yr^{-1} on the whole study area), which gives an indication of the effect that a decline in cover and degradation of willow, has had on the riparian ecosystem. The model predicts that the current elk densities, and the drier conditions, caused by decreased river channel density, both act to limit the extent and productivity of the riparian ecosystem.

INTRODUCTION.

Shrub willows (*Salix spp.*) dominate the riparian community of the elk winter range of Rocky Mountain National Park (RMNP). Changes in hydrological conditions and biota that have occurred in this area have affected willow cover and characteristics. Willow cover decreased by 20 % in two of the main watersheds on the elk winter range of RMNP over a time span of 50 years (1946-1996) or less (Chapter 3). A considerable proportion of the willow cover has probably shifted from communities dominated by tall (>2 m) to communities mostly comprised of short (<1.5 m) willow morphotypes. During this time, the elk population wintering within the RMNP boundaries has increased from 400 to 1,000 individuals (Larkins 1997), and beaver decreased to near disappearance (Zeigenfuss et al. 2000). The beaver decline and probable human alterations to the hydrology have resulted in a decrease in riparian area and stream channel density (Chapter 3). This has likely resulted in reduced areas of shallow water tables, since surface water flow is hydraulically connected to the alluvial water table (Patten 1998). Changes in water availability combined with an increase in elk browsing on willow could have modified the character of the riparian community. In this paper, willow population dynamics and growth on the elk winter range of RMNP were analyzed using simulation modeling. Information taken at the individual, population and landscape levels was integrated in the model with the following objectives; (a) to evaluate willow population changes under different elk densities, and plant water availability; (b) to determine the conditions producing a population shift from a tall to a short willow dominated population; (c) to compare past (1946) and current (1998) willow productivities.

MODEL DESCRIPTION AND PARAMETRIZATION.

We adapted the SAVANNA model (Coughenour 1993) to simulate the Moraine Park area of the Big Thompson River watershed (2481 m) in the northeastern quadrant of RMNP. SAVANNA is a process-oriented, spatially explicit model composed of several submodels that account for water balance, nitrogen cycling, litter decomposition, plant biomass production, and plant and herbivore population dynamics. The entire area covered by willow in Moraine Park was represented by grid-cells of 50x50 m. In each grid-cell, the model simulates on a weekly time-step, the change in cover of herbaceous and willow vegetation. Vegetation cover was defined in terms of rooted area; i.e. the area of the ground which corresponds to the exploited soil volume. Cover was defined in terms of rooted area mainly because soil water and nutrient budgets are computed on a soil volume basis.

The population and biomass productivity submodels of SAVANNA were used to simulate willow dynamics. Willow population dynamics were represented in terms of the number of individuals in six discrete size classes. When the model is initialized, biomass and morphological attributes are ascribed to each size class to represent the mean individual of that size class. Upon initialization, it is assumed that the size classes are arrayed in terms of increasing plant size. Values for plant size (height and canopy diameter) and above and belowground dry weight were assigned to each size class according to allometric relationships (Table 1). Size and aboveground biomass were based on field data (Chapters 1 and 2). Total root biomass was considered to be approximately equal to 70% of the aboveground biomass (Kovalchik 1991), and fine root biomass was considered to be approximately equal to leaf biomass.

Vegetation maps of willow cover generated from a 1998 ground survey (Chapter 3) were used to initialize the model. These maps include information on willow types defined based on the proportion of individuals in each size class

(Table 2), and on willow density. Four willow density classes were defined: few (0-250 plant ha^{-1}), low (250-1,500 plant ha^{-1}), moderate (1,500-3,000 plant ha^{-1}), and high (3,000-4,500 plant ha^{-1}). The initial number of individual in each size class was obtained by the combination of willow types and density maps.

Numbers of individuals in size class 1 could increase only through plant establishment. For our purposes, the number of individuals in the other classes will not increase above their initial numbers because no promotion between size classes will be simulated here. Plant size within size class can change, however. This representation is adequate for modeling short-term population dynamics (shorter than 10-year) but not for long-term dynamics. The rate of establishment was assumed to be proportional to the number of willows in size classes 2 through 6 (it was assumed that individuals in class 1 do not produce seeds). Individuals of classes 2 to 6 have the same contribution to plant establishment. Establishment depends only on current seed production since willow does not develop a seed bank (Densmore and Zasada 1983). However, willow produces numerous wind-dispersed seeds that disperse easily. Consequently, seeds probably are not as important a constraint on willow establishment as are surficial soil moisture and plant competition (Keigley, 1993, Cottrell 1995). The presence of moist soils at the time of seed dispersion is one of the primary factors controlling willow establishment, because willow produces recalcitrant seeds that lose viability rapidly when they are desiccated (Martens and Young 1991). In the model, potential willow establishment was reduced by 0-1 multiplier factors representing water stress (ratio of available water to potential evapotranspiration), and plant competition (woody canopy cover and grass biomass). An additional effect of temperature was used to inhibit establishment outside the growing season. All classes were affected by a nominal mortality rate that was class specific. We assumed a higher mortality rate in size class 1 (0.15 plant year^{-1}) than in the other classes (from 0.02 to 0.008 plant year^{-1} as size class increased from 2 to 6). Low water availability and temperature were assumed to have no direct effect on mortality. Instead, these variables were included in the production submodel as factors affecting plant growth rate and death rate of woody biomass and other tissues. No direct effects of elk on plant mortality or establishment were considered in the model. Willow colonization occurred under the high elk densities of 1996-1998, and it is not clear if heavy elk browsing increases plant mortality (Chapter 3).

The production submodel estimates plant growth and tissue mortality for each size class, which then determines changes in the biomass and size of the mean individual in each size class. Growth initiation at the start of the growing season is a function of phenological stage and carbon reserves stored in stems and roots. Reserves were primarily allocated to initiate leaf growth. Carbon fixation rate is a function of a maximum photosynthesis rate and light, and was reduced by 0-1 functions of temperature, CO2, plant nitrogen and plant available water. Incident light intensity on leaves in each size class is calculated based on plant canopy height using Beer's law. Water uptake is equal to potential transpiration rate if total water demands do not exceed available water. If total demand exceeds supply, water is partitioned among competitors in proportion to demands in each soil layer. Willows were assumed to be deeper rooted (150 cm) than herbaceous plants (85 cm).

Soil water and water table water were modeled as two distinct sources of water. This representation follows the finding of Alstad et al. (1998), that a large proportion of the total water used by willow comes from the water table. Willows relied on water table water more than did herbaceous plants. Limited information exists on willow physiological responses to water stress, in particular to falling water tables. Willow responses to drier conditions are represented in the model by assuming a proportional reduction of plant water availability as the water table depth falls from 50 to 150 cm. Additionally, plants will not have access to the water table if it is deeper than 150 cm. The water table was not considered to be a source of nitrogen even though it was demonstrated that < 10% of the nitrogen uptake of willow is derived from the water table (Menezes 1999). If plant nitrogen uptake from water table was represented, it would result in a large net input of nitrogen into the system, which is probably unrealistic since N leaching losses back to the water table are not represented. The uptake of inorganic nitrogen was represented as a Michaelis-Menten function of soil nitrogen concentration (Thornley 1976).

Net primary productivity (NPP) calculated in each time step is first allocated to leaves and current annual growth of stems during green-up. Excess NPP is then allocated to woody and root biomass. After green-up, NPP is allocated allometrically. The fact that willow leaves are produced only on current annual growth shoots means that NPP can be allocated between leaves and stems in the ratio observed in current shoots. Plant biomass was affected by tissue death due to water, temperature, and herbivory. Tissue death due to herbivory was represented as a function of the amount of plant tissue removed.

As the number and sizes of plants increase, the area covered by willow in the grid-cell also increases. Under high canopy cover, the remaining area available for plant expansion is reduced, resulting in a reduction of potential growth (Mithen et al. 1984). This process is considered in the model through a factor that reduces growth of individual plants under high canopy cover (>60%). In this situation, plant sizes will not change substantially between time-steps, particularly smaller plants, which will remain suppressed in the understory.

The herbaceous functional group is simulated with simpler versions of the submodels described previously. Population dynamics is simulated in terms of potential biomass, as a surrogate for basal cover. Potential biomass changes in response to actual biomass production. NPP is simulated as described above for willow, except there are no woody perrenniating stems. Herbaceous biomass dynamics were calibrated using observed values of standing biomass (Zeigenfuss et al. 2000), however no spatial maps were available.

Neither soil nor water table maps were available for this area. It was assumed that all grid-cells had a Blackwell alluvial floodplain soil type (Moreland 1980). Texture is clay-loam to 85 cm, and sandy below that.

Water table maps were created containing information on the spatial distributions of 4 water table depth types (Fig. 1). Areas were determined by using 1946 and 1998 vegetation maps, and a 1937 hydrological map (Chapter 3). The 4 strata were defined as; Type 1- Tall willow cover in 1998. Type 2- Buffer within 13 m of the main river. Type 3- Buffer within 1 m of the current meanders. Type 4- Areas covered by willow in 1946 that were not included in the other categories, which were considered as the remainder of the potential willow areas. Each water table type was assigned a monthly water table depth based on observed values (Zeigenfuss et al. 2000) assuming that the water table will be shallowest in type 1 and deepest in type 4 (Fig.1).

Weather records used in the model were obtained from weather stations and SNOTEL sites in and around RMNP. These data were spatially interpolated and corrected for elevation differences to estimate weather conditions in the simulated area (Coughenour 1993).

MODEL PERFORMANCE - COMPARISON OF SIMULATED AND OBSERVED DATA.

Individual plant. The simulated total shoot production of an individual plant, with no competition or interference from neighbors, was compared to experimental data. Experimental data were from measurements of total shoots produced in 1997 by willow plants protected from elk herbivory since fall of 1994 (Chapter 1). Simulated data were model outputs for the growth of individual plants of size classes 1, 2 and 3 (other size classes were not considered because they were outside the range of plant sizes in the experimental data). In order to obtain values for shoot production for a wide range of plant sizes, simulations were performed for a period of 10 years with the environmental conditions observed in 1997 for all 10 years (Zeigenfuss et al. 2000).

The ratio of shoot dry weight to aboveground plant dry weight was higher in the simulated data; 0.14 (0.034) and 0.10 (0.014), (means and standard deviations, respectively). The model tended to overestimate shoot production, however values were within the range of variation of the experimental data (Fig. 2).

Simulated plant height increases for short willow were compared with observed values (Fig. 3). The height increase of individual plants under no neighbor interference was simulated over the 5-year period from 1994 to 1998. Simulated growing conditions corresponded to those of plants that were protected from elk browsing by exclosures built in 1994 (Chapter 2). Model estimates of short willow plant height during the period 1994-1998 were in close agreement with observed values (Fig. 3a). Tall willow height growth estimated by the model was within the range of variation of the data for plants with heights < 2.5 m (Fig. 3b). In this case the simulation was for a 10-year period (1990-1999). The model tended to underestimate height growth of plants taller than 2.5 m (Fig. 3c).

Plant Populations. The height frequency distribution of willow populations was compared with the height distributions of simulated data. The model was initialized with data from a survey that was conducted during the summer of 1998 in a short willow area in Horseshoe Park (Chapter 2). The willow population growing in a 50X50 m grid-cell was represented. This willow cover type represents approximately 10 to 20 % of the total willow cover observed in riparian areas of the elk winter range (Chapter 3). The simulation was run for the period 1994-1998. Model output was compared with data from a willow survey conducted on an area of short willows protected from browsing since the fall of 1994 (Chapter 2). Model data were grouped into 3 height classes based on the values of plants height resulted in the model output, and the survey data were grouped accordingly (Fig. 4).

The total number of individuals in the simulated protected population at the end of the 5 year run was similar to that observed in the survey of protected willow plants (3,400 and 3,200 plant ha^{-1}, respectively). Plant height increases during the 5 year period resulted in a reduction in the frequency of smallest individuals (20-180 cm), and an increase in the frequency of the larger size class (180-320 cm) (Fig. 4) in agreement with data. Few individuals were classified in the tallest height class. Thus, changes in frequencies of different height classes were well represented in the model, as there was good agreement between observed and simulated data.

SIMULATION EXPERIMENTS.

Willow productivity under different water conditions and herbivory. The effect of different water table depths on aboveground net primary productivity (ANPP) of willows in the entire watershed was analyzed with the model by simulating years with different precipitation levels and imposing different values for water table depth. The 30-year precipitation average for Estes Park is approximately 370 mm for the period May through September (National Climate Center 1995 and 1996). The years simulated were 1991 and 1995, which had May-September precipitation totals of 281 and 475 mm, respectively in Estes Park. Precipitation data in the model were corrected for elevation and location so at the site the totals were 367 and 476 mm in 1991 and 1995 respectively. The generated water table map with the four water table types (Fig 1) was used to create different water table experiments. The monthly variation of the water table in each experiment was obtained by increasing or decreasing the depth of the water table types by a fixed factor (Table 3).

Changes in water table depth had large effects on willow productivity (Fig. 5). A slight reduction in willow ANPP was predicted under saturated soil conditions. These occurred under the combination of high precipitation (1995) and shallow water table level. Soil saturation caused anaerobic conditions, which reduced net N-mineralization rate (NNMR), producing a nitrogen limitation on plant productivity. Conversely, a deeper water table led to stressful conditions for willow growth. With a deep water table, an increase in precipitation could ameliorate growing conditions. Grass was much less dependent than willow on the water table and an increase in the depth of the water table did not decrease grass productivity.

The combined effects of stressful water conditions and changes in herbivory were analyzed with the model by estimating willow ANPP for the entire Moraine Park study area under different water table levels and elk densities (Fig. 6 a to c). Simulations were run for four years starting from 1990. During these years, precipitation was below the 30-year average (294, 281, 100, and 170 mm, for the period May through September of 1990,1991,1992, and 1993, respectively). In each simulated year the elk migration to the summer range was represented by reducing the simulated elk density to 50% of the winter maximum on May 1st, and then to 10% on June 1st. It was held at this level through the end of August. On September 1st the simulated density was returned to 50% and then to the winter maximum on October 1st. In this simulation elk herbivory did not affected willow productivity in 1990 since it started after the growing season of this year.

Reductions of willow ANPP due to elk herbivory occurred mainly under saturated and dry water conditions. Elk effects on willow productivity increased through time as plants under low or no elk herbivory increased in size and plants under high herbivory became suppressed. An elk density of 50 elk km^{-2} had little effect on willow ANPP with an intermediate reduction of water table (water table experiment equal to F (Fig. 6). Further decrease in the depth of the water table produced a large reduction in willow productivity under this elk density.

Herbaceous ANPP was not reduced by increased elk densities. Increase in elk densities up to 200 elk km^{-2} did not produce differences in the proportion of grass and willow in elk diets (Table 4). However, the percentage of willow ANPP consumed increased considerably (Table 4).

Effect of elk herbivory on nitrogen dynamics. Simulation experiments were performed to analyze the effect of elk on the dynamics of nitrogen and NNMR. These simulations were for a 10 year period (1990-1999), on a 50x50 m grid-cell, with either a short or a tall willow population, under different elk densities. The means of the last 5-years of the simulation were used to represent model outputs (Fig. 7). The model version used here only simulates active cycling N in the litter, plants and active soil organic matter pools. N in slow turnover pools is assumed to be at a steady state at this time scale.

Increasing elk density caused a slight reduction in the total amount of nitrogen in the system, as well as in the total amount of nitrogen in the plant compartment (Fig. 7a, b). Similarly, soil nitrogen content in long-term elk enclosures in Moraine Park were not different compared with similar areas open to herbivory (D. Binkley, pers. comm. 1999). Increase in elk herbivory greatly changed the proportions of nitrogen that were in willow and herbaceous components. This pattern was the result of a decrease in willow and an increase in herbaceous biomass as elk herbivory increased. Simulation results are consistent with 5-year experimental studies conducted in Moraine Park comparing nitrogen dynamics of grazed and ungrazed plots (Menezes 1999). In this experiment elk herbivory reduced willow leaf litterfall, but no differences between treatments in soil inorganic nitrogen availability and NNMR were found. The model predicted a small increase in NNMR in a period of 10 years. This was probably the result of a higher herbaceous proportion in the litterfall under herbivory, as well as elk urine and feces deposition. Similarly, N losses in willow litter where found to be lower than from *Carex* litter (Menezes 1999). Similar N dynamics were found in short and tall willow, but elk stimulation of NNMR was higher in the short willow.

Short to tall willow transition. It is expected that a short willow population will gradually change to a tall willow population under good growing conditions, without plant death due to disturbance effects, and without herbivory (Chapter 2). The model was used to estimate the period of time that is expected for this transition to occur. A short willow population with a 25% willow canopy cover and a density of 4,400 plant ha^{-1} was simulated for a 10-year period (1990-1999), with no elk herbivory. Model outputs were compared with data collected in tall and short willow populations protected from elk browsing for 5 years, with 65 and 45 % willow canopy covers, respectively (Chapter 2) (Fig. 8).

After 10 years, the height distribution of the simulated population differed from that of the original short willow as well as that of short willow after 5-years of protection. Plant canopy cover increased in the simulated population from 23% to 58% after 10-years. Simulated data had a lower proportion of individuals in the shortest height class (20-240 cm), and a higher proportion in the intermediate class (240-300 m) as was observed in the tall willow population. However, a smaller proportion of plants were found in the tallest height class (> 300 cm) compared to the tall willow population. This suggests that 10 years is not enough time for a short willow population to completely shift to tall willow population characteristics. However, it is probable that the model underestimated height increases of the tallest individuals in the population (Fig. 3c). The model estimated that during the transition from a short to a tall willow population, there will be more than 2-fold increases of shoot and root biomass, an approximately 30g m^{-2} increase of leaf and shoot biomass, and < 1 g m^{-2} increase in plant nitrogen (Fig. 9 a-c).

Plant height increase is reduced under elk herbivory, which should slow or prevent the transition from short to tall willow (Chapter 2). The model was used to estimate how different elk densities affect this transition. A short willow population growing in a representative 50x50-m grid-cell was simulated. Initial canopy cover was 23% and water table characteristic correspond to treatment B (Table 3). In this case several runs of four-year periods (1994-1997) were performed with different elk densities, and the effect of elk on willows was analyzed by considering changes in heights of individuals in size classes 1 and 2. Although the model represents elk browsing on willows of all size classes, willow of larger sizes were not included in the current analysis because short-term effects of elk on plants taller than 2.5 m (Table 2) are relatively unimportant.

The mean height of individuals in size class 1 was increased due to plant growth and decreased by establishment of new, smaller individuals. Under good growing conditions and no herbivory mean height increase of size class 1 tended to decrease sharply after a few years of growth (Fig. 10a). Elk hervibory caused a reduction of plant height growth in both size classes. A major reduction occurred with a density of 50 elk km^{-2} and complete height growth suppression occurred with densities of 75 elk km^{-2} (Fig. 10 a, b) at this willow cover (23%).

Willow productivity in past and current conditions. Willow ANPP with past (1946) and current (1998) conditions of willow cover were estimated with the model. The characteristics of willow cover were determined by combining information from digital maps generated from a 1946 aerial photo interpretation, and from a 1998 ground field survey (Chapter 3). In 1998, willow cover was 20% lower than in 1946 (Chapter 3). Although total cover could be determined from aerial photos, the size class distribution could not. Thus, I made the following assumptions to create the 1946 maps with willow size class distribution; a) areas with tall willow in 1998 were also tall willow type (Table 2) in 1946 with high density (3,750 plants/ha), b) the remnants of willow areas in 1946 maps were considered to be intermediate willow type (Table2) with moderate density (2,250 plants/ha). c) areas with willow in 1998 and no willow in 1946 were considered to be comprised of young willow type (Table 2) with low density (500 plants/ha). Overall willow cover in 1998 map was 20% lower than in 1946 (chapter 3).

Willow productivity was estimated for one growing season with no major restriction of plant water availability. In the simulation I used climatic conditions that corresponded to a wet year (1994), and the same water table maps (water table treatment equal B (Table 3)) for both scenarios. However hydrological conditions for willow growth were drier in 1998 due to a higher proportion of type 4 water table (Fig. 1), determined by a reduction in river meander density (chapter 3).

Mean current shoot production for the whole study area was 517 and 311 kg ha^{-1} for 1946 and 1998, respectively. The primary differences in shoot production between the old and current willow covers occurred in the central and southern part of the distribution (Fig. 11). A reduction of 50 % in total willow aboveground productivity (ANPP) was estimated in the 1998 willow cover compared to the 1946 willow cover (132 and 63 tons yr^{-1} on the whole study area).

DISCUSSION.

Ecological research is usually conducted over short temporal and small spatial scales with the aim of predicting processes at larger scales. However in contrast to other sciences, the issue of scale is a relatively new subject in ecology (Tilman and Kareiva 1997, Wiens 1989). So far, scaling ecological processes has been mostly based on empirical approaches, driven by the availability of new technological tools, and using few scaling laws. Simulation modeling has become recognized as being the most useful tool for accomplishing this translation of knowledge through different scales (Ehleringer and Field 1993). Ecological modeling can take into account landscape heterogeneity, which often determines different outcomes of species interactions

(DeAngelis and Waterhouse 1987, Hanski, 1991, Pacala and Levin 1997). However, predictions are largely dependant on the availability of high-resolution spatial data. This was an important limitation in this case, in particular the lack of information on the spatial dynamics of water table depth, since willow performance is largely dependent on hydrological conditions (Svejcar et al 1991, Patten 1998).

At the beginning of the growing season saturated soil conditions are normally expected on areas suitable for willow growth i.e. areas close to the main or temporary river courses (Zeigenfuss et al. 2000). Saturated soil creates stressful conditions for growth even though willow is considered tolerant of flooding (Kozlowski 1984). Reductions in willow and grass ANPP estimated by the model under saturated soils were determined by a decrease in mineralization rate and in nitrogen availability for plant growth. Other effects of flooding produced by the generation of low redox potentials were not included in the model (Kozlowski 1984). Under aerobic soil conditions a decrease in precipitation does not affect willows growing on sites with a shallow water table, but it will reduce productivity where the water table is deep (deeper than 1 m). As the season progresses, the water table drops, and willows become more dependent on precipitation. Thus, the best conditions for willow growth include a combination of high water table and lower precipitation at the beginning of the season, and an increase in precipitation in late season, to offset the seasonal drop in water table.

Water table dynamics are largely determined in this valley by beaver activities. Reduction in beaver populations that had occurred during the last 50 year period in the study area (Zeigenfuss et al. 2000) was associated with a reduction in river length and density of meanders (Chapter 3). This hydrologic modification could lead to deeper water table and drier conditions for willow growth. Even though beaver population dynamics were not explicitly simulated with the model, an estimation of the differences in willow growth with and without beaver could be obtained by comparison of plant responses to different water table levels.

Reductions in willow productivity under stressful conditions were increased by elk herbivory. It is interesting to note that there was an interaction between water and herbivory producing the greatest decrease in willow ANPP under stressful conditions and elk density of 50 elk km^{-2}. In contrast the effect of elk on willow productivity was small under good growing conditions, but increased as water stress increased. These results were consistent with experimental data, in which differences in plant productivity on willow growing under protected and browsed conditions in Moraine Park were found after only 5 years of protection (Zeigenfuss et al. 2000).

The model predicted that the number of plants in a willow population could increase or decrease under increasing elk density. The outcome will depend mainly on the original characteristics of the willow population i.e. canopy cover, and water availability. The model predicted that elk density could be the primary factor affecting the transition from short to tall willow morphotypes. Current elk density in RMNP appears to be high enough to suppress willow growth and prevent this transition (Chapter 2). In Moraine Park the estimated densities were generally between 50-90 elk per km^{-2} in 1995-1997, however densities >90 elk km $^{-2}$ could have been experienced in the core area (F Singer pers. comm. 1999). The model predicted that willow height suppression will occur with elk densities of 75 to 100 elk km^{-2}. Higher elk densities will have little additional effect on willow height because shoots at the top of the canopy, which determine plant height increase, are being completely consumed by elk at this density. However not all the shoots formed in the previous growing season would be removed. Elk normally remove only a portion of the stem axis, and some of the shoot growing inside the canopy could escape browsing. A significant portion of the axes of the browsed shoots die because of damage to the bark caused by browsing (unpublished results). This effect was considered in the model by the incorporation of a factor that reduces plant biomass in proportion to elk tissue removal. Not only will transitions from short to tall willow be suppressed by high elk density, but also, elk will over the long term reduce the height of a tall willow population. Changes in the structure of willow population could lead to other changes at the ecosystem level, such as solar radiation inputs, material fluxes, and species interactions (Naiman and Décampus 1997).

Large herbivores could stimulate or decrease the return of plant available nutrients to the soil by altering litterfall biomass and composition, and by returning nutrient to the soil through deposition of urine and feces (Hobbs 1996). The increase in elk could have altered long-term nitrogen dynamics in this valley by stimulating NNMR (Menezes 1999), but short-term effects (<10 years) of increasing elk densities on NNMR or plant nitrogen availability do not seem to be quantitatively important. The alteration of the nitrogen cycle that could have occurred in this valley during the last 50-years can not be fully understood unless other factors besides the elk increase are included in the analysis. Nitrogen dynamics in riparian ecosystems include additional fluxes to those normally considered in analyses of terrestrial ecosystems (Naiman and Melillo 1984, Naiman and Décampus 1997). Fluxes between the aquatic and terrestrial ecosystem, and between the riparian and upland ecosystem need to be considered to assess nitrogen dynamics in riparian ecosystems. Riparian vegetation plays a major role in regulating these fluxes (Gregory et al. 1991, Naiman and Décampus 1997). Modifications of the structural characteristics or plant species composition of the riparian ecosystem could greatly alter the role of the riparian vegetation in controlling these nutrient fluxes. Here, willow uptake of nitrogen from the water table could represent an important input of nitrogen to the system (Menezes 1999). However the contribution of riparian vegetation to nutrient retention may decline as trees mature, or under restricted accessibility to water (Naiman and Decampus 1997). Suppressed willow under elk browsing will be less able to reach the water table due to a reduction in root development, and consequently, willow will be less able to move nitrogen from the aquatic to the terrestrial system. In addition the decline in beaver populations could have produced important modifications to the long-term nitrogen budget (Naiman and Melillo 1984, Naiman et al 1988). It is highly probable that physical and biologic alterations that have occurred in this riparian ecosystem have caused significant biogeochemical changes, such as changes in the pattern of sediment trapping and deposition that could have occurred because of a reduction of channel complexity, a probable increase in the movement of nutrients to the stream because of the reduction of the functional role of ripairan vegetation, a probable increase in nitrogen cycling and in the movement of nitrogen from upland to lowland ecosystems driven by an increase in the elk population, etc.

The number of elk in RMNP has steadily increased since the late 1960s, which has produced concern about the appropriate balance between ungulate populations and vegetation and soil conditions (Berry et al. 1997). Different concepts and criteria have been developed to determine ungulate population sizes that could be supported by an ecosystem without leading to overgrazing (Coughenour and Singer 1991). The conversion of tall to short willow by elk could be considered an indication of overgrazing in a National Park if it is deemed to be an unnatural situation. Current elk density in Moraine Park does not seem to affect grass production or biomass, but willows are heavily used. This result is similar to the conditions described for Yellowstone, where similar interactions among willow, grass and elk occurs (Coughenour and Singer 1991 and 1996). The resultant high elk numbers could reduce willow productivity and height, in particular if combined with lower water tables. If willow productivity or height suppression is considered to be a primary criterion for elk carrying capacity i.e.

that natural conditions should support higher and taller willow cover, then the number of elk that could be supported in this watershed would probably have to be reduced to approximately half the number present in recent decades.

CONCLUSIONS

Loss of riparian habitats with high water tables and increases in elk densities have affected willow productivity in RMNP. Interactions between these factors have produced a larger than additive effect. High elk density (higher than 75-100 elk km^{-2}) concentrated on the riparian zone also reduces willow productivity under high water availability. However this effect will be evident only after 5-10 years of continuous browsing. The model predicts that elk densities greater than 75 elk km^{-2} will prevent a net annual height increase of short willow, but important reduction in the net annual height increase will occur at a density of around 50 elk km^{-2}. These elk denstiy values are within the range of densities observed in Moraine Park. The changes that have occurred in this valley during the last 50 years due to beaver decline, riparian habitats loss, elk herbivory, and possibly climatic change, have resulted in a large decrease (>50%) in willow productivity and hence changes in the structure and function in the riparian ecosystem.

Increased elk browsing on willow and the consequent reductions of willow biomass and productivity could have negatively affected beaver. The reasons for the reduction of the beaver population are not fully understood but elk could have indirectly contributed to the beaver decline. Whether or not this would be considered to be a natural situation is not addressed in this paper. The loss of beaver caused a reduction of water subsidized surface area and the replacement of riparian vegetation by meadows. Thus the loss of willow cover and productivity was due to a combination of reduction in riparian habitats and an increase in the elk population, but whether these changes are acceptable relative to the goals of a National Park, is beyond the scope of this paper.

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Table 1. Morphometric characteristics of plants in the initial size classes.

	Size class					
	1	**2**	**3**	**4**	**5**	**6**
Height (m)	0.50	1.2	2.4	2.9	3.4	3.8
Canopy bottom (m)	0	0	0	0.3	0.5	0.7
Canopy diameter (m)	0.70	1.4	2.0	2.4	2.6	2.8
Woody biomass (kg)	0.21	0.77	1.59	3.37	6.9	13.6
Fine wood (kg)	0.06	0.12	0.14	0.40	0.6	1.0
Leaf biomass (kg)	0.07	0.22	0.30	0.63	1.0	1.6
Root biomass (kg)	0.13	0.50	1.00	2.20	5.0	9.80
Fine root	0.09	0.19	0.35	0.74	1.20	1.90

Table 2. Proportion of individuals in each size class in different willow types used to initialize the model.

Willow types	**Size class**					
	1	**2**	**3**	**4**	**5**	**6**
Young	1	0	0	0	0	0
Short	0.86	0.12	0.009	0.004	0.002	0.002
Intermediate	0.54	0.26	0.09	0.06	0.03	0.01
Tall	0.21	0.41	0.18	0.12	0.06	0.02

Table 3. Monthly water table depth (cm) during the growing season of different water tables experiments. Experiment B corresponds to the water table type described in figure 1. Others water table experiments were created by increasing or decreasing by a fixed proportion the depth of the water table of experiment B.

Water table experiment	**Water table type**	**Multiplying factor**	**Month**				
			May	**June**	**July**	**August**	**September**
A	1 and 2	0.5	10	9	9.5	10	10
	3		15	10	15	20	21
	4		40	20	35	40	45
B	1 and 2	1	20	18	19	20	20
	3		30	19	30	40	41
	4		80	40	70	80	90
C	1 and 2	1.5	30	27	29	30	30
	3		45	29	45	60	62
	4		120	60	105	120	135
D	1 and 2	2	40	36	38	40	40
	3		60	38	60	80	82
	4		160	80	140	160	180
E	1 and 2	3	60	54	57	60	60
	3		90	57	90	120	123
	4		240	120	210	240	270
F	1 and 2	4	80	72	76	80	80
	3		120	76	120	160	164
	4		320	160	280	320	360
G	1 and 2	5	100	90	95	100	100
	3		150	95	150	200	205
	4		400	200	350	400	450
H	1 and 2	6	120	108	114	120	120
	3		180	114	180	240	246
	4		480	240	420	480	540
I	1 and 2	7	140	126	133	140	140
	3		210	133	210	280	287
	4		560	280	490	560	630

Table 4. Percentage of elk willow offtake of the total willow productivity, and percent of willow in elk diets under different elk densities. Willow and herbaceous ANPP were in all cases equal to 70 and 370 g m^{-2}, respectively.

Elk density (elk km^{-2})	% of elk offtake of total willow ANPP	% of willow in the diet
50	14	25
100	29	27
150	43	27
200	57	25

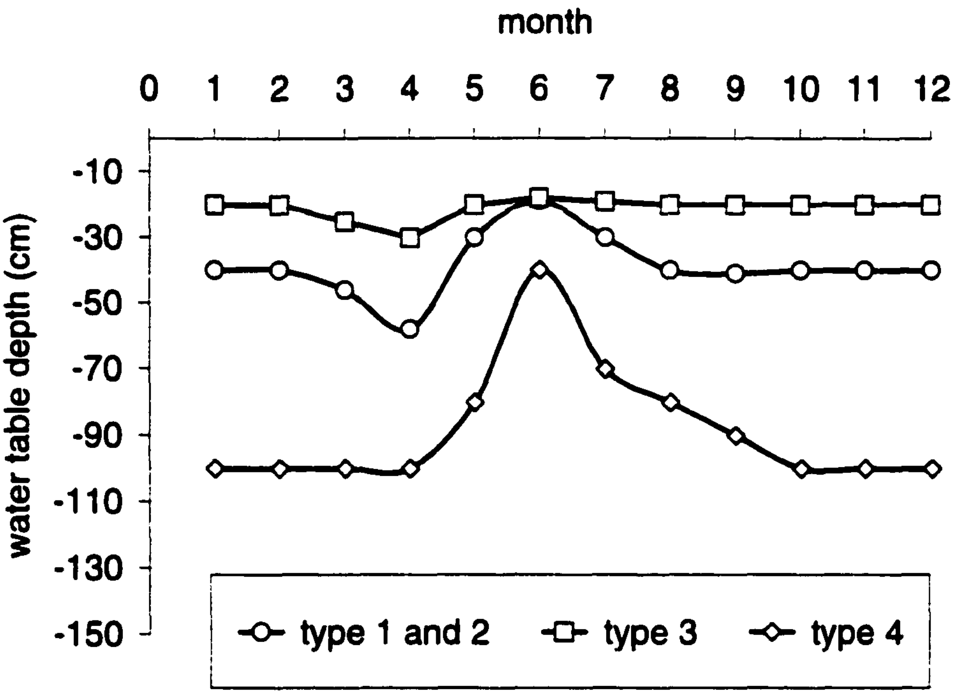

Figure 1. Monthly changes in water table depth for different types represented on the water table maps.

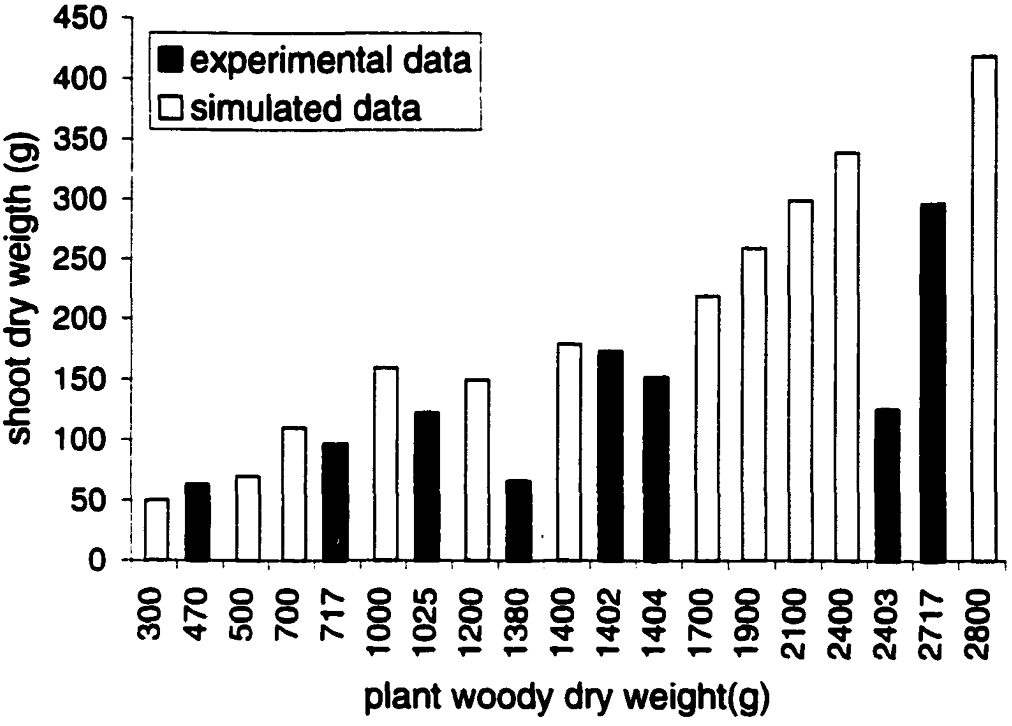

Figure 2. Experimental and simulated annual shoot production of willow plants of different sizes.

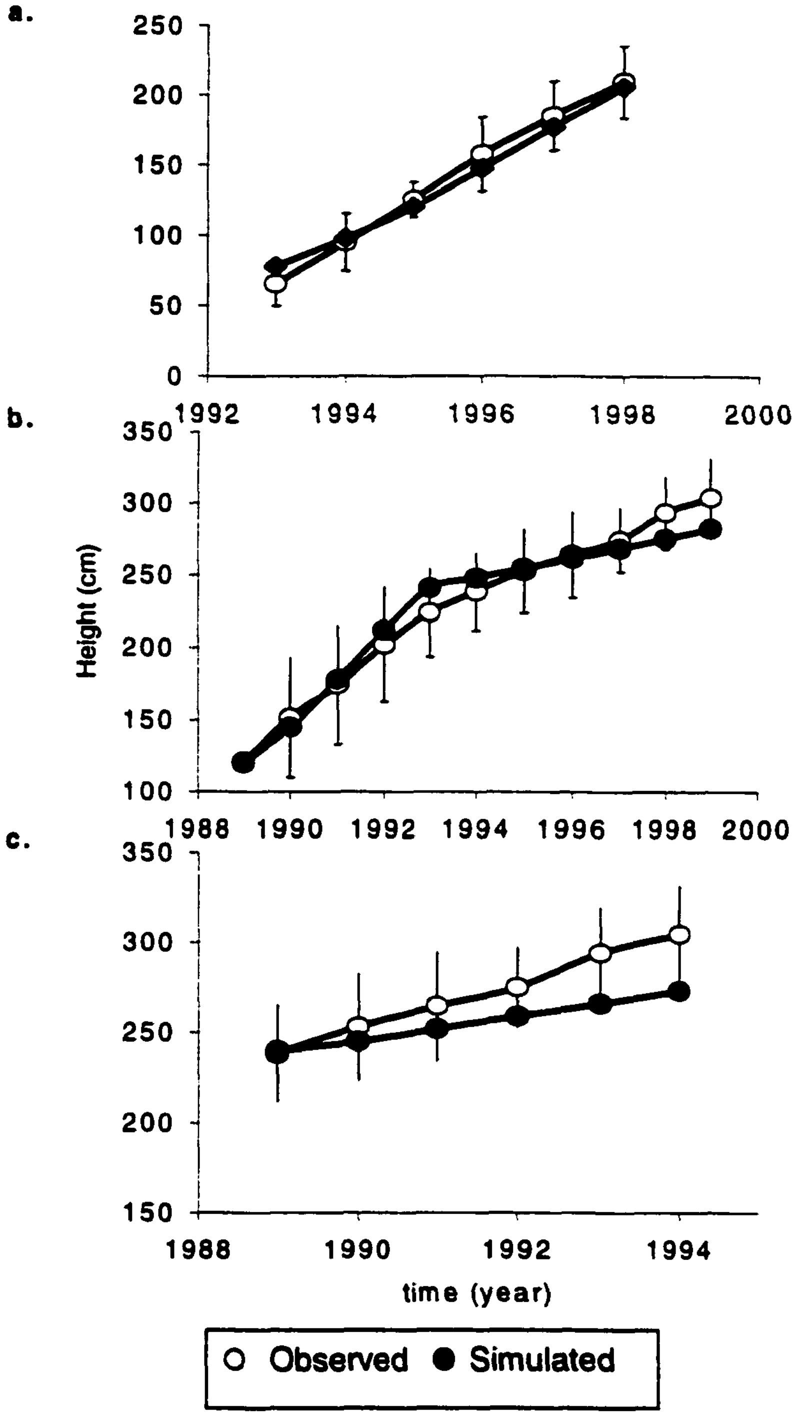

Figure 3. Observed and simulated height increase of individual plants. a). Height increase of short willows protected from elk herbivory since 1994, and simulated values of a combined size class1 and 2. Observed height increase of tall willow plants and simulated values of size class 2 (b) and 3 (c). Observed values correspond to a mean of 8 plants and vertical bars represent standard deviations.

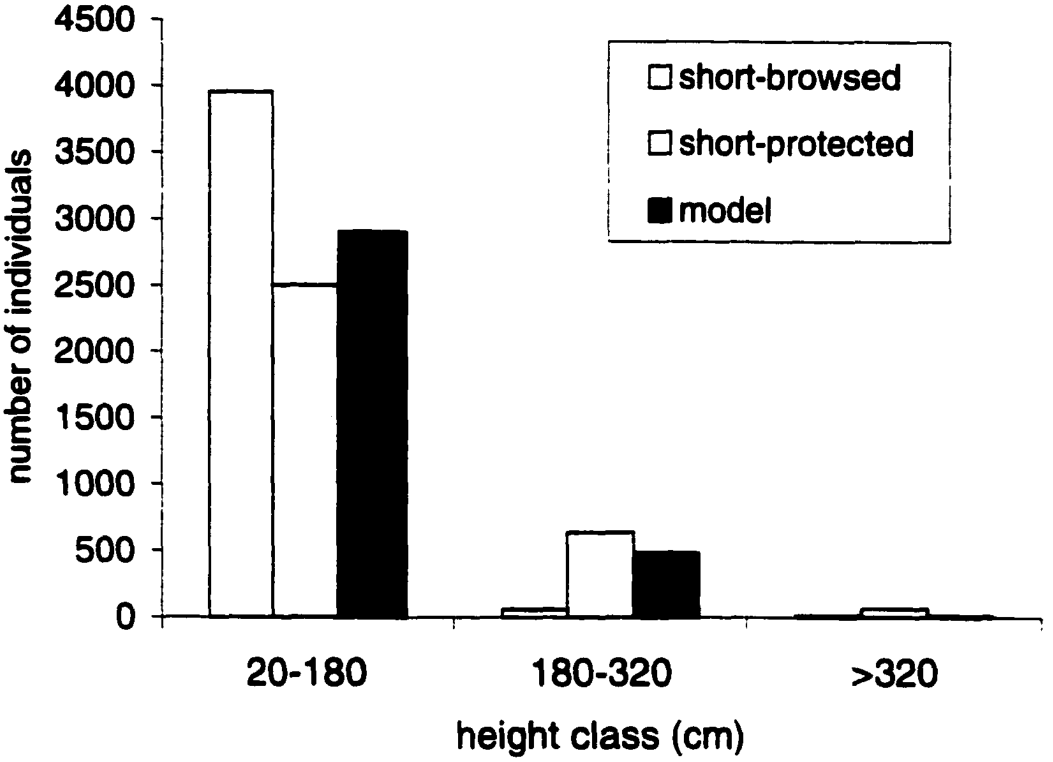

Figure 4. Observed and simulated distribution of individuals of different willow populations in three heights classes. Short-browsed.- short willow population that were used to initialize the model. Short-protected.- short willow population protected from elk browsing during a 5-year period. Model.- willow population estimated with the model (5 year run).

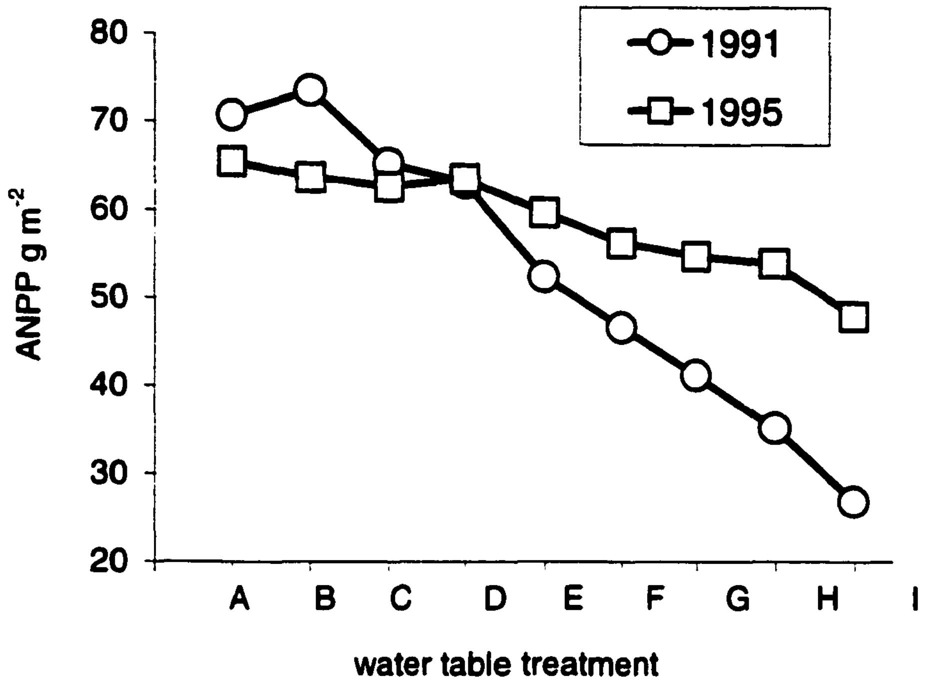

Figure 5. Simulated aboveground net primary productivity (ANPP) of willow over the entire study area in dry and wet years, 1991 and 1995, and under different water table conditions. Letters indicates different water table treatments from shallow to deep water table (Table 3).

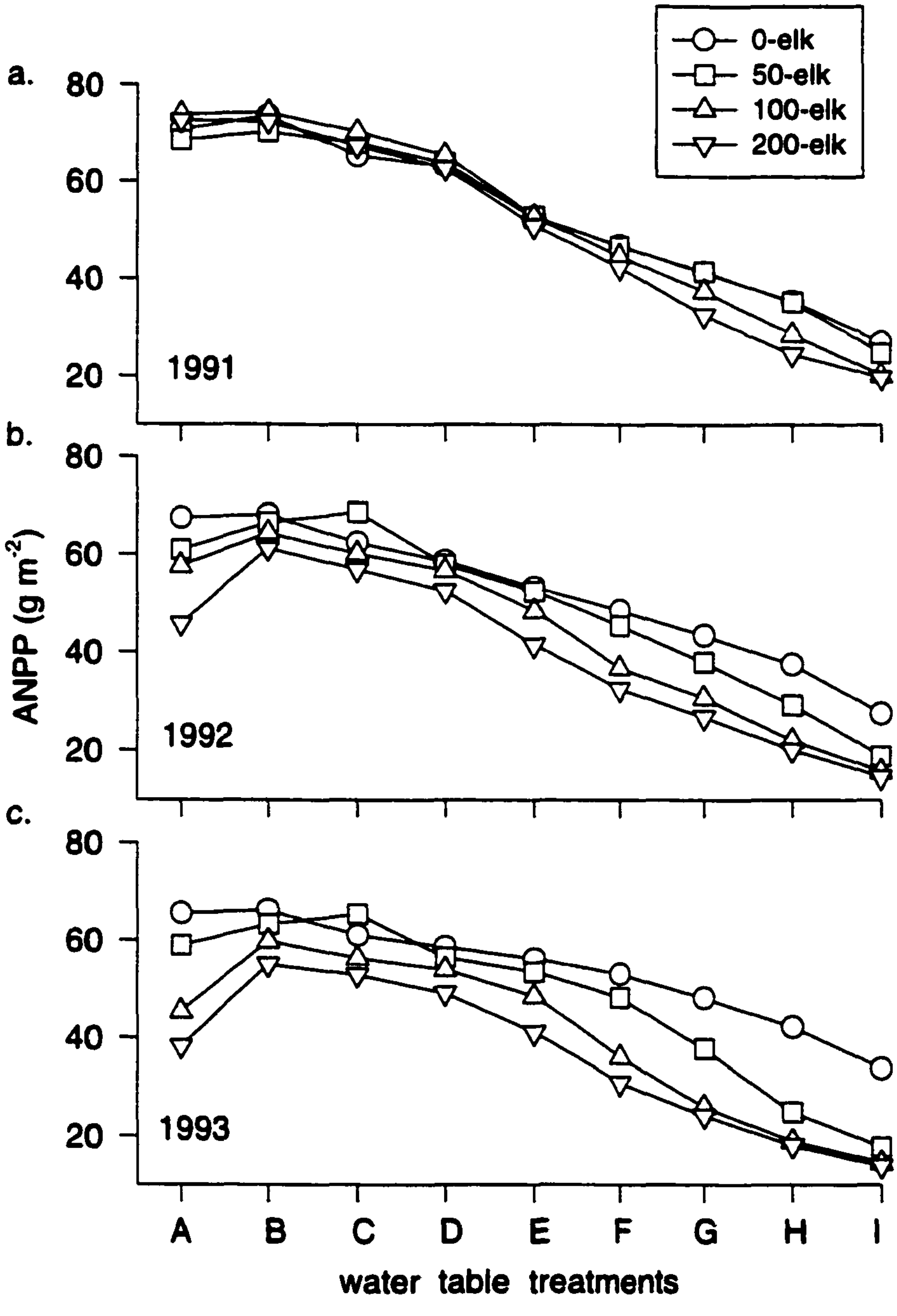

Figure 6. Simulated abovegroung net primary productivity (ANPP) of willow in the entire study area, under different water tables levels and elk densities (elk km^{-2}). Water tables treatments are detailed in Table 3. a. 1991, b. 1992, c. 1993.

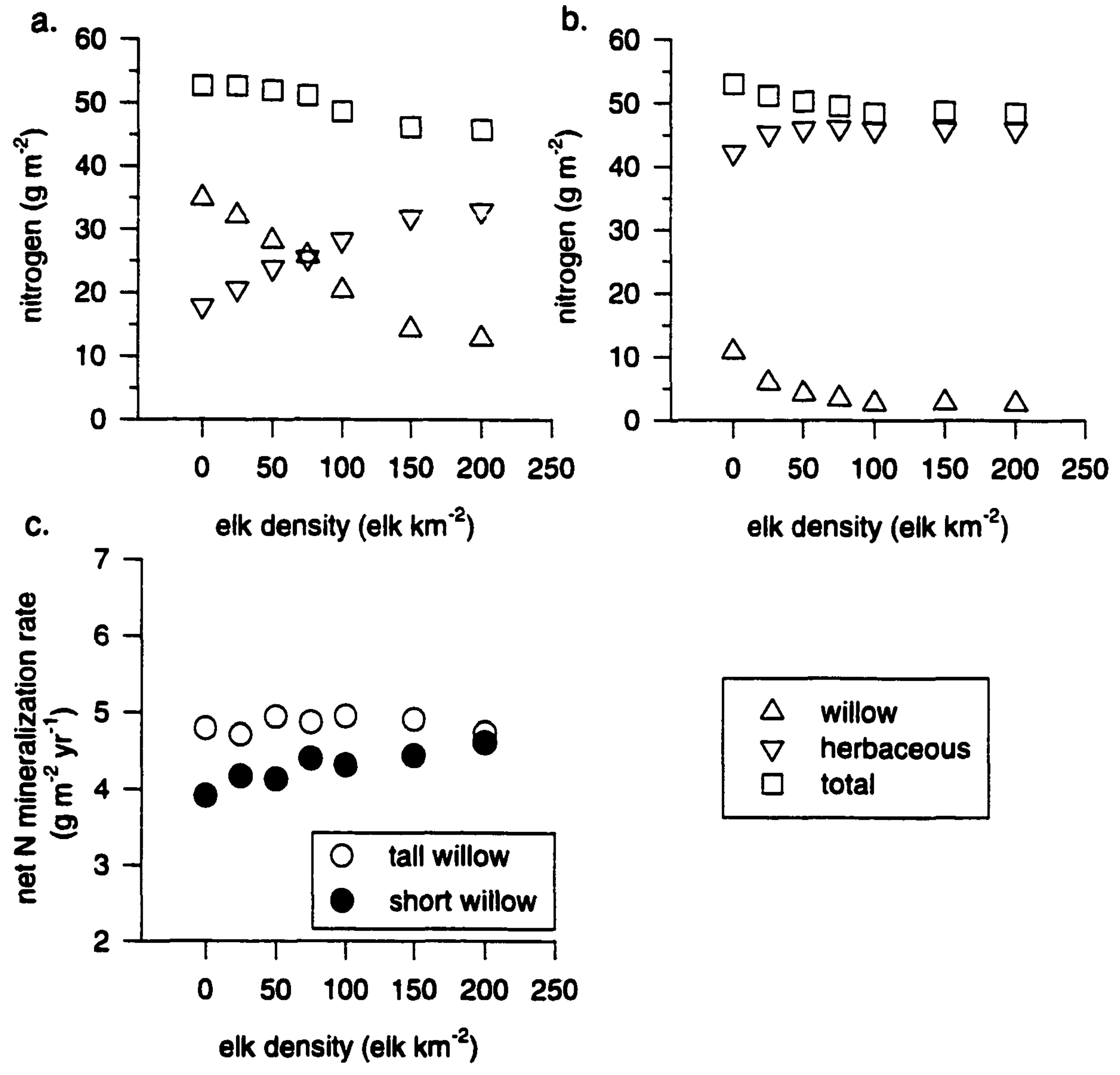

Figure 7. Simulated nitrogen under different elk densities. Values represent the mean of the last 5 years in a 10-year simulation of a grid-cell of a 50x50 m of a) tall willow b) short willow. c) Net nitrogen mineralization rates of tall and short willow.

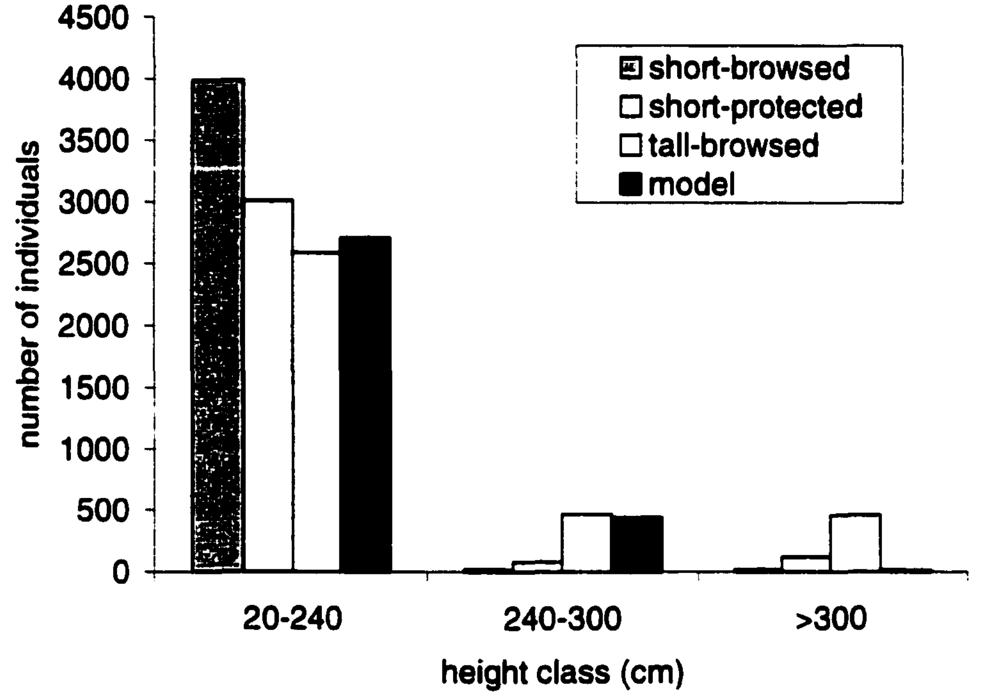

Figure 8. Observed and simulated distribution of individuals of different willow plants among three heights classes. Short-browsed.- short willow population that were used to initialize the model. Short-protected.- short willow population protected from elk browsing during a 5-year period. Tall.- tall willow population. Model.- simulated willow population after ten years simulation starting from a short willow population.

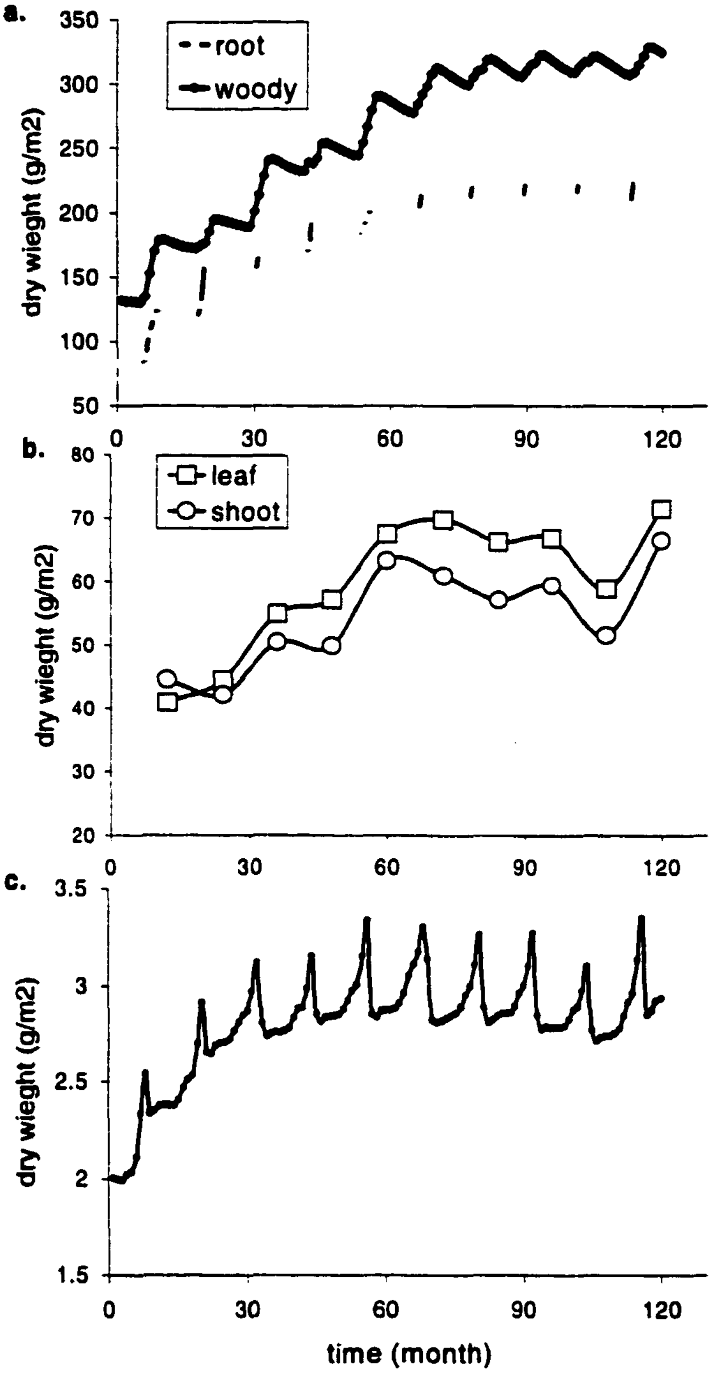

Figure 9. Predicted changes in the transition from short to tall willow population. a. Woody and root biomass. b. Shoot and leaf biomass. c. Mean nitrogen content in willow plants (above and below ground). Values represent the mean of a grid cell of a 50x50 m.

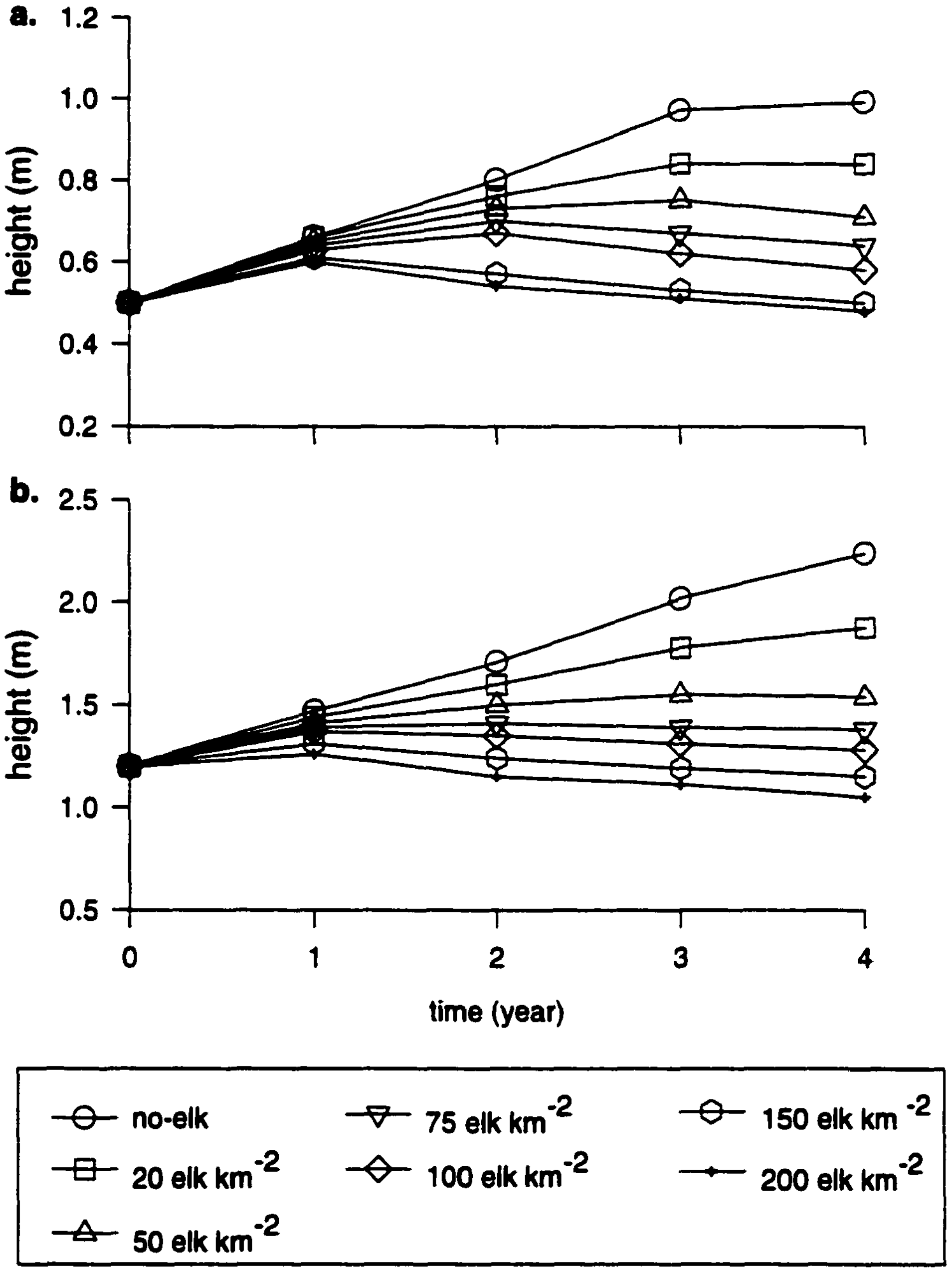

Figure 10. Simulated height of willow plants in size class 1 (a) and 2 (b) under different elk densities.

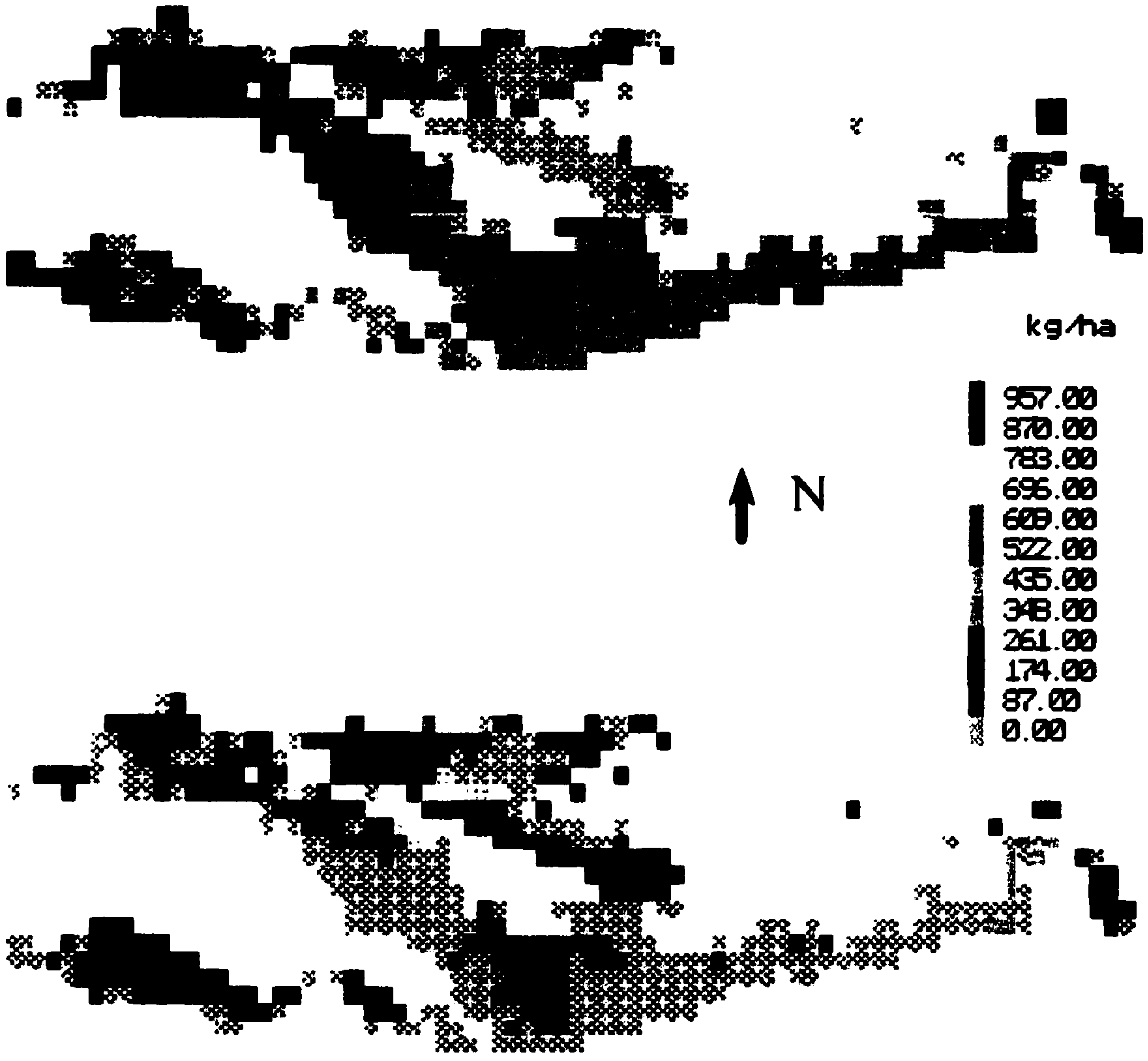

Figure 11. Spatial distribution of simulated willow shoot production in Moraine Park in 1946 (upper map) and 1998 (lower map).

CONCLUSION

The condition of the riparian willows in Moraine and Horseshoe Park valleys of the elk winter range of Rocky Mountain National Park, markedly degraded sometime during the last 50 years. Even though humans intensively used these valleys since the late 1800 willow communities were abundant in the late 1930's and 40's. From this time to the 1990's the spatial extent of willow areas was reduced approximately 20% and the functional contribution of willow to the riparian ecosystem has been reduced by a higher proportion. During this period the area covered by river channels was largely reduced, in particular in Moraine Park. This hydrologic change was mainly driven by a decrease in beaver, however human impacts on river channels could also have contributed. Since water table depth in the open floodplain of these valleys is dependent on the river, we infer that the area with a sufficiently high plant water availability to support riparian willow growth was also reduced. Results showed that areas where willow declined and areas dominated by short willow morphotypes were spatially correspond to areas where river branches disappeared. Considering the link between riparian willows and water table, we conclude that decrease in channel density and riparian habitat were the primary factors determining the reduction in the area of the landscape covered by willow. Drier climatic trends observed during this 50-year period could intensify drier conditions generated by lower water tables, but it is unprobable that lower precipitation could cause a willow decline in areas with high water tables. The increase in elk density and the consequent increase in browsing pressure on willows contribute to a willow decrease, but probably only in areas with low water tables. Thus, we infer that the willow decline was mainly determined by a reduction in the extent of the abiotic conditions for riparian vegetation growth, which in turn was liked to a decline in beaver.

The increase in elk densities was an important factor driving changes in the functional role of willow in the riparian ecosystem. Results indicated that willow could support high elk browsing pressure without reducing aboveground productivity as long as water tables are high. Even though aboveground productivity was maintained by reducing belowground carbon allocation, plant-level physiological performance was not affected. However in the long-term, the morphological characteristic of browsed willow will be modified. Constraints imposed by elk tissue removal on willow plant morphology will result in an increase in the area of the landscape dominated by short willow morphotypes. The functional role of the resulting short willow population in the riparian ecosystem will be less pervasive than that of a tall willow population.

These riparian ecosystem are largely depend on beaver, which created riparian habitats by increasing stream channel complexity and the area of land surface with a high water table. An increase in beaver would promote willow productivity as well as an increase in the extent of the riparian vegetation. These conditions would reduce the negative effects of elk browsing on willow.

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