MORPHOLOGICAL AND PHYSIOLOGICAL RESPONSES OF PLANELEAF WILLOW (*Salix planifolia* Pursh.) TO SIMULATED BROWSING

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ABSTRACT
Morphological and physiological responses of planeleaf willow *(Salix planefolia* Pursh.) to simulated browsing were studied under controlled conditions. The treatments consisted of every combination of three clipping intensities (30%, 60% and 90% of current twigs length removal) and three clipping timings (late winter, early spring and mid-summer). Increased clipping intensity stimulated bud activation; increased total leaf area and leaf size and increased the length of current year's twigs. Mid-summer browsing increased the total number of leaves, the number of current twigs and decreased the length of current twigs. Higher browsing intensity resulted in higher photosynthetic rate of recently matured leaves.

KEYWORDS
willow *(Salix*), intensity and timing of browsing, morphological response, photosynthesis

INTRODUCTION

Willows (*Salix sp.*) are important as food and shelter for terrestrial herbivores and aquatic organisms. Willow root systems stabilize streambanks (Kindschy, 1989) and are frequently used for evaluating riparian zone and wetland health (Atchley and Marlow, 1989). Schulz and Leininger (1990) found that improper livestock grazing results in degradation of willow communities. However, the mechanisms involved with willow response to browsing remain unclear. Therefore, a better understanding of these mechanisms is needed for future livestock, wildlife, riparian zone and watershed management.

The mechanisms of plant response to herbivory include physiological and morphological (Prins et al., 1992). Responses vary with species genetic capacity, growth form, type of herbivory, grazing intensity, frequency and time of grazing and abiotic conditions (Crawely, 1983). The purpose of this study was to investigate how physiological and morphological characteristics change in response to different clippings of planeleaf willow. The objectives of our study were to determine if different intensities and timings of clipping of willow twigs altered bud activation and /or formation, the number and surface area of leaves, the number and length of twigs and photosynthetic rates.

METHODS

Stem cuttings were collected from a mountain meadow at 2,675 m in elevation dominated by bog birch (*Betula glandulosa* Michx.) and planeleaf willow in the Bighorn National Forest of northern Wyoming. Cuttings were taken on 19 June 1995 before leaf and shoot buds broke dormancy. The stems with basal diameter ranging from 13-20 mm were cut to 45 cm lengths. The cuttings were rooted in containers filled with perlite on a misting bench. After the stems had developed several 3-4 cm long roots and emerging leaves the plants were transferred to 4-liter pots filled with pure sand. The cuttings were regularly watered and fertilized to maintain health and vigor. During the winter they were stored in a non-heated building in North Dakota.

A completely randomized design was used in this experiment. Clipping treatments (9) consisted of every combination of three intensities (light, moderate and heavy browsing of current year's twigs) and three timings (pre-bud break, immediately after bud break and two months after bud break) simulating late winter, early spring and mid-summer browsing, respectively. One group was not treated and served as a control.

Morphological responses: Five plants were randomly assigned to each treatment group and grown in a greenhouse (temperature was about 25^{o}C/17^{o}C, day/night, and the photoperiod was 15-h). The timing of clipping treatments were conducted on 5 April, 15 April and 15 June. The morphological characteristics (i.e. number, location and status of buds, number and area of leaves, number and length of twigs) of each plant were measured before and after treatment and at 15 d intervals until 30 August. To determine leaf area non-destructively, an extra group of 10 plants were used to randomly collect leaves to determine the regression relationship between leaf area (with Li-3100 Area Meter, Lincoln, NE) and leaf length. Regression equations were then used to estimate leaf area of observed plants based on leaf length.

Photosynthetic rate: Five plants were randomly assigned to each treatment group and moved into the greenhouse on 30 April. Treatments were imposed on 30 April, 3 May and 2 July. Gas-exchange measurements were determined for recently matured leaves (the fifth leaf from the apex) with a Li-Cor (Lincoln, NE) 6200 instrument one month after treatment. Oven dry weight of leaves was measured after drying 72 h at 60^{o}C. Data were analyzed using a two-way PROC GLM procedure ($P<0.05$). Duncan's multiple-range test was applied to determine significant differences between means (SAS, 1990).

RESULTS AND DISCUSSION

Bud size varied by locations on twigs (upper 1/3, middle 1/3 and lower 1/3). The buds on the upper 1/3 of the twig were larger than on the lower 1/3 of the twig. Bud density (the number of buds/cm) did not vary with location on the twigs. The percentage of buds breaking dormancy 15 d after treatments increased as browsing intensity increase. This is consistent with responses of grasses to herbivory (McNaughton, 1979: Coughenour et al., 1984). Late winter and early spring browsing stimulated activation of dormant buds of the previous year's twigs and mid-summer browsing stimulated axillary buds of current year twigs. These responses support the view that the number, type and activity of meristems remaining on defoliated plants affect the pattern of growth following defoliation (Briske, 1986).

As clipping intensities increased, total leaf area (Table 1) and average leaf size (data not shown) increased. Timing of clipping did not significantly influence total leaf area, but mid-summer treatments increased leaf numbers. Our results clearly demonstrate that plants either increase individual leaf size or increase the number of leaves to provide maximum photosynthetic area for compensatory growth following browsing. The results indicate that intensity and timing as well as the interactive effect of these factors significantly affect the number and length of twigs. The length of current twigs increased with clipping intensity and decreased during mid-summer browsing. Heavy late winter and early spring clipping treatments had the longest twigs, heavy mid-summer treatments had the shortest twigs. In contrast, the former treatments yielded the fewest twigs and the latter treatments provided the most twigs.

Increased browsing intensity enhanced photosynthetic rates on recently matured leaves (Table 2). There was a significantly higher photosynthetic rate of heavy browsing compared to control plants. The increase in photosynthetic rate was related to an increase in specific leaf area. This study demonstrated that both morphological and physiological mechanisms govern responses of planeleaf willow to simulated browsing.

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Table 1
Effects of browsing on the area and number of leaves, the number and length of current twigs.

Treat	Area of leaf (cm^2/plant)	Number of leaf (per plant)	Number of current twig (per plant)	Length of current twig (per plant)
Intensity				
30%	2380.8^{b}	324.43^{b}	10.71^{c}	27.70^{bc}
60%	2954.0^{a}	486.40^{ab}	15.80^{ab}	30.70^{ab}
90%	3075.6^{a}	459.22^{ab}	14.25^{bc}	37.08^{a}
Check	2139.3^{b}	551.11^{a}	20.00^{a}	22.21^{c}
Timing				
Mid-summer	2915.5^{a}	574.27^{a}	21.55^{a}	13.39^{b}
Early spring	2595.2^{a}	397.17^{b}	13.18^{b}	37.72^{a}
Late winter	2498.8^{a}	428.75^{ab}	12.08^{b}	34.83^{a}

Means in a column followed by the same superscript are not significantly different (P>0.05)

Table 2
Effects of browsing on photosynthetic rate and specific leaf area of recently matured leaf (5th leaf).

	Photosynthetic rate(μmol $m^{-2}s^{-1}$)	Specific leaf area (cm^2 g^{-1} ODW)
Intensity		
30%	11.4763^{ab}	210.599^{b}
60%	11.8934^{ab}	250.739^{a}
90%	12.7975^{a}	266.823^{a}
Check	10.4402^{b}	220.072^{b}
Timing		
Mid-summer	12.0372^{a}	188.709^{c}
Early spring	11.4372^{a}	286.289^{a}
Late winter	11.3498^{a}	249.544^{b}

Mean in a column followed by same superscript are not significantly different(P>0.05)