The Basis of Browsing Tolerance in Shrubs of the Intermountain West: Growth Rates and Meristematic Potential

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THE BASIS OF BROWSING TOLERANCE IN SHRUBS OF THE INTERMOUNTAIN WEST: GROWTH RATES AND MERISTEMATIC POTENTIAL

by

Jackson L. Wandera

A dissertation submitted in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Range Ecology

UTAH STATE UNIVERSITY
Logan, Utah
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Relative growth rates (RGRs) and meristematic potential of big sagebrush (Artemisia tridentata, in some experiments ssp. tridentata Nutt. and in other experiments ssp. vesevana [Rydb] Beetle), bitterbrush (Purshia tridentata [Pursh] DC), serviceberry (Amelanchier alnifolia Nutt.), birchleaf mountain mahogany (Cercocarpus montanus Raf.), curlleaf mountain mahogany (C. ledifolius Nutt.) and big tooth maple (Acer grandidentatum Nutt.) were quantified under both glasshouse and field conditions. The relationships between the RGRs, meristematic potential and regrowth capacity of the shrub species were then determined. Sagebrush exhibited a significantly higher RGR than the other species at both high and low nutrient levels under glasshouse conditions. Four of the other shrub species had similar RGRs. The shrub species also exhibited different patterns of biomass and nutrient allocation. Sagebrush allocated most of its resources to leaf production, and in contrast, the other species tended to allocate similar amounts of resources to both leaf and root
production. In the glasshouse experiment, neither RGRs nor patterns of biomass and nutrient allocation were related to growth form. Under field conditions, curlleaf and birchleaf mountain mahogany exhibited similar RGRs, while both serviceberry and maple had similar but significantly lower growth rates. Except for sagebrush, which died following simulated browsing, four other shrub species exactly compensated for lost tissues. The mean RGRs of those shrub species were correlated significantly with compensatory growth capacity. Loss of 90% of buds on previous year's growth did not cause a meristematic constraint to regrowth production. Instead, it stimulated regrowth production. The shrub species we evaluated also exhibited differences in meristematic potential. Curlleaf and birchleaf mountain mahogany had a greater number of buds and long shoots per plant but a lower percentage of long shoots at the basal position on twigs. In contrast, serviceberry and maple had fewer buds and long shoots per plant but a higher percentage of long shoots at the basal position on twigs. The meristematic potential of the shrub species correlated with regrowth capacity.
CHAPTER 1

INTRODUCTION

In the Intermountain Region of western North America, many species of shrubs are found in the basins and foothills where both wild and domestic ungulates winter. The most abundant species include basin big sagebrush (Artemisia tridentata ssp. tridentata Nutt.), mountain big sagebrush (A. tridentata ssp. vaseyana [Rydb.] Beetle), bitterbrush (Purshia tridentata [Pursh.] DC), serviceberry (Amelanchier alnifolia Nutt.), birchleaf mountain mahogany (Cercocarpus montanus Raf.), curileaf mountain mahogany (C. ledifolius Nutt.) and big tooth maple (Acer grandidentatum Nutt.). Some of these species are an essential source of highly nutritious browse for both wild and domestic ungulates and may provide a viable alternative to feeding costly hay to livestock during winter (Welch 1983a, Otsyina et al. 1984, Gade and Provenza 1986).

When browsed, the shrubs lose 1) stored carbon and nutrients in the plant parts removed; 2) carbon gain capacity because of loss of photosynthetic surface which secondarily affects nutrient uptake; and 3) a certain degree of the potential to regrow because of loss of meristems. However, the amount and kind of loss may vary with the season of browsing and the shrub growth form. Evergreen shrubs contain high levels of nutrients in their leaves during all seasons of the year, while deciduous shrubs retranslocate nutrients from leaves to roots and/or stems before winter, leaving less nutritious stems for grazing during winter (Chapin 1980a). Evergreen shrubs therefore lose more nutrients and plant tissues than deciduous shrubs when browsed in winter.
In ecosystems where heavy browsing is prevalent, such as on the rangelands of the Intermountain Region, the survival, growth and reproduction of shrubs is influenced by their ability to either tolerate or avoid the damage associated with browsing. Mechanisms of herbivory avoidance have been the focus of intensive research (Bryant et al. 1983, Rhoades and Cates 1976). The avoidance mechanisms include chemical, morphological or phenological characteristics that deter feeding by herbivores or reduce the probability of herbivores utilizing the plant. By contrast, mechanisms which allow shrubs to tolerate browsing have been studied less and are not well understood.

Inherent growth capacity may be the major determinant of a plant’s capacity to tolerate herbivory (Chapin 1980a, Bryant et al. 1983, Coley et al. 1985). Coley et al. (1985) have suggested a growth rate hypothesis that predicts that plants adapted to growing in high resource habitats have evolved high inherent growth rates and less chemical defense. The high inherent growth rate provides the potential to rapidly replace photosynthetic foliage, which minimizes the effects of herbivory. Plants with high inherent growth rates are, therefore, expected to tolerate herbivory. On the other hand, plants with low inherent growth rates have limited capacity to refoliate and are less able to tolerate herbivory.

This relationship between relative growth rates (RGRs) and herbivory tolerance has not been evaluated for semiaridland shrubs. This is partly because basic data on RGRs and tolerance capacities of the shrubs are lacking. Several clipping studies have been conducted on some shrubs growing in semiarid environments, but they did not estimate the shrub’s inherent growth rates or indicators of browsing tolerance such as compensatory growth (Garrison 1953, Shepherd 1971). Field observations of shrubs growing...
on the semiarid rangelands of the Intermountain Region in western North America suggest that inherent growth properties may not be related to herbivory tolerance or growth form. Probably, high inherent growth rates would correlate with browsing tolerance only if they also correlated with a suite of other characteristics such as abundance and activation of meristems. The absence or inability to activate meristems may limit the ability of shrubs to rapidly refoliate and tolerate herbivory, irrespective of their inherent growth rates (Caldwell 1984).

The present study was designed to quantify the relative growth rates (RGR) and meristematic potential of six semiaridland shrub species and to determine whether the RGRs and meristematic potential are related to compensatory growth capacity (an indicator of browsing tolerance). The specific objectives of the study were:

1) To quantify the relationship of biomass and nutrient allocation patterns to RGR of seedlings of five shrubs that differ in growth form.
2) To determine the relationship between RGR and compensatory growth capacity (tolerance) of the six shrubs following simulated browsing in winter and spring.
3) To quantify the meristematic potential of four shrubs for bud abundance, ability to initiate long shoot growth from remaining buds and the location of buds on twigs that grow into long shoots.
4) To determine the influence of loss of buds on regrowth capacity of four shrub species.

The study included both glasshouse and field experiments. The glasshouse experiment was conducted at Utah State University, Logan, Utah, while the field experiments were located at the Green Canyon Ecology Center.
about 4 km north of Utah State University, near Logan. The details of the experimental sites are presented in Chapters II - IV.

The woody species used in the study included: big sagebrush (*Artemisia tridentata* ssp. *tridentata* Nutt. and ssp. *vaseyana* [Rydb] Beetle), bitterbrush (*Purshia tridentata* [Pursh.] DC), serviceberry (*Amelanchier alnifolia* Nutt.), birchleaf mountain mahogany (*Cercocarpus montanus* Raf.), curlleaf mountain mahogany (*C. ledifolius* Nutt.) and big tooth maple (*Acer grandidentatum* Nutt.), henceforth referred to as sagebrush, bitterbrush, serviceberry, birchleaf, curlleaf and maple, respectively. The sagebrush (*Asteraceae*) is perhaps the most dominant shrub species in the Intermountain Region of western North America (Welch 1983a). Bitterbrush, serviceberry, birchleaf and curlleaf (*Rosaceae*) are also abundant in the basins and foothills of the Intermountain Region and are more preferred for browsing by both wild and domestic ungulates than big sagebrush (Smith and Hubbard 1954). Big tooth maple (*Aceraceae*) is the most common maple in canyons of the Intermountain Region and is rarely browsed by ungulates, except when browse choices are limited. The six shrubs were chosen because they are among the most abundant and important browse species in the Intermountain Region.

The second chapter of this dissertation reports RGRs and resource allocation patterns of seedlings of five of these semiaridland shrubs. In chapter III, the relative growth rates and compensatory growth capacity of six semiaridland shrubs following simulated browsing in winter and spring are discussed. Chapter IV focuses on the relationship between meristematic potential and regrowth capacity of four semiaridland shrubs. The summary and conclusions from the research project are presented in Chapter V.
CHAPTER II
RELATIVE GROWTH RATES AND RESOURCE ALLOCATION PATTERNS AMONG SEEDLINGS OF FIVE SEMIARIDLAND SHRUBS

Summary. Among woody plants, patterns of biomass and nutrient allocation and growth rates are often related to growth forms. Because few studies supporting this generalization have been conducted with semiaridland shrubs, I quantified the relationships between patterns of biomass and nutrient allocation and relative growth rates (RGR) of seedlings of five semiaridland shrubs that grow in association but differ in growth form. The seedlings were grown at high and low nutrient levels under glasshouse conditions. All five shrub species had higher RGRs when grown at the high than the low nutrient level, however, only basin big sagebrush (Artemisia tridentata ssp. tridentata Nutt) exhibited a statistically significant increase in RGR. The RGRs positively correlated with biomass and nutrient allocation to leaves regardless of growth form. Sagebrush, which allocated significantly more biomass and nutrients to leaves, had the highest RGR. The other shrubs, including both deciduous and evergreen species, had a lower RGR and allocated less biomass and nutrients to leaves than sagebrush. The RGRs and patterns of biomass and nutrient allocation of the five semiaridland shrubs I evaluated were not related to growth form, suggesting that these species have different constraints to growth and nutrient storage than woody plants in other ecosystems.
Introduction

Growth rate is a useful indicator of a plant's growth potential and correlates with many plant characteristics of ecological significance (Chapin 1980a, Coley et al. 1985, Grime 1977). The growth rate of a plant is determined primarily by resource allocation patterns within a plant (Chapin et al. 1987, Chapin et al. 1989, Dijkstra and Lambers 1989). Among woody plants, patterns of biomass and nutrient allocation and growth rates are thought to be related to deciduous and evergreen growth forms (Archer and Tieszen 1980, Chapin et al. 1980, Chapin 1980b, Johnson and Tieszen 1976). Deciduous growth forms are expected to have high rates of nutrient absorption and to allocate more of their carbon and nutrients to tissue growth than to defense against herbivory. Conversely, evergreen growth forms are expected to have low rates of nutrient absorption and to allocate a large proportion of their resources to tissue defense. The defense compounds that are found in high concentrations in tissues of most evergreen species are costly to produce and store (Swain 1979). At least partly as a consequence of this, species with an evergreen growth form have slower growth rates than those with a deciduous growth form. Although evidence to support the above propositions is available from several ecosystems, few studies have examined these relationships on sympatric semiaridland species (Archer and Tieszen 1980, Chabot and Hicks 1982, Chapin et al. 1980, Chapin 1980b, Johnson and Tieszen 1976, Mooney and Gulmon 1982).

Basin big sagebrush [Artemisia tridentata Nutt. ssp. tridentata] is a late successional species that is dominant in the semiarid basins and foothills of western North America (Humphrey 1984, West 1979). Its leaf habits are both deciduous and evergreen. During a growing season, basin big sagebrush
produces two kinds of leaves: large leaves that are shed after approximately three months and relatively small leaves that are maintained throughout the year (Depuit and Caldwell 1975). Basin big sagebrush has a well developed chemical defense against herbivory, as is expected in a late successional species (Kelsey 1986). However, it successfully colonizes disturbed areas (West 1979), and field observations suggest that it grows faster than associated deciduous shrub species (Richards et al. unpublished data, Bilbrough, 1990).

The observed growth characteristics suggest that among semiaridland shrubs, patterns of biomass and nutrient allocation and growth rates may not be related to growth form. To test this hypothesis, I quantified patterns of biomass and nutrient allocation and relative growth rates (RGRs) of seedlings of sagebrush and four other sympatric shrub species. I then determined 1) whether the RGRs and patterns of biomass and nutrient allocation of the semiaridland shrubs were related to growth form, and 2) which patterns of biomass and nutrient allocation correlated with RGR and, therefore, might explain the differences in RGR. I also examined plasticity in RGR because in semiarid environments, where temporal variation in resource availability (water and nutrients) is particularly high, the ability to change RGR to take advantage of unpredictable, favorable environmental conditions may be an important factor determining competitive success and dominance (Jackson and Caldwell 1988).

The shrub species selected for this study, besides sagebrush, were bitterbrush (Purshia tridentata [Pursh] DC), serviceberry (Amelanchier alnifolia Nutt.), birchleaf mountain mahogany (Cercocarpus montanus Raf.) and curlleaf mountain mahogany (C. ledifolius Nutt.), henceforth referred to as bitterbrush, serviceberry, birchleaf and curlleaf. Bitterbrush is a highly branched shrub
varying in stature from low prostrate forms to erect forms as tall as 4 m. Its leaf habit is intermediate between evergreen and deciduous. It is often a pioneering species, and because of its ability to grow on depleted and severe sites, it is used for stabilizing disturbed areas. Serviceberry is an erect deciduous shrub 1 to 4.5 m tall. It is more productive on sloping, moist habitats. Birchleaf is also an erect deciduous shrub rarely more than 4 m tall. Curlleaf is an evergreen shrub that sometimes grows into a small tree. Both birchleaf and curlleaf are difficult to establish because seedlings are vulnerable to herbaceous competition (Horton 1989). The four shrub species are highly preferred over sagebrush by ungulates (Smith and Hubbard 1954). On a continuum, the ranking of the five shrub species from the true evergreen to the true deciduous growth form is curlleaf, sagebrush, bitterbrush and birchleaf or serviceberry. The five species were chosen because they are widely distributed and they commonly grow in close association, often in mixed species stands, in semiarid montane and basin habitats in western North America.

**Materials and methods**

Plants of all five species were grown from seed in a glasshouse at Utah State University, Logan, Utah, USA, from July to December 1989. The experimental design was a 2 X 3 X 5 split-plot using a randomized, complete block design with 10 blocks. Two nutrient levels were assigned to the main plots. Three harvesting times and the five shrub species were randomly assigned to the subplots. Seeds used in the experiment were purchased from NPI Inc. (Salt Lake City, Utah) and had been collected from native populations in semiarid areas of Utah and Nevada, USA.

The seeds, except sagebrush, were moist stratified at 1°C for 8 weeks.
before sowing in 0.58 L plastic Conetainers (Ray Leach Conetainer Nursery, Canby, Oregon) filled with fritted clay (Van Bavel et al. 1978). Three days following seedling emergence, the plants were thinned to one plant per Conetainer, and the nutrient treatment was started. Data concerning nutrient concentrations and biomass for current annual growth of sagebrush (Nagy 1979) were used to determine the high and low nutrient levels. These rates were similar to those suggested by Ingestad (1970) for birch seedlings. The amount of nutrients added was increased through time as the seedlings grow larger. Thus, the two nutrient levels were twice weekly applications of 2 ml (low nutrient level) and 50 ml (high nutrient level) per plant of a diluted and modified Hoagland's solution (Hoagland and Arnon 1950; modified by addition of FeEDTA and micronutrients). The modified Hoagland's solution was diluted to 1/4, 1/3, 1/2, and 3/4 strength before applying to the seedlings at the ages of 1, 2, 3, and 4 to 5 months, respectively. In addition to nutrient application, plants were watered with a small volume of tap water every two days to maintain high soil moisture but avoid leaching of nutrients. The plants were grown in the glasshouse for 21 weeks during which time the maximum and minimum temperatures were 38 and 15°C, respectively. A day length of 13 to 15 h was maintained throughout the experiment by supplemental light from fluorescent lamps. The plants were harvested after 7, 14 and 21 weeks. At each harvest, 5 seedlings were harvested as sub-samples within each block for each treatment.

The measurements taken at each harvest included root, shoot and total plant biomass and leaf area. At each harvest, leaf area was measured using a Licor LI-3100 area meter. Weights of the roots, leaves and stems were obtained after drying at 80°C for 72 h. The roots, stems and leaves from the final harvest
(21 weeks) were ground and analyzed for concentrations of total nitrogen and phosphorus using the Kjeldahl and perchloric methods, respectively. Total nutrient pools (nutrient concentrations X biomass) were then calculated. To determine seed dry weights, seeds were soaked in water for 14 h to remove pericarps and seed coats on sagebrush, bitterbrush, birchleaf, curlleaf achenes and seed coats on serviceberry seeds. The embryos were then dried in an oven at 80°C for 48 h before weighing.

RGR values were calculated using the interval approach (Evans 1972): 

\[
RGR = \frac{\ln(W_2) - \ln(W_1)}{(t_2 - t_1)},
\]

where \(W\) is total biomass (g per plant), \(t\) is time and subscripts indicate the beginning (1) and ending (2) times. RGR values were estimated for three time intervals 0 to 7, 7 to 14 and 14 to 21 weeks. For each shrub species, the ability to change RGR when grown under the two nutrient regimes was used as an indicator of the degree of plasticity in RGR. To assess allocation patterns, the proportion of total biomass allocated to roots and stems was calculated. Allocation to leaves was assessed by calculating leaf area ratio (LAR) using the formula: 

\[
LAR = \frac{[(A_2W_2) + (A_1W_1)]}{2},
\]

where \(A\) is total leaf area (cm² per plant), \(W\) is total biomass (g per plant) and subscripts indicate the beginning (1) and ending (2) times. The LAR was determined for only one age interval of 7 to 14 weeks because seedlings had no leaves at zero weeks of age, and sagebrush seedlings grown at the high nutrient level became root bound after 14 weeks and started losing some leaves.

The data were analyzed using analysis of variance (SuperANOVA, Abacus Concepts Inc., Berkeley, California). Differences in RGR between treatments were statistically evaluated as a treatment by time interaction in an ANOVA procedure with ln-transformed plant weight as the dependent variable (Poorter
and Lewis 1986). To separate the RGR means, the calculated RGR data were analyzed by ANOVA with time interval as a repeated measure. This was necessary because each harvest was used twice in the calculation of RGR, hence, RGR at time interval 1, 2 and 3 were not completely independent observations. Least square correlations of seed weight, total biomass, leaf area, LAR, allocation to stems and roots, and nutrient pools with RGR were also determined. The 0.05 level of probability was used for all tests of significance.

Results

Seed mass, total biomass, and leaf area
Seed mass, with pericarp and/or testa removed, differed 69-fold among the shrub species. The mean weights (n=100 seeds) for sagebrush, bitterbrush, serviceberry, birchleaf and curlleaf were 0.2, 13.8, 7.1, 4.8 and 3.1 mg, respectively.

At all harvests seedlings grown at the high nutrient level produced significantly more biomass than those grown at the low nutrient level (Fig. 1). On the average sagebrush, bitterbrush, serviceberry, birchleaf and curlleaf produced 16, 3, 5, 5 and 4 times more biomass at the high than at the low nutrient level, respectively.

Leaf area was also significantly greater for seedlings grown at the high than low nutrient level (Fig. 2). At the low nutrient level, sagebrush had the lowest leaf area at 7 weeks but by 21 weeks sagebrush had surpassed the other species. On the average, from 7 to 21 weeks at the high nutrient level, sagebrush produced 3, 2, 4, and 6 times more leaf area than bitterbrush, serviceberry, birchleaf and curlleaf, respectively, (Fig. 2).
Fig. 1. Total biomass for seedlings of five shrub species grown at high and low nutrient levels and harvested at 7, 14 and 21 weeks after emergence. Seed masses, with testa removed, are shown for time 0 weeks (see text for details). The SE bars are shown except where smaller than the size of the symbols, n = 10. Note scale differences between upper and lower panels.
Fig. 2. Leaf area for seedlings of five shrub species grown at high and low nutrient levels and harvested at 7, 14 and 21 weeks after emergence. The SE bars are shown except where smaller than the size of the symbols, n = 10. Note scale differences between upper and lower panels.
Sagebrush had significantly higher RGR than the other species at both nutrient levels (Fig. 3a). On the average, the RGR of sagebrush was two-fold greater than that of the other species at both the low and high nutrient levels. All seedlings had greater RGRs when grown at the high than the low nutrient level, however, only sagebrush had a significantly higher RGR (0.084 compared to 0.048). The increases in RGR ranged between 30 and 80% as a result of the 25-fold increase in nutrient supply rate from the low to the high nutrient level. The RGR declined with age (Fig. 3b) but the decrease was greatest for sagebrush seedlings. The ranking of the shrub species for mean RGR was similar at both nutrient levels: sagebrush > curlleaf = serviceberry = birchleaf = bitterbrush.

*Allocation of biomass to roots, stems and leaves*

Overall, all species allocated at least 10% more biomass to roots when grown at the low than at the high nutrient levels (Fig. 4). At both nutrient levels, serviceberry allocated significantly more resources to root production than any other species. On the average, 41.8 and 54.6% of the serviceberry seedling biomass was allocated to roots when grown at the high and low nutrient levels, respectively, and this allocation tended to increase with age.

Except for serviceberry, seedlings produced more stem biomass when grown at the high than at the low nutrient level (Table 1). However, the increase was significant only in sagebrush and bitterbrush. All five shrub species allocated more to leaf area production when grown at the high than at the low nutrient level (Table 1). Within each nutrient level, sagebrush allocated significantly more to leaf area production than other species.
Fig. 3. The RGR for total biomass for seedlings of five shrub species grown at high and low nutrient levels averaged across time intervals (a) and estimated for three time intervals 0 to 7, 7 to 14 and 14 to 21 weeks averaged across high and low nutrient treatments (b). Bars within nutrient level or time interval with the same letter are not significantly different at $P < 0.05$. 
Fig. 4. Root biomass as a percentage of total biomass for seedlings of five shrub species grown at high and low nutrient levels and harvested at 7, 14 and 21 weeks after emergence. The SE bars are shown except where smaller than the size of the symbols, n = 10.
Table 1. Mean values of allocation to stems (% of total biomass) and leaf area ratio (LAR). Values within columns followed by the same letter are not significantly different. Mean values between nutrient levels for: allocation to stem were significantly different except for birchleaf and curlleaf; and LAR values were significantly different except for sagebrush.

<table>
<thead>
<tr>
<th>Species</th>
<th>Stem (%)</th>
<th>LAR (cm² g⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Nutrient level</td>
<td>Nutrient level</td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td>Sagebrush</td>
<td>15.8b</td>
<td>19.8b</td>
</tr>
<tr>
<td>Bitterbrush</td>
<td>16.1b</td>
<td>17.9c</td>
</tr>
<tr>
<td>Serviceberry</td>
<td>19.2a</td>
<td>14.8d</td>
</tr>
<tr>
<td>Birchleaf</td>
<td>20.0a</td>
<td>20.3b</td>
</tr>
<tr>
<td>Curlleaf</td>
<td>21.5a</td>
<td>21.9a</td>
</tr>
</tbody>
</table>
Allocation of nutrients to roots, stems and leaves

Seedlings had more nutrients in the leaves and roots than in the stems, except for phosphorus pools in the roots of seedlings grown at the high nutrient level (Fig. 5). Among the shrub species, sagebrush allocated significantly more nitrogen and phosphorus to the leaves and proportionately less to the stems and roots. The other species tended to allocate similar amounts of nitrogen and phosphorus to leaves and roots, except for phosphorus pools in the roots of seedlings grown at the high nutrient level.

Correlation of the various traits with RGR

In the results presented in Figs. 6 and 7 the two data points for each species are joined by a line to show the change in RGR when seedlings were grown at the low and high nutrient levels. Correlations of LAR, leaf area and total biomass with RGR were significant (Fig. 6). Allocation to stems was not significantly correlated with RGR. Allocation to roots and seed weight correlated negatively with RGR, although the correlations were not statistically significant. Overall, sagebrush had unique biomass allocation patterns compared to the other species (Fig. 6). However, the unique patterns of sagebrush did not drastically influence the overall correlations of resource allocation with RGR, except for allocation to roots. When sagebrush data were omitted from the correlations, the correlation coefficients of RGR with LAR, leaf area, total biomass, allocation to stem and allocation to roots were 0.79, 0.74, 0.75, 0.10, and -0.72, respectively, as compared to the 0.84, 0.86, 0.85, 0.05, and -0.49, respectively, when sagebrush was included.

Except for the root phosphorus pool, nutrient pools were significantly
Fig. 5. Mean values of total nitrogen and phosphorus pools (n = 9) in the roots, stems and leaves of seedlings of five shrub species grown at two nutrient levels. Bars between species and within root, stem and leaf with the same letter are not significantly different at \( P < 0.05 \). Note the differences in scales.
Fig. 6. Correlations of LAR, leaf area, total biomass, allocation to stem and root and seed mass with relative growth rate (RGR).
* indicates significant correlation at $P < 0.05$. Except for seed mass, $n = 10$, i.e. five species $\times$ two nutrient levels. For seed mass, $n = 5$ species. Note that for each shrub species, low and high RGR values are for seedlings grown at low and high nutrient levels, respectively, except for allocation to roots and to serviceberry stems where RGR are low and high at high and low nutrient levels, respectively.
correlated with RGR (Fig. 7). Sagebrush exhibited greater RGRs per gram of nutrient than any of the four species.

Discussion

RGR patterns among the shrub species

Results suggest that patterns of biomass and nutrient allocation and growth rates of the semiaridland shrub species evaluated are not related to growth form. These results differ from previous studies with tundra shrubs where species with similar growth forms exhibited similar biomass and nutrient allocation patterns and growth rates (Archer and Tieszen 1980, Chapin 1980b, Chapin et al. 1980, Johnson and Tieszen 1976). Unlike in the present experiment, studies from the tundra determined absolute growth rates rather than RGRs and were performed in the field with mature plants. In my glasshouse experiment, sagebrush, which exhibits both evergreen and deciduous leaf characteristics, had different biomass and nutrient allocation patterns to various plant parts, and exhibited a different RGR compared to the other species (Table 1, Figs. 3 and 6). The four species that were compared with sagebrush ranged from strictly deciduous (serviceberry and birchleaf) to plants with long-lived evergreen leaves (curlleaf) and had varied allocation patterns but similar RGRs. Even the closely related birchleaf, a deciduous species, and curlleaf, an evergreen species, had similar RGRs. The same relationship also was observed in a field study conducted in 1989 and 1990 where three and four-year-old birchleaf and curlleaf had statistically similar RGRs (Chapter III). In addition, mature plants of sagebrush had higher growth rates under field conditions than interspersed mature bitterbrush (Bilbrough, 1990). The lack of a relationship between growth form and characteristics such
Plasticity in RGR

The large differences in RGR of sagebrush seedlings grown at the low and high nutrient levels (Fig. 3) suggests that sagebrush is more capable of large responses to resource changes in the environment than the other species. In semiarid environments, where nutrients are available in pulses, sagebrush may have an advantage over the other species in tapping and exploiting the periodically available nutrients (Caldwell et al. unpublished data). Both mountain mahogany species and bitterbrush form actinorrhizal associations in their natural environments (McKell 1989). In my experiment, these shrubs were not inoculated with actinomycetes and lack of their usual symbiotic associates could have influenced their nutrient uptake capacity. Sagebrush also maintained a higher RGR than the other species when grown under low nutrient level. This may be a disadvantage because a high RGR in low nutrient environments can result in resource exhaustion and increased mortality (Chapin 1980a).

In summary, my results confirm that sagebrush has a higher RGR than the four other species that often grow in association with it. The high growth rates of sagebrush, which invests heavily in chemicals for herbivory defense (Kelsey 1986, Welch and McArthur 1979), suggests that allocation to defense compounds does not always limit growth. Briggs and Schultz (1990) also observed a similar pattern where plants investing in high tannin concentrations exhibited higher growth. The lack of relationship between patterns of biomass and nutrient allocation and RGR with growth form does not support the results found in other ecosystems. Further experiments are needed to confirm the
relationships of resource allocation patterns and RGR with growth form among mature semiaridland plants in the field. An explanation of why patterns of biomass and nutrient allocation and RGR of the semiaridland shrubs are unrelated to growth form should be sought.
CHAPTER III
COMPENSATORY GROWTH CAPACITY AND GROWTH RATES OF SIX SEMIARIDLAND SHRUBS FOLLOWING SIMULATED BROWSING.

Summary. Inherent plant factors that limit compensatory growth in plants following herbivory have not been extensively studied. I investigated the relationship between compensatory growth capacity and relative growth rate (RGR) in six semiaridland shrubs following removal of 90% of previous year's growth in winter and spring. Four-year-old shrubs growing under field conditions were used in the study. Except for big sagebrush (*Artemisia tridentata* ssp. *vaseyana* [Rydb.] Beetle), which died following simulated browsing, compensatory growth was observed for bitterbrush (*Purshia tridentata* [Pursh] DC), serviceberry (*Amelanchier alnifolia* Nutt.), birchleaf mountain mahogany (*Cercocarpus montanus* Raf.), curlleaf mountain mahogany (*C. ledifolius* Nutt.) and big tooth maple (*Acer grandidentatum* Nutt.). By the end of a four-month growing season, the clipped shrubs had exactly compensated for tissues removed by clipping. Overall, clipped plants produced more new growth than unclipped plants. Although the mean RGRs of five shrub species averaged over two years were significantly correlated with compensatory growth capacity, the death of sagebrush, a species with rapid growth rate, suggests that inherent growth rate is not the only factor that determines compensatory growth capacity in plants. Other factors that may influence compensatory growth capacity of shrubs are discussed.
Introduction

Compensatory growth refers to a positive response of plants to tissue removal and is a very useful indicator of the capacity of a plant to tolerate herbivory (Dyer 1975, McNaughton 1983, Belsky 1986). Grazed, browsed or clipped plants that produce more cumulative dry weight than control plants, and those that produce cumulative dry weights equal to control plants, overcompensate and exactly compensate for lost tissues, respectively, and are considered relatively tolerant of herbivory. Plants that undercompensate (i.e. produce less cumulative dry weight than controls), and those that do not compensate for lost tissues are considered relatively intolerant of herbivory. Whether plants exhibit compensatory growth or not is still a subject of discussion (Belsky 1986, 1987; McNaughton 1983, 1986). The most commonly held view is that plants do not overcompensate or exactly compensate for lost tissues and, therefore, herbivory is generally detrimental to plants (Belsky 1986, Crawley 1983, Whitham and Mopper 1985). There is limited evidence that some plants overcompensate or exactly compensate for lost tissues as long as the external environment is favorable for growth (McNaughton 1983, 1986; Paige and Whitham 1987, Maschinski and Whitham 1989).

The discussion concerning compensatory growth has persisted partly because the inherent mechanisms and constraints that limit or facilitate compensatory growth are not well understood. Inherent growth capacity may be a major determinant of a plant's capacity for compensatory growth (Coley et al. 1985, Bryant et al. 1983, Gulmon and Mooney 1986, Chapin 1980a). Plants with high inherent growth rates have the potential to rapidly replace photosynthetic tissues and are considered capable of compensating for lost tissues and consequently, tolerating herbivory. Conversely, plants with low
inherent growth rates have limited capacity to refoliate and are expected to be less capable of compensating for lost tissues.

The relationship between inherent growth rate and compensatory growth capacity has received very little research attention particularly for plants in semiarid lands. Field observations of shrubs growing on arid and semiarid rangelands of the Intermountain Region in western North America suggest that inherent growth rates may not be related to compensatory growth. For instance, sagebrush has relatively high growth rates, yet it does not compensate for lost tissues and is intolerant of browsing (Chapter II, Welch and McArthur 1979, Bilbrough 1990). On the other hand, bitterbrush has relatively low growth rates, yet it compensates for lost tissues and tolerates even severe herbivory (Chapter II, Bilbrough 1990).

In this study, I quantified the relationship between relative growth rate (RGR) and compensatory growth capacity of six semiaridland shrubs following simulated browsing in winter and spring. I expected simulated browsing during winter to cause a loss of leaves, nutrients in the leaves and meristems among evergreens and mainly meristems in deciduous species. Spring browsing was expected to cause a loss of leaves, nutrients and meristems in both deciduous and evergreen species. This is because evergreen shrubs contain high levels of nutrients in their leaves during all seasons of the year, while deciduous shrubs re-translocate nutrients from leaves to roots and/or stems before winter, leaving less nutritious stems for grazing during winter (Chapin 1980a). The specific questions I sought to answer were 1) Do these semiaridland shrubs exhibit compensatory growth? 2) Does browsing influence RGR? 3) Does the season of browsing influence compensatory growth capacity and RGR? 4) Is compensatory growth capacity correlated with RGR?
The shrub species included in this study were mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana* [Rydb.] Beetle), bitterbrush (*Purshia tridentata* [Pursh] DC), serviceberry (*Amelanchier alnifolia* Nutt.), birchleaf mountain mahogany (*Cercocarpus montanus* Raf.), curlleaf mountain mahogany (*C. ledifolius* Nutt.) and big tooth maple (*Acer grandidentatum* Nutt.), henceforth referred to as sagebrush, bitterbrush, serviceberry, birchleaf, curlleaf and maple, respectively. The sagebrush, (*Asteraceae*), is perhaps the most dominant shrub species in the Intermountain Region (Welch 1983a). It exhibits both deciduous and evergreen leaves. In a growing season, it produces two kinds of leaves: large leaves that are shed after approximately three months and relatively small leaves which are maintained throughout the year and are photosynthetically active during the following growing season (Depuit and Caldwell 1975). Sagebrush leaves have high concentrations of crude protein, total digestible nutrients, calcium, phosphorous and carotene (Welch 1983b). However, the forage value of sagebrush is reduced because the plants are not as palatable to wildlife and livestock as other shrubs (Smith and Hubbard 1954). Bitterbrush, serviceberry, birchleaf and curlleaf (Rosaceae), are preferred by both wild and domestic ungulates over big sagebrush (Smith and Hubbard 1954). Serviceberry and birchleaf are deciduous species, bitterbrush has deciduous and evergreen leaves, but overwintering leaves are much smaller than in sagebrush, and curlleaf is evergreen. These shrubs grow in close association with sagebrush, often in mixed species stands. Big tooth maple (*Aceraceae*) is deciduous and is the most common maple in canyons of the Intermountain Region. It is a hard wood that normally grows into a small tree and is rarely browsed by ungulates, except when browse choices are limited. The six shrubs were chosen because they are among the most
abundant and important browse species that grow in the basins and foothills of the Intermountain Region in western North America.

**Materials and methods**

The experiment was performed near Logan, Utah (41° 45' N, 111° 48' W, 1460 m above sea level). The site is characteristic of cold-desert shrub steppe (West 1983a,b). Soil on the site is a stony mollisol (Typic Haploxeroll) which was formed from calcareous alluvial fan deposits (Southard et al. 1978). Details of the site, climate and soils are contained in Caldwell et al. (1981).

The experimental design was a 6 X 3 factorial using a randomized block design with 10 blocks. The six experimental shrub species were established from three-year-old shrubs in September 1988. At planting time, deep holes (40 cm deep) capable of covering the root system of the young shrubs were dug at a 2-m spacing. A slow-release fertilizer (Osmocote 17-16-10 NPK) was mixed with the soil in the holes before planting to provide optimal nutrient supply while reducing the risk of fertilizer damage to the roots of the young shrubs. In April 1989, during the spring rains, a top-dressing of fertilizer (16-16-8 NPK) was applied at a rate of 50 g per shrub. Throughout the experiment, weeds were removed by hand to reduce competition for water, light and nutrients.

Three kinds of simulated browsing were assigned to the shrubs, and they included: the control (no browsing), reduction of the previous year's growth by 90 % in winter, and the same browsing treatment in spring. The removal of 90% of previous years growth was chosen because it represents a common browsing patterns of large ungulates on these shrubs. The winter and spring treatments were applied to the shrubs in December 1989 and April 1990.
respectively, more than one year after planting.

The measurements taken included 1) basal-stem diameter measured at ground level for use as an estimator of plant size, 2) leaf area on current annual growth measured non-destructively during the growing season and destructively at the end of the experiment and 3) cumulative aboveground biomass (dry weight per plant). For clipped plants cumulative aboveground biomass included old growth, removed tissues and regrowth. For unclipped plants, cumulative biomass was the aboveground biomass at the end of the experiment.

To determine leaf area non-destructively, leaves were removed from non-experimental shrubs of similar size and age as the experimental shrubs and established at the same time as the experimental shrubs. For each species leaf lengths were regressed against leaf area (determined with a LI-3100 area meter) and the $r^2$ for serviceberry, birchleaf, curlleaf and maple were 0.96, 0.93, 0.90 and 0.98, respectively. Leaf lengths of all leaves on each experimental shrub were then measured and converted to leaf area using the linear regression equations. By summation the leaf area of each experimental shrub was estimated at each measurement interval. Because sagebrush and bitterbrush produced so many small leaves, it was not possible to estimate their leaf area at intervals, consequently, their relative growth rates on a leaf area basis ($RGR_{LA}$) could not be estimated. At the end of the experiment (end of July 1990), leaf area was determined destructively by harvesting all the leaves from each experimental shrub and measuring their area using a LI-3100 area meter.

The $RGR_{LA}$ of four of the six shrubs (i.e. serviceberry, birchleaf, curlleaf
and maple) were estimated from the leaf area data collected during the growing season (April to July) in 1989 and 1990. The $R_{\text{RGRLA}}$ were calculated by the interval method (Evans 1972) using the formula: 

$$R_{\text{RGRLA}} = (\ln A_2 - \ln A_1)/(t_2 - t_1)$$

where $A$ is total leaf area (cm$^2$ per plant), $t$ is time and subscripts indicate the beginning (1) and ending (2) times. The $R_{\text{RGRLA}}$ were calculated for three time intervals each year. Each time interval was 28 and 20 days in 1989 and 1990, respectively. The $R_{\text{RGRLA}}$ values for the first, second and third time intervals represented growth rates during the early (May), mid (June) and late (July) parts of the growing season, respectively.

The aboveground plant tissues removed in winter and spring and harvested at the end of the experiment were dried in an oven at 90°C for five days before weighing. Whether shrubs overcompensated, exactly compensated, or undercompensated for removed tissues was determined as suggested by Belsky (1986). To determine the influence of browsing on plant size, I disregarded the biomass removed by browsing and compared the aboveground biomass of clipped and unclipped shrubs at final harvest.

Plant biomass data were analyzed using covariance procedures (SuperANOVA, Abacus Concepts Inc. Berkeley, California) with basal-stem size as the covariate to adjust for the effects of plant size on biomass yield. The $R_{\text{RGRLA}}$ differences between treatments were statistically evaluated as the interaction between treatment and time in an ANOVA procedure with In-transformed leaf area as the dependent variable (Poorter and Lewis 1986). To separate the $R_{\text{RGRLA}}$ means, the calculated $R_{\text{RGRLA}}$ data were analyzed by ANOVA with time interval as a repeated measure. This was necessary because each harvest was used twice in the calculation of $R_{\text{RGRLA}}$, hence, $R_{\text{RGRLA}}$ at
time intervals 1, 2 and 3 were not completely independent observations. Least square correlations of cumulative aboveground biomass and aboveground new growth biomass with $\text{RGR}_{\text{LA}}$ were also determined. The 0.05 level of probability was used for all tests of significance.

**Results**

*Compensatory growth capacity*

Except for sagebrush which died following clipping, the aboveground cumulative biomass of clipped and unclipped plants were statistically similar (Fig. 8A). Consequently, these shrubs exactly compensated for lost tissues. Irrespective of shrub species, clipped plants produced slightly more new growth than the unclipped plants (Fig. 8B) but the increases were not large enough to be significant. Season of simulated browsing had no significant influence on aboveground cumulative biomass or new growth production. Similarly, shrub size, expressed as total aboveground biomass of plants at harvest was not significantly influenced by the one-time browsing in my experiment.

$\text{RGR}_{\text{LA}}$

Birchleaf and curlleaf exhibited greater $\text{RGR}_{\text{LA}}$ than serviceberry and maple in both the 1989 and 1990 spring growing seasons (Table 2). The mean $\text{RGR}_{\text{LAS}}$ for the two spring growing seasons averaged over the two years were 0.009, 0.024, 0.026, 0.006 for serviceberry, birchleaf, curlleaf and maple, respectively. In 1990 all shrubs had the greatest $\text{RGR}_{\text{LA}}$ during the early part of the growing season (Fig. 9A). Late in the growing season $\text{RGR}_{\text{LAS}}$ declined. Maple produced most of its leaves within a short time interval early in the growing season and as the growing season progressed, it shed old leaves.
Fig. 8. Effect of winter and spring simulated browsing on cumulative aboveground biomass and aboveground new growth compared with unclipped (control) plants of five shrub species. All sagebrush plants died as a result of the 90% browsing treatment. Each value is the mean ± S.E; because plants in some blocks died, n varied from 6 to 10 plants. Note scale differences between the upper and lower panels.
Table 2. Mean leaf area RGRs of unclipped young shrubs grown under field conditions and estimated during the spring seasons in 1989 and 1990. (n = 30 except for curlleaf and maple in 1990, n = 27 and 15, respectively.) Data are means ± S.E. Values within a column followed by the same letter are not significantly different at $P \leq 0.05$

<table>
<thead>
<tr>
<th>Species</th>
<th>$\text{RGR}_{\text{LA}}$</th>
<th>1989</th>
<th>1990</th>
</tr>
</thead>
<tbody>
<tr>
<td>Serviceberry</td>
<td>0.005 ± 0.002b</td>
<td>0.012 ± 0.003b</td>
<td></td>
</tr>
<tr>
<td>Birchleaf</td>
<td>0.020 ± 0.003a</td>
<td>0.028 ± 0.004a</td>
<td></td>
</tr>
<tr>
<td>Curlleaf</td>
<td>0.018 ± 0.002a</td>
<td>0.033 ± 0.004a</td>
<td></td>
</tr>
<tr>
<td>Maple</td>
<td>0.009 ± 0.005b</td>
<td>0.003 ± 0.005b</td>
<td></td>
</tr>
</tbody>
</table>
Fig. 9. Time course of relative growth rate within species averaged across treatments (A) and for plants subjected to simulated winter and spring browsing or control treatments combined across species (B). The time intervals 1, 2 and 3 represent early (May), mid (June) and late (July) spring growing season. Each point represents the mean RGR with associated ± S.E, n varied from 15 to 34 plants.
Consequently, the $RGR_{LA}$ of maple became negative. Unlike the other species, curlleaf continued to produce new leaves throughout the growing season. Overall, clipped plants had slightly greater $RGR_{LAS}$ than unclipped plants early in the growing season but this difference was not significant (Fig. 9B).

Correlation of $RGR_{LA}$ with compensatory growth capacity

The cumulative aboveground biomass and aboveground new growth biomass were significantly and positively correlated with the mean $RGR_{LA}$ for the two spring growing seasons, averaged over two years (Fig. 10). In contrast, the correlation of compensation (cumulative biomass of clipped/cumulative biomass of unclipped plants) with the mean RGR was significantly negative (Fig. 10).

Discussion

Except for sagebrush, the shrubs responded to simulated browsing by producing more new growth and exactly compensating for lost tissues. Similar neutral or positive effects on shrubs subject to long-term browsing or simulated browsing have been shown in the Serengeti (Pellew 1983), western North America (Bilbrough 1990, Provenza et al. 1983) and in Sweden (Bergstrom and Danell 1987). In this experiment, both intra- and inter-specific competition for nutrients, water and light were reduced by using fertilized and spaced individual plants. In semiaridland environments competition and nutrient limitations occur and may decrease compensatory growth (Maschinski and Whitham 1989, Chapin and McNaughton 1989).

While no data were collected on belowground growth responses of the shrubs, I speculate that the regrowth biomass produced was not necessarily a
Fig. 10. Correlation of cumulative aboveground biomass, aboveground regrowth biomass and compensation by winter- and spring-browsed plants with mean RGR of two spring growing seasons. * indicates significant correlation at $P \leq 0.05$, $n = 8$ i.e. 4 species X winter and spring browsing treatments.
consequence of a shift in allocation of photosynthate and nutrients to new shoot growth at the expense of root growth. The shrubs were grown in an environment rich in nutrients and light where current photosynthate and nutrient uptake could have provided the required carbon and nutrients for regrowth. In addition, browsing treatments apparently did not cause a severe nutrient stress because shrubs that lost more nutrients in leaves (evergreen shrubs browsed in winter and deciduous shrubs browsed in spring) had similar regrowth to shrubs that lost minimal nutrients (deciduous shrubs browsed in winter). Assuming that both carbon and nutrients required for regrowth were available, the shrubs could have allocated the carbon and nutrients necessary to support shoot growth without sacrifice of root function (Chapin 1980b).

The mechanisms that can lead to compensatory growth capacity can be divided into intrinsic mechanisms that involve physiological and developmental changes and extrinsic mechanisms that involve a modification of the environment (McNaughton 1983). My experiments showed that the browsed shrubs had a slightly greater RGR\textsubscript{LA} early in the growing season (Fig. 9B). Although the increase in RGR\textsubscript{LA} was not statistically significant, an increase in RGR\textsubscript{LA} is a necessary condition for the exact compensation I observed (Hilbert et al. 1981). The increase in RGR\textsubscript{LA} following clipping supports the suggestion that physiological and developmental changes occur following browsing and can result in compensatory growth (McNaughton 1983). The high correlation coefficients of RGR\textsubscript{LA} and cumulative biomass (Fig. 10) suggests that a plant's inherent growth rate is likely to influence its compensatory growth capacity. The negative correlation between compensation and mean RGR supports the prediction by Hilbert et al. (1981) that plants with rapid RGRs have to exhibit a greater increase in RGR compared to plants with lower RGRs to be able to
compensate for lost tissues.

The deleterious effects of browsing on sagebrush have also been reported in other studies (Shepherd 1971, Bilbrough 1990). The death of sagebrush, a species with rapid inherent growth capability (Chapter II; Welch and McArthur 1979), suggests that constraints other than slow growth rate may limit compensatory growth. The study by Bilbrough (1990) suggests that in sagebrush, meristematic limitations or low allocation plasticity are likely to limit compensatory growth because buds with the highest potential to produce vegetative growth are vulnerable to removal by browsing. Studies on grass species also suggest that differences in the ability to activate buds better explains the differences in grazing tolerance capacity of two bunchgrasses that exhibit similar characteristics, including growth rate (Eissenstat and Caldwell 1987, Richards and Caldwell 1985, Caldwell et al. 1981). The intrinsic constraints that may limit compensatory growth, even in plants with rapid growth rates, are poorly understood and require further research.
CHAPTER IV
THE RELATIONSHIP BETWEEN MERISTEMATIC POTENTIAL AND REGROWTH CAPACITY AMONG FOUR SEMIARIDLAND SHRUBS

Summary: Absence of active apical meristems following grazing by large herbivores limits regrowth capacity of grasses. Whether regrowth capacity of shrubs also is limited by insufficient numbers of active meristems following browsing has been studied less and is not known. In this study, I determined the influence of loss of buds on regrowth capacity and the relationship between meristematic potentials and regrowth capacity of four semiaridland shrub species. Four-year-old shrubs growing under field conditions were used in the study. Loss of 90% of the buds on the previous year’s growth did not limit regrowth capacity of any of the browsing tolerant shrubs. Instead, shrubs that lost buds produced more regrowth biomass than the controls. The ranking of the four species in descending order of regrowth capacity, were: curlleaf mountain mahogany (Cercocarpus ledifolius Nutt.) > birchleaf mountain mahogany (C. montanus Raf.) > big tooth maple (Acer grandidentatum Nutt.) = serviceberry (Amelanchier alnifolia Nutt.). The four species exhibited significantly different meristematic potentials. Curlleaf followed by birchleaf had a greater number of buds and long shoots per plant, and a lower percentage of buds at the basal section on twigs. In contrast, maple and serviceberry had fewer buds and long shoots per plant, and a higher percentage of long shoots at the basal sections. The number of long shoots that were produced following bud removal was highly and positively correlated with regrowth biomass, while
the percentage of long shoots produced at the basal position on twigs was highly and negatively correlated with regrowth biomass. My results suggest that the ability of shrubs to initiate long shoot growth and allocation plasticity are likely to influence their ability to produce regrowth biomass.

Introduction

When plants are browsed or grazed by large herbivores, they lose meristems on the plant parts removed. Loss of active meristems may be a major constraint that limits the capacity of plants to rapidly replace photosynthetic foliage and consequently, tolerate herbivory (Caldwell 1984, Dahl and Hyder 1977, Caldwell et al. 1981, Richards and Caldwell 1985). Once active meristems are lost to herbivores, any further growth must originate from axillary buds that must be activated. Activation of the axillary meristems may depend on how flexibly and efficiently a plant allocates resources to bud growth. It may also depend on the suitability of environmental conditions for initiating growth. A plant that delays activating meristems, delays producing photosynthetic foliage and risks depleting its carbon reserves by respiratory demands before achieving a positive carbon balance. The delay in producing foliage may also slow uptake of resources such as nutrients and water, which may be lost to competing neighbor plants that are not as severely damaged by herbivores.

Studies with grasses suggest that bud activation is of prime importance in determining regrowth production and, consequently, tolerance of grazing (Richards et al. 1988, 1987, Caldwell et al. 1981, Richards and Caldwell 1985). For instance, *Agropyron desertorum*, which rapidly activates buds to produce tillers, rapidly re-establishes its photosynthetic canopy and as a result tolerates grazing. By contrast, *Pseudoroegneria spicata*, which is similar to *Agropyron*
desertorum in most physical and biological characteristics, is less capable of rapidly activating buds following grazing and is less tolerant of grazing.

Whether regrowth capacity of shrubs is also limited by a lack of meristems or inability to activate meristems following browsing has been studied less. This is partly because most shrubs seem to have abundant meristems, some of which are protected in the canopy (Dahl and Hyder 1977). Consequently, the potential, for shrubs to replace photosynthetic tissues lost to herbivores has always been expected to be high because, a large number of leaf-producing units are available (Archer and Tieszen, 1980). However, some shrubs, such as sagebrush, that have the characteristics that should favor rapid regrowth capacity, such as, abundance of meristems and rapid inherent growth rates, are incapable of regrowing following browsing (Chapter II, Welch and McArthur 1979, Bilbrough 1990). Probably, it is the ability to initiate growth and the location of buds that initiate growth rather than a redundancy of buds that determine regrowth capacity. Although a shrub may have abundant axillary buds it may fail to activate them. In addition, buds with the greatest potential to produce vegetative growth may be located on current annual growth that is mostly vulnerable to removal by browsing (Bilbrough 1990).

In this study, I determined whether loss of potentially active buds influences regrowth capacity of four semiaridland shrubs. I also tested the hypothesis that the regrowth capacity of a shrub is dependent on its ability to initiate growth and the location of buds that initiate growth. To test this hypothesis, I first quantified the meristematic potential of the four semiaridland shrubs in terms number of buds, ability to initiate long shoot growth and the location of long shoots on twigs. I then determined the correlation between regrowth capacity and ability to activate long shoot growth as well as the
location of long shoots on twigs. The buds were removed from the shrubs in winter and again in spring to simulate both winter and spring loss of buds to herbivores. In this study buds were removed leaving leaves and stems intact. Results from this study were compared with results from a similar experiment (Chapter III) in which buds, leaves and stems were removed.

Four shrub species were chosen for this study based on ease of bud removal and their abundance and importance as browse species in the Intermountain Region of Western North America. The species included: serviceberry (Amelanchier alnifolia Nutt.), birchleaf mountain mahogany (Cercocarpus montanus Raf.), curlleaf mountain mahogany (C. ledifolius Nutt.) and big tooth maple (Acer grandidentatum Nutt.) henceforth referred to as serviceberry, birchleaf, curlleaf and maple, respectively. Serviceberry, birchleaf and maple are all deciduous while curlleaf is evergreen. Maple is rarely browsed by ungulates except when browse choices are limited, whereas the three other shrubs are highly preferred by both wild and domestic ungulates (Smith and Hubbard 1954).

**Materials and methods**

The experiment was located at a site characteristic of the cold-desert shrub steppe (West 1983a,b) near Logan, Utah (41° 45' N, 111° 48' W, 1460 m elevation). Soil on the site is a stony mollisol (Typic Haploxeroll), which was formed from calcareous alluvial fan deposits (Southard et al. 1978). Details of the site, climate and soils are contained in Caldwell et al. (1981).

The experimental design was a 4 X 3 factorial using a randomized block design with 10 blocks. The four experimental shrub species were established from three-year-old shrubs in September 1988. At planting time, deep holes
(40 cm deep) capable of covering the root system of the young shrubs were dug at a 2 m spacing. A slow-release fertilizer (Osmocote 17-16-10 NPK) was mixed with the soil in the holes before planting to provide optimal nutrient supply while reducing the risk of fertilizer damaging the roots of the transplants. In April 1989, during the spring rains, a top-dressing of fertilizer (16-16-8 NPK) was applied at a rate of 50 g per shrub. Throughout the period of the experiment, weeds were removed by hand to reduce competition for water, light and nutrients.

Three kinds of bud removal were assigned to the shrubs: the control (no bud removal), reduction of distal-most buds on the previous year’s growth by 90% in winter and the same bud removal treatment in spring. The winter and spring bud removal treatments were applied to the shrubs in January and April 1990, respectively, more than one year after planting.

During the course of the experiment, I observed that most of the long shoots, (i.e. shoots with elongated internodes), were produced on one and two-year-old twigs and a few on three-year old twigs, where a twig is an annual growth increment (Bilbrough, 1990). The long shoots produced most of the vegetative biomass on the shrubs. At the start of spring growth in 1990, curlleaf plants on which buds had been removed in winter initiated multiple shoot growth from the same leaf axil positions where a lateral apical bud had been removed. A sample of leaf axils observed under a microscope revealed that at each leaf axil position there was a compressed short shoot with many lateral buds. Apparently, when the short shoot terminal buds were removed, the remaining lateral buds initiated growth.

The measurements taken included 1) basal-stem diameter measured at ground level for estimating plant size, 2) number of buds per plant, 3) total
number of long shoots per plant, 4) percentage of long shoots at the basal and distal section on twigs (i.e the lowermost and uppermost 1/3 of the length of two and three-year-old twigs), 5) number of stump sprouts at the base of each plant, 5) biomass of regrowth per plant at the end of the experiment and 6) leaf area on current annual growth of each plant measured non-destructively during the course of the spring growing season and destructively at the end of the experiment. The percentage of long shoots in the middle section of the twigs was estimated as 100% minus the percentage of long shoots at the distal and basal section of the twigs.

To determine leaf area non-destructively, leaves were removed from non-experimental shrubs of similar size and age and established at the same time as the experimental shrubs. For each species, leaf lengths were regressed against leaf area, determined with a LI-3100 area meter (Licor, Lincoln, Nebraska), and the $r^2$ for serviceberry, birchleaf, curlleaf and maple were 0.96, 0.93, 0.90 and 0.98 respectively. Leaf lengths of all leaves on each experimental shrub were then measured and converted to leaf area using the linear regression equations. By summation the leaf area of each experimental shrub was estimated at each measurement interval. At the end of the experiment (end of July 1990), leaf area was determined destructively by harvesting all the leaves from each experimental shrub and measuring their leaf area using the LI-3100 area meter.

Relative growth rates on a leaf area basis ($RGR_{LA}$) were estimated from the leaf area data collected during the growing season (April to July) in 1990. The $RGR_{LA}$s were calculated using the interval method (Evans 1972) using the formula: $RGR_{LA}=(\ln A_2-\ln A_1)/(t_2-t_1)$ where $A$ is total leaf area (cm$^2$ per plant), $t$
is time and subscripts indicate the beginning (1) and ending (2) times. The $\text{RGR}_{\text{LA}}$s were calculated for three time intervals and each time interval was 20 days. The $\text{RGR}_{\text{LA}}$ values for the first, second and third time intervals represented rates of growth during the early (May), mid (June) and late (July) parts of the growing season, respectively. The aboveground regrowth harvested at the end of the experiment was dried in an oven at $90^\circ\text{C}$ for five days before weighing.

Data on abundance of buds, ability to initiate long shoot growth, percentage of long shoots at the basal and distal locations, stump sprouts and regrowth were analyzed using a covariance procedure (SuperANOVA, Abacus Concepts Inc. Berkeley, California) with basal-stem size as the covariate to adjust for the effects of plant size on biomass yield. The $\text{RGR}_{\text{LA}}$ differences between treatments were statistically evaluated as the interaction between treatment and time in an ANOVA procedure with In-transformed leaf area as the dependent variable (Poorter and Lewis 1986). To separate the $\text{RGR}_{\text{LA}}$ means, the calculated $\text{RGR}_{\text{LA}}$ data were analyzed by ANOVA with time interval as a repeated measure. This was necessary because each harvest was used twice in the calculation of $\text{RGR}_{\text{LA}}$, hence, $\text{RGR}_{\text{LA}}$ at time intervals 1, 2 and 3 were not completely independent observations. Least square correlations of number of long shoots per plant at final harvest and percentage of long shoots at the basal and distal locations with regrowth biomass were also determined.

**Results**

**Regrowth capacity**

Irrespective of species, plants that lost buds in spring produced significantly
more regrowth biomass than the control plants (Fig. 11a). Regrowth biomass production also was significantly influenced by species (Fig. 11b). Curlleaf produced the greatest regrowth biomass whereas birchleaf produced more regrowth biomass than serviceberry and maple.

**Abundance of buds**

The mean number of buds per shrub (scaled by basal stem diameter to account for differences in plant size) varied six fold among the four shrub species just prior to the application of bud removal treatment (Fig. 12a). Curlleaf had the highest number of buds and serviceberry had the lowest.

**Long shoots**

The total number of long shoots per plant at harvest was influenced by the interaction of species and bud removal at $P = 0.056$ (Fig. 12b). Serviceberry and maple that had buds removed in winter or spring had recovered to similar numbers of long shoots as the controls by the end of the growing season. Curlleaf and birchleaf that lost buds produced more long shoots than the controls. Overall, the number of long shoots produced by the four species paralleled the number of buds available for each species (Fig. 12a and b).

**Percentage of distal and basal long shoots on twigs at final harvest.**

Removal of buds had no significant influence on the location of long shoots on twigs. Most of the long shoots were produced on the portion of the one-year-old twigs that remained with buds following removal of 90% of the buds and on two-year-old twigs (Fig. 12c). Three-year-old twigs also had a few long shoots. Shrubs of all species tended to produce more long shoots at the distal end (uppermost 1/3 of twig length starting from the tip) than at the basal end.
Fig. 11. Mean new growth biomass ± SE combined across species for plants whose buds were removed in winter and spring compared to controls (a) and mean regrowth biomass ± SE for plants of each species that had buds removed in winter and spring (b); n=32. Bars between bud removal treatments or species with the same letter are not significantly different at $P < 0.05$. 
Fig. 12. Mean ± SE number of buds just prior to bud removal (a), mean ± SE number of long shoots at final harvest (b), and mean ± SE percentage of long shoots produced at the distal, middle and basal part of two-year-old twigs (c) for the four shrub species. In (a), bars with different letters are significantly different at $P < 0.050$. In (b), bars within species with the same letter are not significantly different at $P < 0.056$. In (c), bars between species for distal and basal long shoots with the same letter are not significantly different at $P < 0.050$. 
(lowermost 1/3 of twig length starting from the base; Fig. 12c) of two-year-old
twigs, irrespective of bud removal treatment. Birchleaf and curlleaf had a very
small percentage of long shoots on the basal portions of their twigs. In contrast,
serviceberry had approximately 25% of its long shoots on the basal portion of
twigs and only 50% of its long shoots on the distal portion.

**Stump sprouts**
Shrubs that produce stump sprouts are considered to be capable of producing
regrowth even after severe loss of buds following browsing. Curlleaf and
maple did not produce any stump sprouts, while birchleaf and serviceberry had
1 and 5 sprouts per plant, respectively. Overall, all four shrub species exhibited
a low production of stump sprouts.

**RGR on leaf area basis**
An accurate estimation of $\text{RGR}_{LA}$ was not possible for maple because it
produced most of its leaves within a very short time interval early in the spring
growing season, and then dropped leaves as the season progressed. Bud
removal treatments, species and the interaction of these two factors significantly
influenced the $\text{RGR}_{LA}$ of the shrubs (Fig. 13). Birchleaf and curlleaf increased
$\text{RGR}_{LA}$ after spring bud removal. Other differences were not significant.

**Correlation of various traits with regrowth capacity.**
The number of long shoots per plant at final harvest was highly and positively
correlated with spring season growth biomass (Fig. 14). The percentage of
long shoots at the distal end of the twigs was not significantly correlated with
spring growth biomass. In contrast, the percentage of long shoots at the basal
end of twigs was strongly and negatively correlated with spring growth biomass.
Fig. 13. The mean leaf area relative growth rates ± SE of plants whose buds were removed in winter and spring, compared to controls of three shrub species. Bars within species with same letter are not significantly different at $P < 0.05$. 
Fig. 14. Correlations of long shoots per plant, and percentage of distal and basal long shoots with dry weight of spring growth. * indicates significant correlation at $P < 0.05$, $n = 12$ i.e 4 species $\times$ 3 bud removal treatments.
Discussion

Removal of 90% of buds on the previous year’s growth was expected to cause a meristematic constraint to regrowth production. On the contrary, my results show that shrubs that lost buds, produced greater regrowth biomass than the controls. Apparently, when apical meristems were removed, ‘correlative inhibition’, defined as the inhibitive effects of the terminal buds on other buds (Hillman 1984), was overcome and axillary buds lower on the branches or apical meristems on short shoots were activated to grow into long shoots. Resources required for regrowth were apparently not limiting, probably because both intra- and inter-specific competition were reduced by weeding and the wide spacing of individual plants, and nutrient availability was increased by addition of NPK fertilizer.

The regrowth capacity exhibited by the shrubs following loss of buds alone were not statistically different from the regrowth capacity exhibited by the same shrub species following simulated browsing where buds, leaves and stems were removed (Chapter III). This again suggests that in the simulated browsing experiment, clipping did not severely interfere with nutrient and carbon balance of the shrubs. The stimulated regrowth in both studies was probably a response to a loss of ‘correlative inhibition’ (Hillman 1984, Brown et al. 1967). Other studies have also shown that different intensities of clipping stimulated regrowth in some shrub species (Ellison 1960, Garrison 1953).

Studies from other ecosystems have shown that production of many long shoots positively influences biomass production in plants (Provenza et al. 1983, Bergstrom and Danell 1987, Bilbrough 1990). A species that activates a larger proportion of buds to grow into long shoots would be expected to produce more biomass. In this study, the correlations between number of long shoots and
spring season growth were positive and significant. However, the correlations between percentage of long shoots at the basal position of twigs and spring season growth were negative and significant. Long shoots at the basal position on twigs will likely be shaded by leaves on upper long shoots. In my experimental plants, the basal long shoots were relatively small in size and produced fewer and smaller leaves, suggesting that they produced relatively less biomass than the long shoots at the distal end on twigs. This might explain the negative correlation between regrowth biomass and the percentage of long shoots at the basal position. The low biomass productivity of long shoots at basal positions also has been reported for mature sagebrush and bitterbrush (Bilbrough 1990). However, production of long shoots at basal positions may help protect a greater number of active apical meristems from being removed by large herbivores. Serviceberry had the highest percentage of buds at the basal position on twigs and may have this advantage.

The low correlations between percentage of long shoots at the distal position on twigs and regrowth capacity suggests that in some shrubs such as curlleaf, the long shoots at the mid part of the twigs also contribute significantly to regrowth biomass.

The low production of stump sprouts indicates that either winter or spring removal of buds did not cause a severe meristematic limitation to regrowth or these shrubs have a low inherent capacity for resprouting. Results from clipping studies suggest that when more than current annual growth is removed, curlleaf, birchleaf and serviceberry have the capacity to produce stump sprouts (Shepherd 1971).

In conclusion these results support the generalization that browsing-tolerant shrubs have abundant meristems for regrowth (Dahl and Hyder 1977),
therefore, loss of 90% of buds from the previous year's growth may not cause a meristematic constraint that would limit regrowth production. However, these results may not apply to browsing-intolerant species, such as sagebrush, which have viable buds located on current annual growth that are vulnerable to removal by browsing (Bilbrough 1990). Results from this study also suggest that the ability to initiate long shoot growth from the abundant axillary or apical meristems on short shoots will probably influence the regrowth capacity of shrubs. The shrubs in this study were not limited in activating buds to grow into long shoots.

Although removal of buds stimulated regrowth production, plants in this study were grown in an environment where nutrient limitations were reduced by the wide spacing of individual plants, weeding and addition of NPK. Further research is needed to determine the regrowth capacity of these shrubs following loss of buds under conditions of high resource competition. Limited resource availability possibly could reduce the capacity of these shrubs to rapidly activate meristems and produce regrowth.
CHAPTER V
SUMMARY AND CONCLUSIONS

Proposed mechanisms for browsing tolerance in shrubs were evaluated in this study. The specific questions addressed in a series of experiments included:

1) Are the RGRs of the shrub species different? Are RGRs of very young shrub seedlings and three- and four-year-old shrubs similar? Do the shrub species exhibit plasticity in RGR depending on availability of nutrients?

2) Are the patterns of biomass and nutrient allocation of the shrub species different? Which patterns of biomass and nutrient allocation are correlated with RGRs and therefore, might help explain the differences in RGR among the shrub species?

3) What is the relationship between RGRs, resource allocation patterns and growth form of semiaridland shrubs?

4) Do the shrubs exhibit compensatory growth following simulated browsing? What is the relationship between compensatory growth capacity and RGR of the shrub species?

5) Does bud removal influence regrowth capacity of the shrub species?

6) Do the shrub species exhibit differences in meristematic potentials? What is the relationship between meristematic potential and regrowth capacity?

Results from this study showed that at the very early seedling age, sagebrush had faster growth rates than the other shrub species. The RGRs for curlleaf at the very early seedling age and at the age of three and four years
were similar. Serviceberry and birchleaf had lower RGRs at the age of three and four years than at the very young seedling age. The lower RGRs of serviceberry and birchleaf were associated with their tendency to produce most of their leaves early in the growing season and gradually drop them as the season progressed. Unlike the other shrub species sagebrush significantly increased its RGR in response to nutrient availability.

The shrub species exhibited differences in both biomass and nutrient allocation patterns. Sagebrush allocated more biomass and nutrients to leaves whereas the other species allocated similar amounts of nutrients to leaves and roots. Differences in allocation of biomass and nutrients to photosynthetic tissues probably explains the differences in RGRs of the shrub species.

The RGRs of the semiaridland shrubs were not related to their growth form. In addition, resource allocation patterns exhibited by these shrub species were also not related to their growth form.

Except for sagebrush, which died following clipping, the other shrub species exactly compensated for lost tissues. The clipped plants compensated for lost tissues by producing greater regrowth biomass than control plants. Both cumulative and regrowth biomass were significantly correlated with RGR suggesting that shrubs with rapid growth rates would compensate for lost tissues as long as viable meristems remain on the plants.

Removing 90% of the buds on previous years growth did not limit regrowth production. Instead, bud removal stimulated production of regrowth biomass. Apparently, when buds were removed, correlative inhibition effects of apical meristems on other buds were removed. Consequently, buds lower on the branches initiated growth and produced regrowth biomass.

The shrub species also exhibited differences in meristematic potentials.
The ranking of species for the abundance of buds and long shoots per plant are: curlleaf > birchleaf > serviceberry = maple. Both the number of long shoots per plant and the percentage of long shoots at the basal position on twigs were significantly related to regrowth capacity. This suggests that meristematic potential probably influences regrowth capacity of shrubs.

In conclusion, results from this study show that RGR and meristematic potential of the shrub species evaluated are related to their regrowth capacity. This relationship suggests that both RGR and meristematic potentials are at least part of the basis for browsing tolerance among these shrub species.

This study also raised questions that require further research investigation:

1) Are the RGRs and patterns of biomass and nutrient allocation of mature semiaridland shrubs related to growth form? If they are not related, which constraints have shaped the RGRs, resource allocation patterns and growth forms of semiaridland shrubs? Are these constraints different from those that have shaped RGRs, allocation patterns and growth form in other ecosystems?

2) Do the shrub species evaluated in this study exhibit compensatory growth in environments where intra- and inter-specific competition and nutrient stress are high?

3) Does removal of more than 90% of the buds from previous years growth cause a meristematic constraint to regrowth production of browsing-tolerant shrubs?

Answers to these questions will contribute towards an understanding of why some shrubs tolerate herbivory and should also be useful for developing management practices for the sustained productivity of shrubs.
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