Responses of *Caragana korshinskii* to Different Aboveground Shoot Removal: Combining Defence and Tolerance Strategies

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**Background and Aims** It is generally assumed that plants respond to natural enemies by either allocating resources to resistance traits or compensating for damage. This study evaluated how different methods of artificial shoot removal influence two alternative strategies (i.e. tolerance and defence) of *Caragana korshinskii* in the semi-arid area of China.

**Methods** Zero per cent (control), 30 % (30 %) and 60 % (60 %) of the main shoot length and 25 % (25 %), 50 % (50 %) and 100 % (100 %) of the numbers of main shoots were removed from shrubs.

**Key Results** Moderate clipping treatments [30 % removal of partial shoot length (RSL), 25 % removal of shoot number (RSN) and 50 % RSN] improved seed production, whereas the most intensive clipping treatments (60 % RSL and 100 % RSN) with most or total removal of potential flower buds reduced current reproduction fitness compared with controls. All treatments produced a similar leaf phenolic content, with the exception of 100 % RSN which resulted in a low leaf phenolic content. In spite of a substantial investment in regrowth, clipped plants increased biomass allocation to physical defence. Control plants almost did not grow, had lower levels of physical defence and a lower photosynthetic rate, mobilized fewer carbohydrates from roots and produced more flowers. However, their current fitness was lower than that of plants undergoing clipping treatments (30 % RSL, 25 % RSN and 50 % RSN) because of the high level of abortion of flowers and fruits.

**Conclusions** *Caragana korshinskii* responded to aboveground shoot removal through combining defence and tolerance strategies.

**Key words:** Clipping, damage response, defence, *Fabaceae*, resource allocation, seed number, sprouting shrub, tolerance.

**INTRODUCTION**

Induced defence and tolerance are principal responses of plants to herbivory (Karban and Baldwin, 1997; Strauss and Agrawal, 1999; Juenger and Lennartsson, 2000). Compensation for herbivory is frequently reported in grasses (McNaughton, 1983; Milchunas and Lauenroth, 1993; Bush and Vanauken, 1995; Milchunas et al., 1995; Varnamkhasti et al., 1995), and has also been found in herbs (Paige, 1992; 1999), shrubs (Oba, 1994; Tolvanen and Laine, 1997; Oba et al., 2000) and trees (Honkanen et al., 1994; Bergström et al., 2000). The degree of growth and reproductive compensation following tissue loss may depend on a number of variables, including resource availability and the ability to allocate these resources after damage, the life form of the host plant and seasonal timing of tissue removal (Maschinski and Whitham, 1989; Obeso, 1993; Trumble et al., 1993), higher reproductive efficiency through increased percentage of fruit set (Mabry and Wayne, 1997) and increased branching or tillering after the release from apical dominance (Escarre et al., 1996; Sacchi and Connor, 1999; Simons and Johnston, 1999; Lortie and Aarsen, 2000).

Plants can also respond to herbivory by increasing their defence levels. This induced defence can be adaptive in situations where herbivory is variable, and current herbivory is a good predictor of future herbivory (Karban and Baldwin, 1997; Strauss and Agrawal, 1999). Defensive responses include chemical defences such as synthesis of secondary chemicals and physical defences such as an increase in structural and morphological characteristics, which include hairs, prickles, spines and thorns.

The hypothesis that plants respond to natural enemies by either allocating resources to defensive resistance traits or compensating for damage through a growth-related response has been tested often in the literature (van der Meijden et al., 1988; Fineblum and Rausher, 1995; Sagers and Coley, 1995). With the presence of allocational costs associated with both alternatives of defence, a negative correlation between them is expected (van der Meijden et al., 1988; Fineblum and Rausher, 1995). This particular trade-off is expected if high investment in resistance reduces resources needed for regrowth after damage (Rosenthal and Kotanen, 1994; De Jong and van der Meijden, 2000).

In the disturbed environment, sprouting species often suffer from all types of damage such as grazing, clipping, frost, trampling or windthrow. Shoots of woody plants are usually partially lost and the remaining shoots still grow new sprouters and flowers, and maintain fruit production. After damage, carbohydrates for compensatory growth and induced defence are supplied from two sources: current assimilation (Kruger and Reich, 1997; Fleck et al., 1998; Omari et al., 2003) and mobilization of pre-damage reserves stored in roots and other parts (DeSouza et al., 1986; Pate et al., 1990; Bowen and Pate, 1993; Van der Heyden and Stock, 1996; Canadell and López-Soria, 1998). Under these
conditions, physiological trade-offs may be caused by allocation decisions between growth, maintenance, reproduction and defence (Stearns, 1992; Zangerl and Bazzaz, 1992; Mole, 1994). Therefore, the selection by herbivores or damage may create sufficient environmental variability to affect the allocation pattern that is adapted as a result of the plant response to damage.

We carried out a study on the sprouting shrub *Caragana korshinskii*, which was different from our previous studies in that we monitored compensatory regrowth, reproduction and induced defence by removing different amounts of tissue from shoots. Tolerance was defined as the capacity of a plant to maintain its fitness through regrowth and reproduction, chemical defence was defined as phenol content, and physical defence was defined as spine length and spine biomass allocation. The objective of this study was to test whether removing different amounts of shoot tissue affects the investment in regrowth, defence and fitness as measured by the plant’s reproductive performance. We predicted that as the amount of shoot removal increases, plants would increase their regrowth capacity to compensate for the damage. According to the hypothesis, defence against herbivory or damage would result in trade-offs between this investment and other plant functions such as regrowth and reproduction.

**MATERIALS AND METHODS**

**Species and study site**

*Caragana korshinskii* is a long-lived shrub and is commonly found in desert, semi-desert and Loess Plateau in northwestern China, where its shoots are cut by local farmers to use as fuel energy or browsed by many sheep before the grasses turn green (removal of approx. 30% of shoot length). Following destruction of aboveground shoots by cutting, it typically develops a stout taproot from the crown of which multiple shoot sprouts arise (Niu, 1998). Flowers open for approx. 20 d during early spring. Fruits maturate in the late summer. The shoots usually grow at the end of the flowering period. The root system of *C. korshinskii* can extend over 6 m in depth, and the ratio of root to shoot is about 6:0:5:0 (Liu et al., 2003).

This study was conducted in artificial *C. korshinskii* land, approx. 90–100 km north of Yuzhong County (104°25'E, 36°20'N), Gansu Province, northwestern China. The average altitude is about 2400 m and average annual temperature is 6.5 °C. The area receives an average of 395 mm rainfall per year (Shi et al., 2003).

**Experimental design**

Clipping treatments were applied in the late winter of 2004 (i.e. 21–25 March) prior to bud swell, at a time when sheep and goat commonly browse this species. One hundred and twenty 16-year-old shrubs (20 per treatment) were randomly selected from the *C. korshinskii* wood stand. Selected plants had an average shoot number of 33, an average canopy diameter of 1.5 m and good vigour. Before clipping, the basic diameter of shoots in each shrub was measured and the total number of shoots was calculated. In order to test the effect of removal of partial shoot length (RSL) on shoot regrowth, 30 (30% RSL) and 60% (60% RSL) of the main shoot length was removed, and to test the effect of removal of shoot number (RSN) on regrowth of remaining shoots and resprouts, 25% (25% RSN), 50% (50% RSN) and 100% (100% RSN) of the main shoots were removed at 1 cm above the soil surface. With 30% RSL treatment, 30% of the length of all main shoots of each shrub was removed and in 60% RSL treatment, 60% of the length of all main shoots of each shrub was removed. In 25% RSN treatments, 25% of the total number of main shoots of each shrub was removed, and in the 50% RSN treatment, 50% of the total number of main shoots of each shrub was removed, whereas the remaining shoots were left intact. In 100% RSN treatment, all shoots were cut at 1 cm above the soil surface and thus there was no aboveground biomass. Intact plants were the control group. Three typical shoots were randomly selected from each shrub in each treatment and labelled. Each shrub biomass was obtained from a regression relationship developed from the sub-samples of shoot biomass (g) and shoot basic diameter (mm) ($r^2 = 0.921, P < 0.001$). The 30% RSL, 60% RSL, 25% RSN, 50% RSN and 100% RSN treatments removed approx. 19, 52, 23, 46 and 100% of the total shoot biomass, respectively.

**Sampling procedure and measurements**

To determine seasonal changes in total non-structural carbohydrates (TNC), samples were harvested at different time according to the plant phenology. The harvest time during 2004 was: flower bud development and flush of new foliage (10 May), fruit set (3 July) and fruit ripeness (6 August). Root samples were collected carefully by excavating roots originating from the selected shrubs, and then fine roots and coarse roots of lateral roots were combined. All samples were immediately immersed in ice, taken to the laboratory, dried at 70 °C for 48 h and then ground to a fine powder. The ground samples were well sealed over with silica gel and stored at 4 °C until analysis. The part of the roots which was removed was so small that it did not affect the growth of the whole shrub. For each harvest time, six sub-samples were taken from six randomly chosen shrubs of each treatment group. During the experimental period, each individual shrub was sampled only once. Flowers, initial fruits and final fruits of three typical shoots per shrub in each treatment group were counted to determine initial fruit set and fruit abortion. The number of seeds per shrub was used to estimate current fitness. Reproductive compensatory capacity was determined as an increased percentage of actual seed number per shrub compared with the estimated seed number per shrub if the clipped shrubs had the same initial fruit set, abscission rate and seed number per pod as the control plants.

At the end of the growing season, three resprouts and three current year shoots were randomly harvested from each shrub in each treatment group to determine spine length (mm). The samples were then sorted into leaves, stems and spines, dried to constant weight at 70 °C and
TABLE 1. Effects of different clipping treatments on flower number per shrub, initial fruit set, abscission rate, seed number per shrub and reproductive compensatory capacity of Caragana korshinskii in 2004 and in the following year (2005) (mean ± s.e., n = 20)

<table>
<thead>
<tr>
<th></th>
<th>Control</th>
<th>30 % RSL</th>
<th>60 % RSL</th>
<th>25 % RSN</th>
<th>50 % RSN</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>2004</td>
<td></td>
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</tr>
<tr>
<td>Flower number per shrub (10^3)</td>
<td>2.83 ± 0.45</td>
<td>2.72 ± 0.21</td>
<td>0.79 ± 0.11</td>
<td>2.63 ± 0.29</td>
<td>1.99 ± 0.41</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Initial fruit set (%)</td>
<td>54 ± 5</td>
<td>68 ± 4</td>
<td>69 ± 4</td>
<td>61 ± 4</td>
<td>69 ± 6</td>
<td>0.025</td>
</tr>
<tr>
<td>Abscission rate (%)</td>
<td>18 ± 1</td>
<td>13 ± 6</td>
<td>6 ± 7</td>
<td>15.8 ± 1.2</td>
<td>7.2 ± 0.2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Seed number per shrub (10^3)</td>
<td>2.93 ± 0.21</td>
<td>5.45 ± 0.44</td>
<td>1.27 ± 0.18</td>
<td>3.83 ± 0.23</td>
<td>4.11 ± 0.48</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Reproductive compensatory capacity (%)</td>
<td>0.45 ± 2.72</td>
<td>41 ± 9</td>
<td>55 ± 8</td>
<td>41 ± 7</td>
<td>95 ± 14</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>2005</td>
<td></td>
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</tr>
<tr>
<td>Flower number per shrub (10^3)</td>
<td>2.73 ± 0.55</td>
<td>2.51 ± 0.11</td>
<td>1.44 ± 0.28</td>
<td>2.54 ± 0.14</td>
<td>2.38 ± 0.17</td>
<td>0.036</td>
</tr>
<tr>
<td>Initial fruit set (%)</td>
<td>65 ± 5</td>
<td>72 ± 3.6</td>
<td>75 ± 5</td>
<td>71 ± 6</td>
<td>71 ± 7</td>
<td>0.013</td>
</tr>
<tr>
<td>Abscission rate (%)</td>
<td>18 ± 1.7</td>
<td>15 ± 3.5</td>
<td>11 ± 2</td>
<td>15 ± 1.2</td>
<td>14 ± 2.7</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Seed number per shrub (10^3)</td>
<td>3.89 ± 0.58</td>
<td>5.08 ± 0.37</td>
<td>3.98 ± 0.28</td>
<td>4.30 ± 0.64</td>
<td>4.50 ± 0.16</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Reproductive compensatory capacity (%)</td>
<td>0.29 ± 1.99</td>
<td>40 ± 7</td>
<td>40 ± 8</td>
<td>18 ± 4</td>
<td>32 ± 5</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Probability (P) values denote significance levels from ANOVA. Treatment groups indicated by the same letter do not differ statistically significantly from each other.

The photosynthetic rate was measured with a combined portable open gas exchange system (CIRAS-1, PP-System, Hitchin, UK) and measured at the end of July when seed and vegetative growth rates were high. All tested leaves were at a similar developmental stage and were in the upper shoot. Measurements were made during two consecutive days.

Statistical analysis

To examine the effects of clipping on current year shoot number per shoot, net shoot extension, current year shoot biomass per shrub, resprout number per removed shoot, net resprout height, resprout biomass per shrub, biomass allocation (leaf, stem and spine), spine length, leaf phenolic content and photosynthetic rate, we performed a one-way analysis of variance (ANOVA) with clipping treatments as variables. TNC concentrations in roots at each sampling time were compared with repeated measure ANOVA. Multiple comparisons of the level of clipping treatments were performed using the least significant difference (L.s.d.) procedure. Levene’s test was used to verify the assumption of homogeneity of variance. If variances were heterogeneous, data were log transformed or square-root transformed. The relationship between vegetative growth and seed number per shrub, leaf phenolic content, spine biomass and spine length, between seed number per shrub and spine biomass were explored with linear regression.

RESULTS

Seed production

There was a significant effect of clipping on the seed number per shrub (Table 1). Both RSL treatment plants (30 % RSL treatment) and RSN treatment plants (25 and 50 % RSN treatment) produced more seeds than the control plants, but 60 % RSL treatment plants produced fewer
seeds and 100 % RSN treatment plants (all aboveground tissue removed) had no fruit. Control plants produced more flowers in both years, but seed number per shrub was less, owing to lower initial fruit set and higher fruit abortion. Initial fruit set was higher in all treatments in 2005 (a wet year) compared with that in 2004 (a dry year), whereas the reproductive compensatory capacity decreased from 2004 to 2005 (Table 1).

Vegetative regrowth and biomass allocation

*Caragana korshinskii* displayed a considerable ability to compensate for vegetative tissue loss during both years following shoot damage. Clipping increased the vegetative growth biomass and it was higher in all clipping treatment plants than in controls. Current year shoots of control plants almost did not grow at all, and the vegetative growth biomass was <2 g in both years. Within clipping treatments, the vegetative growth biomass in the 100 % RSN treatment group was highest; >200 g in 2004 and >100 g in 2005. The next largest vegetative growth biomass was that after 60 % RSN treatment, and the vegetative growth biomass in other clipping treatments (30 % RSL, 25 % RSN and 50 % RSN) was relatively lower (Table 2). Vegetative growth biomass per shrub decreased from 2004 to 2005 in all clipping treatments.

Clipped shrubs tended to allocate more resources to the growth of current year shoots. Current year shoot number per shoot, net shoot extension and current year shoot biomass per shrub of clipping treatments were significantly different from those of controls in both years. Current year shoot number per shoot of RSL treatment groups was higher than that of RSN treatment groups. In RSL treatment groups, net shoot extension and current year shoot biomass increased with more shoot biomass removal, but this tendency did not appear in RSN treatment groups (Table 2).

The effect of increased shoot number removal on sprout number per removed shoot and net resprout length was not statistically different between 25 and 50 % RSN treatments. However, the value of each variable was less than that of 100 % RSN treatment plants in 2004, suggesting that there existed competition for resources between resprouts and the remaining intact shoots with 25 and 50 % RSN treatments (Table 2). Net resprout height and net resprout biomass in the 100 % RSN treatment group decreased sharply from 2004 to 2005, while they increased in the 25 and 50 % RSN treatment groups.

The results show that there was an effect of clipping on biomass allocation of current year shoots and resprouts. Within RSL treatments, leaf biomass allocation decreased, while stem biomass allocation and spine biomass allocation increased with more shoot biomass removal. Within RSN treatments, current year shoots tended to have higher leaf biomass allocation than resprouts, while the latter tended to have higher stem biomass allocation and spine biomass allocation (Table 3). Biomass allocation in 2005 had a similar pattern to that in 2004, while leaf allocation slightly increased in all clipping treatments at the expense of stem and spine allocation.

**Induced defence**

In both years, spine length was higher in all clipping treatment groups than in controls and, within clipping treatments, it was higher in resprouts than in current year shoots (Table 3). The leaf phenolic content of current year shoots and/or resprouts in clipping treatment groups (30 % RSL, 60 % RSL, 25 % RSN and 50 % RSN) was similar to that of controls, whereas in the 100 % RSN treatment group it was lower in both years. The difference between 100 % RSN and other treatments was significant ($P < 0.001$) (Table 3).

Vegetative growth biomass in clipping treatments was negatively correlated with seed number per shrub, and was not negatively correlated with leaf phenolic content.

### Table 2. Effects of different clipping treatments on performance characters of current year shoot and resprout of *Caragana korshinskii* in 2004 and in the following year (2005) (mean ± s.e., photosynthetic rate, n = 10; other variables, n = 20)

<table>
<thead>
<tr>
<th></th>
<th>Control</th>
<th>30 % RSL</th>
<th>60 % RSL</th>
<th>25 % RSN</th>
<th>50 % RSN</th>
<th>100 % RSN</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>2004</td>
<td></td>
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</tr>
<tr>
<td>Current year shoot number per shoot</td>
<td>3.71 ± 1.01 &amp;</td>
<td>15.67 ± 2.22 &amp;</td>
<td>17.17 ± 1.28 &amp;</td>
<td>13.02 ± 4.94 &amp;</td>
<td>10.64 ± 1.85 &amp;</td>
<td>–</td>
<td>0.007</td>
</tr>
<tr>
<td>Net extension length (cm)</td>
<td>2.88 ± 0.25 &amp;</td>
<td>6.9 ± 1.37 &amp;</td>
<td>10.57 ± 1.33 &amp;</td>
<td>6.7 ± 2.1 &amp;</td>
<td>5.07 ± 0.55 &amp;</td>
<td>–</td>
<td>0.007</td>
</tr>
<tr>
<td>Current year shoot biomass per shrub (g)</td>
<td>1.94 ± 0.99 &amp;</td>
<td>23.79 ± 7.21 &amp;</td>
<td>80.69 ± 23.4 &amp;</td>
<td>31.83 ± 8.08 &amp;</td>
<td>24.17 ± 3.62 &amp;</td>
<td>–</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Resprout number per removed shoot</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Net resprout height (cm)</td>
<td>1.29 ± 0.16b</td>
<td>1.34 ± 0.229b</td>
<td>2.86 ± 0.215c</td>
<td>2.86 ± 0.215c</td>
<td>2.86 ± 0.215c</td>
<td>–</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Total resprout biomass per shrub (g)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Photosynthetic rate ($\mu$mol m$^{-2}$ s$^{-1}$)</td>
<td>9.02 ± 2.16 &amp;</td>
<td>14.34 ± 2.17 &amp;</td>
<td>16.82 ± 1.74 &amp;</td>
<td>11.06 ± 1.41 &amp;</td>
<td>11.96 ± 2.51 &amp;</td>
<td>20.86 ± 2.93 &amp;</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>2005</td>
<td></td>
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<tr>
<td>Current year shoot number per shoot</td>
<td>2.31 ± 0.51 &amp;</td>
<td>8.24 ± 1.41 &amp;</td>
<td>15.31 ± 4.33 &amp;</td>
<td>5.62 ± 2.83 &amp;</td>
<td>7.68 ± 1.58 &amp;</td>
<td>–</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Net extension length (cm)</td>
<td>3.51 ± 0.38 &amp;</td>
<td>5.32 ± 1.38 &amp;</td>
<td>18.92 ± 2.27 &amp;</td>
<td>5.6 ± 1.96 &amp;</td>
<td>5.5 ± 0.53 &amp;</td>
<td>–</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Current year shoot biomass per shrub (g)</td>
<td>1.66 ± 0.63b &amp;</td>
<td>13.94 ± 4.51b &amp;</td>
<td>56.70 ± 15.74b &amp;</td>
<td>7.72 ± 3.76b &amp;</td>
<td>6.52 ± 1.73b &amp;</td>
<td>–</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Net resprout height (cm)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Total resprout biomass per shrub (g)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Photosynthetic rate ($\mu$mol m$^{-2}$ s$^{-1}$)</td>
<td>11.75 ± 0.79 &amp;</td>
<td>18.23 ± 3.56 &amp;</td>
<td>22.02 ± 5.54 &amp;</td>
<td>14.5 ± 3.22 &amp;</td>
<td>14.11 ± 4.19 &amp;</td>
<td>26.31 ± 6.05 &amp;</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Probability ($P$) values denote significance levels from ANOVA. Treatment groups indicated by the same letter do not differ statistically significantly from each other.
Table 3. Effects of different clipping treatments on biomass allocation of current year shoots and resprouts, spine length and leaf phenolic content of Caragana korshinskii in 2004 and in the following year (2005) (mean ± s.e., leaf phenolic content, n = 10; other variables, n = 20)

<table>
<thead>
<tr>
<th></th>
<th>Control</th>
<th>30 % RSL</th>
<th>60 % RSL</th>
<th>25 % RSN</th>
<th>50 % RSN</th>
<th>P</th>
<th>25 % RSN resprout</th>
<th>50 % RSN resprout</th>
<th>100 % RSN resprout</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>2004 Leaf biomass allocation (%)</td>
<td>68.24 ± 6.82&lt;sup&gt;a&lt;/sup&gt;</td>
<td>61.86 ± 5.36&lt;sup&gt;a&lt;/sup&gt;</td>
<td>46.51 ± 4.75&lt;sup&gt;b&lt;/sup&gt;</td>
<td>62.34 ± 4.12&lt;sup&gt;a&lt;/sup&gt;</td>
<td>64.17 ± 2.81&lt;sup&gt;a&lt;/sup&gt;</td>
<td>&lt;0.001</td>
<td>38.93 ± 5.43&lt;sup&gt;c&lt;/sup&gt;</td>
<td>43.25 ± 7.55&lt;sup&gt;b&lt;/sup&gt;</td>
<td>54.83 ± 4.63&lt;sup&gt;a&lt;/sup&gt;</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>2004 Spine biomass allocation (%)</td>
<td>0.62 ± 0.11&lt;sup&gt;c&lt;/sup&gt;</td>
<td>1.26 ± 0.19&lt;sup&gt;b&lt;/sup&gt;</td>
<td>4.21 ± 0.37&lt;sup&gt;a&lt;/sup&gt;</td>
<td>5.78 ± 0.69&lt;sup&gt;a&lt;/sup&gt;</td>
<td>4.83 ± 0.25&lt;sup&gt;a&lt;/sup&gt;</td>
<td>&lt;0.001</td>
<td>10.10 ± 0.76&lt;sup&gt;a&lt;/sup&gt;</td>
<td>9.55 ± 1.12&lt;sup&gt;a&lt;/sup&gt;</td>
<td>7.18 ± 0.67&lt;sup&gt;b&lt;/sup&gt;</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>2004 Stem biomass allocation (%)</td>
<td>30.81 ± 4.85&lt;sup&gt;c&lt;/sup&gt;</td>
<td>37.20 ± 5.78&lt;sup&gt;b&lt;/sup&gt;</td>
<td>40.51 ± 4.38&lt;sup&gt;a&lt;/sup&gt;</td>
<td>30.27 ± 3.86&lt;sup&gt;a&lt;/sup&gt;</td>
<td>30.63 ± 1.61&lt;sup&gt;a&lt;/sup&gt;</td>
<td>&lt;0.001</td>
<td>51.89 ± 3.91&lt;sup&gt;a&lt;/sup&gt;</td>
<td>45.36 ± 5.51&lt;sup&gt;a&lt;/sup&gt;</td>
<td>38.77 ± 3.62&lt;sup&gt;b&lt;/sup&gt;</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>2004 Spine length (mm)</td>
<td>2.40 ± 0.33&lt;sup&gt;c&lt;/sup&gt;</td>
<td>3.50 ± 0.50&lt;sup&gt;b&lt;/sup&gt;</td>
<td>6.66 ± 0.76&lt;sup&gt;a&lt;/sup&gt;</td>
<td>3.66 ± 0.74&lt;sup&gt;b&lt;/sup&gt;</td>
<td>4.16 ± 0.57&lt;sup&gt;b&lt;/sup&gt;</td>
<td>&lt;0.001</td>
<td>6.24 ± 1.32&lt;sup&gt;b&lt;/sup&gt;</td>
<td>6.16 ± 0.28&lt;sup&gt;b&lt;/sup&gt;</td>
<td>8.16 ± 0.52&lt;sup&gt;a&lt;/sup&gt;</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>2004 Leaf phenolic content (mg g⁻¹)</td>
<td>7.79 ± 0.46&lt;sup&gt;a&lt;/sup&gt;</td>
<td>7.83 ± 0.55&lt;sup&gt;a&lt;/sup&gt;</td>
<td>7.64 ± 0.23&lt;sup&gt;a&lt;/sup&gt;</td>
<td>7.47 ± 0.64&lt;sup&gt;a&lt;/sup&gt;</td>
<td>7.66 ± 0.82&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.549</td>
<td>7.31 ± 0.43&lt;sup&gt;a&lt;/sup&gt;</td>
<td>7.52 ± 0.53&lt;sup&gt;a&lt;/sup&gt;</td>
<td>5.19 ± 0.32&lt;sup&gt;b&lt;/sup&gt;</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>2005 Leaf biomass allocation (%)</td>
<td>69.36 ± 4.19&lt;sup&gt;a&lt;/sup&gt;</td>
<td>63.72 ± 5.89&lt;sup&gt;a&lt;/sup&gt;</td>
<td>54.11 ± 5.69&lt;sup&gt;b&lt;/sup&gt;</td>
<td>65.82 ± 5.37&lt;sup&gt;a&lt;/sup&gt;</td>
<td>66.11 ± 3.88&lt;sup&gt;a&lt;/sup&gt;</td>
<td>&lt;0.001</td>
<td>41.13 ± 3.28&lt;sup&gt;c&lt;/sup&gt;</td>
<td>46.39 ± 4.22&lt;sup&gt;b&lt;/sup&gt;</td>
<td>59.64 ± 5.36&lt;sup&gt;a&lt;/sup&gt;</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>2005 Spine biomass allocation (%)</td>
<td>0.61 ± 0.34&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.96 ± 0.24&lt;sup&gt;c&lt;/sup&gt;</td>
<td>3.31 ± 0.71&lt;sup&gt;b&lt;/sup&gt;</td>
<td>4.91 ± 0.83&lt;sup&gt;a&lt;/sup&gt;</td>
<td>3.86 ± 0.31&lt;sup&gt;a&lt;/sup&gt;</td>
<td>&lt;0.001</td>
<td>7.46 ± 0.33&lt;sup&gt;a&lt;/sup&gt;</td>
<td>7.97 ± 1.21&lt;sup&gt;a&lt;/sup&gt;</td>
<td>6.59 ± 0.81&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.036</td>
</tr>
<tr>
<td>2005 Stem biomass allocation (%)</td>
<td>29.68 ± 5.37&lt;sup&gt;c&lt;/sup&gt;</td>
<td>35.19 ± 3.52&lt;sup&gt;b&lt;/sup&gt;</td>
<td>43.37 ± 4.14&lt;sup&gt;a&lt;/sup&gt;</td>
<td>29.61 ± 2.49&lt;sup&gt;a&lt;/sup&gt;</td>
<td>29.75 ± 1.46&lt;sup&gt;a&lt;/sup&gt;</td>
<td>&lt;0.001</td>
<td>50.28 ± 2.64&lt;sup&gt;a&lt;/sup&gt;</td>
<td>46.13 ± 3.50&lt;sup&gt;b&lt;/sup&gt;</td>
<td>34.17 ± 2.36&lt;sup&gt;c&lt;/sup&gt;</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>2005 Spine length (mm)</td>
<td>2.30 ± 0.41&lt;sup&gt;c&lt;/sup&gt;</td>
<td>3.12 ± 0.50&lt;sup&gt;b&lt;/sup&gt;</td>
<td>4.26 ± 0.22&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2.93 ± 0.54&lt;sup&gt;a&lt;/sup&gt;</td>
<td>3.02 ± 0.55&lt;sup&gt;b&lt;/sup&gt;</td>
<td>&lt;0.001</td>
<td>4.11 ± 0.55&lt;sup&gt;a&lt;/sup&gt;</td>
<td>5.44 ± 0.36&lt;sup&gt;b&lt;/sup&gt;</td>
<td>6.06 ± 0.41&lt;sup&gt;a&lt;/sup&gt;</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>2005 Leaf phenolic content (mg g⁻¹)</td>
<td>7.28 ± 0.35&lt;sup&gt;a&lt;/sup&gt;</td>
<td>7.19 ± 0.55&lt;sup&gt;a&lt;/sup&gt;</td>
<td>7.05 ± 0.31&lt;sup&gt;a&lt;/sup&gt;</td>
<td>7.6 ± 0.36&lt;sup&gt;a&lt;/sup&gt;</td>
<td>6.94 ± 0.73&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.261</td>
<td>7.51 ± 0.38&lt;sup&gt;a&lt;/sup&gt;</td>
<td>6.82 ± 0.56&lt;sup&gt;a&lt;/sup&gt;</td>
<td>5.23 ± 0.45&lt;sup&gt;b&lt;/sup&gt;</td>
<td>&lt;0.001</td>
</tr>
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</table>

Probability (P) values denote significance levels from ANOVA. Treatment groups indicated by the same letter do not differ statistically significantly from each other.
whereas it was significantly positively correlated with spine length and spine biomass in both years. Seed number per shrub, in turn, was negatively correlated with spine biomass (Table 4).

**TNC concentrations in root tissues**

There was dramatic seasonal variation in the concentrations of TNC in roots. During flower bud development and the flush of new foliage, TNC concentrations in clipping treatment groups were lowest. TNC concentrations in control plants had a similar pattern of change to clipped plants, but these were less dramatic. Differences were statistically significant, reflecting the fact that clipped plants transported more carbohydrates from root to support aboveground tissue growth and development. Accumulation of TNC in roots in clipping treatment plants increased quickly after July. However, there was no statistical difference between control plants and clipped plants on 6 August 2004 when fruit ripened (Fig. 1A). The change in the patterns of TNC concentrations in 2005 was similar to that in 2004. However, clipped shrubs drew upon fewer carbohydrates from the root (TNC concentrations in roots of clipping treatment plants increased quickly after July. 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because the cost of regrowth is high in such environments and thus investment in defence to prevent organ loss should be favoured (Grime, 1977). However, in this study, *C. korshinskii* showed high regrow capacity to compensate for shoot loss.

The regrow capacity of *C. korshinskii* could be due to the presence of dormant buds, their activation sensitivity in relation to the tissue loss (Marquis, 1996) and shoot extension length. Intensive clipping treatments (60% RSL and 100% RSN) in which all uppermost meristems were removed prompted more side shoots to sprout and showed higher vegetative regrowth than other treatments. After clipping and defoliation, woody species usually regrow long shoots (du Toil *et al.*, 1990; Bilbrough and Richards, 1993; Riba, 1998), which is an important component of tolerance (Bilbrough and Richards, 1993). Although long shoots constitute a potentially greater energetic investment than short-shoots, such tissue will be able to make damaged *C. korshinskii* gain vertical stature as quickly as possible in a disturbed environment as a competitive advantage of establishing apical dominance.

Within populations, the ability of a plant to compensate for tissue loss appears to be positively related to factors that determine its ability to acquire energy, such as growing season (Oba, 1994; Bush and Vanauken, 1995; Alados *et al.*, 1997), branch size (Honkanen and Haukioja, 1994), fertilization and lack of competition (Mutikainen and Walls, 1995), light availability (Lentz and Cipollini, 1998) and between-shoot competition for nutrients (du Toil *et al.*, 1990). Sexual production normally requires large amounts of resources. As a result of the costs associated with the development of reproductive structures, allocation to other functions, including vegetative reproduction, can be reduced (Sutherland and Vickery, 1988; Reekie, 1991; Westley, 1993). The observation is also confirmed by our data, as vegetative growth biomass was higher with 100% RSN treatment, in which plants had no fruit.

An overall picture of reproduction in *C. korshinskii* shows that control plants invested more in reproduction (flowering), but they had the greatest number of aborted flowers and fruits during 2 years of growth. In contrast, clipped plants invested less in reproduction (flowering) but ultimately they produced a higher number of seeds in the moderate clipping treatment groups (30% RSL, 25% RSN and 50% RSN) than the controls. Previous research has shown that, after initial fruit set, fruit development is especially carbon supply, as has been suggested for cotton (Guinn, 1982), apple (Berüter and Droz, 1991) and pistachio (Nzima *et al.*, 1999). The results of our study suggest that reproductive tissues of clipping treatment groups had more resources available, early from roots and late from an elevated photosynthetic rate, and accordingly had higher fruit set and lower fruit abortion.

Several hypotheses have been proposed to explain the selective advantages of surplus flowers and juvenile fruit production. These hypotheses fall into three broad categories: (a) uncertainties surrounding pollination, fruit/seed predation, and resource availability; (b) the male role of hermaphroditic flowers; and (c) the improvement in fruit/seed quality acquired by selective abscission (Stephenson, 1981). Surplus flower production by *C. korshinskii* is probably a bet-hedging strategy, because it allows plants to take advantage of the occasional ‘good years’ when resources are plentiful. In 2005, all treatments, especially the control, had higher initial fruit set compared with in 2004. In ‘bad years’, the plant is physiologically incapable of providing all the necessary resources to develop mature fruits from all flowers and aborts a portion of flowers and fruits to meet resource limitations and to control offspring quality (Stephenson and Winsor, 1986; Stearns, 1992).

On the other hand, there were indications that shoot removal induced physical defences (spine biomass allocation and spine length), but no chemical defence (phenol). Although many studies have shown that defoliated plants accumulate defensive compounds in leaves (Tuomi *et al.*, 1984; Kamata *et al.*, 1996), we observed that the leaf phenolic content in clipped plants was lower than or similar to that in the control plants. Pisani and Distel (1999) reported that the phenolic content in stump sprouts of *Prosopis caldenia* was higher than or similar to that in the controls, whereas in *Prosopis flexuosa* it was lower than that in the control. A lower leaf phenolic content in the 100% RSN treatment group in our study in both years suggests that the effect of clipping on the leaf phenolic content of *C. korshinskii* only appeared in cases of extensive clipping treatment (up to a certain threshold). The findings of lower or similar leaf phenolic content, greater spine length and more spine production suggest that during the phase of regrowth of *C. korshinskii*, protection of stems may be more important than protection of leaves in order to become established quickly in the disturbed environment.

The hypothesis suggests that plants respond to natural enemies by either allocating resources to defensive resistance traits or compensating for damage through a growth-related response (van der Meijden *et al.*, 1988; Fineblum and Rausher, 1995; Sagers and Coley, 1995). Our results show that *C. korshinskii* combined tolerance and defence strategies to respond to shoot removal. With more potential flower bud removal, clipped shrubs shifted resources from roots and elevated photosynthesis to support vegetative regrowth, whereas an increase in spine biomass allocation may protect stems against herbivores (Gowda, 1996). *Caragana korshinskii* is a long-lived plant and the costs of fruit production and vegetative growth might be expressed in terms of reduced future growth, reproduction or survival, but this is by no means certain (Vail, 1992; Paige, 1999).

After damage, the balance between above- and below-ground resource uptake is shifted. Clipped shrubs have less water and nutrient stress, resulting in more nutrients and water available per unit area of remaining source leaf (Saruwatari and Davis, 1989; Fleck *et al.*, 1996; Thomson *et al.*, 2003). These relative increases in water and nutrient availability induce plants to use their absorbed light more efficiently. With more resource availability from roots and an increased photosynthetic rate, clipped shrubs allocate more resources to sexual production, vegetative regrowth and defence. However, the ability for compensation and
defence will decrease sharply and then slowly during the following years as available nutrients and water decline with vegetation growth, as indicated by vegetative growth, reproductive compensatory capacity and induced defence decreasing from 2004 to 2005. Vegetative growth may not compensate and defence may not increase any more once the balance between the above- and belowground status of the damaged shrub is restored as equal to that of controls. Caragana korshinskii is widespread in arid and semi-arid areas in north-western China, especially in desert, semi-desert zones and Loess Plateau (Wang et al., 2001), and is capable of regenerating from vegetative reproduction and recruiting new individuals from seeds (Wang et al., 1995), facts which are confirmed by our data. However, the increase in induced physical defence contributes to increasing vegetative reproduction through protecting stems against herbivores.

In summary, C. korshinskii responded to shoot removal via tolerance and induced defence strategies. Under different levels of damage, plants allocated different resources to the same function. With more potential flower bud removal, clipped shrubs mobilized more resources from roots and elevated photosynthesis in order to support vegetative regrowth, whereas an increase in spine biomass allocation was to protect stems against herbivores. In this case, tolerance and defence may have evolved as a consequence of adaptation to the disturbed environment.

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