Impact of Biological Control on Two Knapweed Species in British Columbia

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Abstract
Diffuse and spotted knapweed (Centaurea diffusa Lam and C. stoebe L.) are two closely related invasives found in many parts of British Columbia’s Southern Interior, causing substantial economic losses in rangelands. Beginning in 1970, the provincial government initiated a long-term biological control effort against the knapweeds, introducing 10 different insect agents from 1970 to 1987. In an effort to evaluate the efficacy of the program, archival (1983–2008) data was amassed from 19 vegetation monitoring sites that contained knapweed. In 2010, these sites were relocated and re-monitored and cover values were analyzed. Diffuse knapweed showed significant declines at 14 of 15 sites; spotted knapweed declined at three of four sites. Possible alternative explanations for the decline are discussed. Evidence strongly points to a suite of biocontrol agents (seed feeders and root feeders) as the primary drivers of knapweed decline in British Columbia’s Southern Interior.

KEYWORDS: biological control; British Columbia; Centaurea; knapweed; monitoring

Introduction
Diffuse knapweed (Centaurea diffusa Lam.) and spotted knapweed (Centaurea stoebe L.) are two introduced, closely related invasive forbs. These species are most common in the northwestern United States and in western Canada. Centaurea stoebe (also referred to as C. maculosa Lam. and C. biebersteinii DC) is particularly widespread, reported in 45 US states and all provinces of Canada (Marshall 2004; Zouhar 2001). The drought-tolerant C. diffusa has an altitudinal range of 150–900 m, whereas C. stoebe favours mesic sites and is found from sea level up to 1200 m (Watson & Renney 1974). Isolated C. stoebe populations are now found as high as 1700 m (B.C. Ministry of Forests, Lands and Natural Resource Operations 2012). Both species are tap-rooted, insect-pollinated, biennials or short-lived perennials. A single plant can produce as many as 900 seeds, which remain viable for up to 7 years. Infested areas can have soil banks of up to 40 000 seeds per square metre (Watson & Renney 1974; Davis et al. 1993; Sheley & Jacobs 1998). Seedlings form ground-oriented rosettes; bolted plants have either a single stem (C. diffusa) or multiple stems (C. stoebe).

In British Columbia, both knapweeds are found in the dry valleys and plateaus of the Southern Interior, primarily in the Bunchgrass, Ponderosa Pine, and dry phases of the Interior Douglas-fir biogeoclimatic zones. Typical habitat for C. diffusa is semi-arid native
bunchgrass rangeland and adjacent open ponderosa pine woodland. Both of these vegetation types support high biodiversity, as well as concentrations of species at risk, and both face other threats from land conversion, fire suppression, and overgrazing (Austin et al. 2008). Centaurea stoebe extends into the Interior Cedar-Hemlock and Montane Spruce biogeoclimatic zones, typically along forest roads and in cutblocks and can negatively affect regenerating tree seedlings (Powell et al. 1997).

The provincial Invasive Alien Plant Database shows current C. diffusa distribution extending northward to around Williams Lake (52°7' latitude) and C. stoebe reaching to Fort St. John (56°10' latitude), with isolated populations at the Yukon border (B.C. Ministry of Forests, Lands and Natural Resource Operations 2012; see Figure 1). The first North American report of C. stoebe was by Macoun in Victoria, B.C., in 1893 (Groh 1943). Centaurea diffusa was first reported in Grand Forks, B.C., in 1925 and subsequently in the Okanagan Valley in the late 1930s (Groh 1943). Starting in the 1970s, both species began a period of rapid expansion in British Columbia and the US Pacific Northwest (Sheley & Jacobs 1998; Newman et al. 2011).

![Figure 1: Distribution of (a) Centaurea diffusa and (b) C. stoebe in British Columbia (B.C. Ministry of Forests, Lands and Natural Resource Operations 2012).](image)

The impact of the knapweeds is both ecological and economic. Ortega and Pearson (2005) characterized C. stoebe as a “strong invader” in the rangelands of western Montana. Although both knapweed species typically invade after soil disturbance, wildfire, or overgrazing, they can also invade pristine native habitats (Tyser & Kay 1988; Ferguson et al. 2007; Duncan et al. 2011). Researchers have found greater surface water runoff and increased sediment loading in areas affected by C. stoebe (Lacey et al. 1989). Neither species is preferred forage for wild or domestic ungulates, but immature plants will be grazed when more desirable forage is in short supply. Watson and Renney (1974), working in the British Columbia Interior, found a negative correlation between knapweed biomass and available livestock forage. They also found that palatable forage underneath a knapweed canopy was poorly utilized.

Economic damage caused by knapweed in the United States has been well reported elsewhere (Griffith & Lacey 1991; Hirsch & Leitch 1996). In British Columbia, Frid et al. (2009) estimated cumulative economic losses at $20 million (for C. diffusa only) based on a 43% loss of forage production, soil erosional losses, and loss of recreational values in infested rangelands. Both species are on the province’s noxious weed list.2 Traditional weed control methods (i.e., herbicide application, mowing, burning, reseeding, etc.) have had very limited success in controlling knapweeds (Sheley & Jacobs 1998).
Biological control

Following a successful biocontrol initiative against St. John’s-wort (*Hypericum perforatum* L.) in the early 1950s, the provincial government began an aggressive campaign against the knapweeds. They opted for the “classical” approach, searching for insect agents that would self-perpetuate, self-distribute, and create a long-term balance between insect and weed (Powell et al. 1994). The first knapweed agent releases (*Urophora affinis* and *U. quadrifasciata*), small flies whose larvae feed on developing seeds, attack both knapweed species. Later releases included beetle and moth species, some of which feed on knapweed roots (Bourchier et al. 2002; De Clerck-Floate & Carcamo 2011). Early releases were concentrated in the West Kootenay, Boundary, and Kamloops areas, with subsequent propagation and redistribution as the insect habitat preferences became known. With the exception of *Chaetorellia acrolophi*, *Pelochrista medullana*, and *Pterolonche inspersa*, all other knapweed bioagents have now established self-perpetuating populations (see Table 1).

<table>
<thead>
<tr>
<th>Insect</th>
<th>Type</th>
<th>Host knapweed (C. diffusa or C. stoebe)</th>
<th>Year of introduction</th>
<th>Year of first operational redistribution</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Seed feeders:</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Urophora affinis</em></td>
<td>Fly</td>
<td>Both</td>
<td>1970</td>
<td>1977</td>
</tr>
<tr>
<td><em>Urophora quadrifasciata</em></td>
<td>Fly</td>
<td>Both</td>
<td>1972</td>
<td>1977</td>
</tr>
<tr>
<td><em>Chaetorellia acrolophi</em></td>
<td>Fly</td>
<td><em>C. stoebe</em></td>
<td>1991</td>
<td>Not operational yet</td>
</tr>
<tr>
<td><em>Metzneria paucipunctella</em></td>
<td>Moth</td>
<td><em>C. stoebe</em></td>
<td>1981</td>
<td>Not operational yet</td>
</tr>
<tr>
<td><em>Larinus minutus</em></td>
<td>Beetle</td>
<td><em>C. stoebe</em></td>
<td>1991</td>
<td>1994</td>
</tr>
<tr>
<td><em>Larinus obtusus</em></td>
<td>Beetle</td>
<td>Both: prefers <em>C. stoebe</em></td>
<td>1992</td>
<td>1999</td>
</tr>
<tr>
<td><em>Root feeders:</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Sphenoptera jugoslavica</em></td>
<td>Beetle</td>
<td>Mainly <em>C. diffusa</em></td>
<td>1976</td>
<td>1985</td>
</tr>
<tr>
<td><em>Agapeta zoegana</em></td>
<td>Moth</td>
<td>Both: prefers <em>C. stoebe</em></td>
<td>1982</td>
<td>1992</td>
</tr>
<tr>
<td><em>Pelochrista medullana</em></td>
<td>Moth</td>
<td>Both: prefers <em>C. diffusa</em></td>
<td>1982</td>
<td>Not operational yet</td>
</tr>
<tr>
<td><em>Pterolonche inspersa</em></td>
<td>Moth</td>
<td>Both: prefers <em>C. diffusa</em></td>
<td>1986</td>
<td>Not operational yet</td>
</tr>
<tr>
<td><em>Cyphocleonus achates</em></td>
<td>Beetle</td>
<td>Both: prefers <em>C. stoebe</em></td>
<td>1987</td>
<td>1992</td>
</tr>
</tbody>
</table>

Over the past few years, there have been numerous field reports of observed declines in knapweed populations in the province’s Interior. We undertook the project reported here to provide program managers with objective answers to the following questions.

1. Are knapweed populations declining?

2. If populations are declining, what are the possible causes for the decline?

Comparing historical and contemporary vegetation cover data is one of several tools for assessing biocontrol impacts (Morin et al. 2009). Visual assessment of vegetation cover values is a commonly used technique for detecting changes in species dominance in herbaceous plant communities (Daubenmire 1959; Elzinga et al. 1998). Thus, we undertook a broad-scale, metadata survey of previously documented knapweed sites to answer the first question.
Methods

A large number of existing provincial government vegetation data records were scanned. Previous analysis (Gayton 2004) directed us to several areas close to the United States border as invasive plant hotspots. We were fortunate in locating archival data sets for 19 different sites, all of which listed either C. diffusa or C. stoebe. The data sets were either from weed monitoring or livestock grazing impact studies; all sites were located on Crown land. For the knapweed-positive sites that had not been re-monitored recently, a further sort was done to determine whether:

1. the monitoring transects could be relocated, and
2. the monitoring methodology was sufficiently explicit to allow precise re-monitoring.

This latter set of “historical sites” were relocated and re-monitored. These sites had been originally monitored using different variants (foliar and canopy cover; 6-class and 7-class) of the Daubenmire frame methodology (Daubenmire 1959). These were re-monitored with a Daubenmire frame, using the currently preferred method of estimating foliar values to the percent. Re-monitoring cover value averages were compared against cover class midpoints from the archival data. For the sites that were originally monitored using canopy cover, foliar cover re-monitoring values were multiplied by a factor of four to make the data equivalent. One site was originally monitored using the point-intercept method, and so this method was also used for the re-monitoring. The number of observations per site varied from 25 to 100, ranged along 1–5 separate transects. The minimum number of repeat monitoring events was two, the maximum six, with an average of three monitoring events per site. The earliest monitoring event was 1983; the latest occurred in 2010. Site locations are shown in Figure 2, and individual site descriptions and data are tabulated in the appendix at the end of this article. Raw data was located for 13 of the 19 sites, so variances were calculated for those.

The sites were located in the Thompson, Salmon, Nicola, Okanagan, Kettle, and Kootenay river valleys, between 355 and 1010 m, with an average elevation of 700 m, and lying within the Bunchgrass and dry phases of the Ponderosa Pine and Interior Douglas-fir biogeoclimatic zones. These were primarily grassland sites, mid-seral examples of the Pacific Northwest Bunchgrass type (Daubenmire 1988) of which these areas form a northern extension. Typical dominant native grasses were Pseudoroegneria spicata (Pursh) A. Löve, Achnatherum occidentale (Thurber) Barkw., and Hesperostipa comata (Trin. & Rupr.) Barkw.; leading introduced species were Bromus tectorum L., Bromus japonicus (Thunb.), Poa pratensis L., and Potentilla recta L.

Livestock grazing is a potential factor in knapweed population dynamics, so the grazing status for each site was noted. The eight Range Reference Area (RRA) sites consisted...
of 1 ha grazing exclosures with an adjacent grazed control; grazing ceased in the “ungrazed” RRA treatments the year prior to first monitoring. Adjacent grazed and ungrazed treatments were considered as separate sites.

**Results and discussion**

Diffuse knapweed cover declined in 14 of 15 sites; at 11 of the 14 sites no plants were found on the transects at the last monitoring event (see Figure 3). The single exception was Pickering Hills RRA (graph reference “9” in the Appendix), but knapweed presence at this site was minimal, with cover values never exceeding 3% in the five separate monitoring years. At Johnstone Creek Weed Transects (graph reference “2” in the Appendix), cover values declined but were still at 25% in 2010. This site is immediately adjacent to a highway and an access road, and the persistence of knapweed there may be the result of periodic vehicular disturbances. Spotted knapweed cover values declined at three of four sites (see Figure 4). The persistent population at Westwold Station (graph reference “b” in the Appendix) may be due to the slightly cooler and wetter conditions, high levels of livestock disturbance, later insect release dates, or a combination of these factors. In spite of small individual sample sizes and variable data, a composite downward cover value trend is apparent for both species.
The possible proximal causes for the knapweed decline (the second research question) are:

- hand pulling or herbicide use,
- changed weather patterns,
- altered grazing regimes resulting in a more competitive native plant community, and (or)
- the impact of biocontrol agents.

The wide dispersion of knapweed biocontrol agents renders a comparison with a non-attacked control site impossible; thus we must examine the alternative explanations. Spraying and hand pulling of knapweeds was ongoing during the period studied; however, it was confined to new and peripheral infestations along roadsides. Insect biocontrol monitoring and release sites, as well as range reference areas, were specifically excluded from the spraying and hand-pulling program.

Weather is a possible driver of knapweed decline. To test correlations with changing weather patterns, *C. diffusa* cover trends from a group of sites clustered around Midway, B.C., were visually compared with mean annual precipitation and growing season degree-day data from this community (Wang et al. 2009; see Figure 5). Precipitation trended downward and degree-days upward during the period studied, increasing stress on the entire plant community. However, the 1999–2003 period showed a reversed trend toward warmer, drier conditions, but no corresponding increase in knapweed cover was detected. The warmest and driest years for the Midway sites during the period of analysis are still well within the climatic ranges for *C. diffusa*-infested rangelands as cited by Watson & Renney (1974) (see Table 2). In addition, the geographical ranges of both knapweeds extend southward into regions both warmer and drier than the British Columbia Interior (U.S. Department of Agriculture 2011).

### Table 2: Comparison of knapweed climate parameters as per Watson & Renney (1974) with values from Midway, B.C., 1983–2009

<table>
<thead>
<tr>
<th>Climatic range of knapweed infested areas, British Columbia Interior</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mean annual precipitation</strong></td>
<td><strong>Mean annual temperature</strong></td>
</tr>
<tr>
<td>241–417 mm</td>
<td>7.2–9.4°C</td>
</tr>
<tr>
<td><strong>Driest and warmest years, Midway, B.C., 1983–2009</strong></td>
<td></td>
</tr>
<tr>
<td>(1985) 345 mm</td>
<td>(1998) 8.8°C</td>
</tr>
</tbody>
</table>
Drought stress has been identified as a source of seedling mortality in *C. diffusa* (Myers & Berube 1983; Powell 1990); however, Powell (1990) demonstrated that a majority of the established rosettes that died during midsummer drought also showed signs of attack by *S. jugoslavica*. Corn et al. (2007) grew *C. stoebe* in field trials under different soil moisture regimes. These trials revealed that both total plant biomass and plant height were relatively insensitive to moisture deficit but were negatively affected by the presence of biocontrol agent *Cyphocleonus achates*. Story et al. (2006) monitored *C. stoebe* in western Montana from 1993 to 2004, during which time plant density declined significantly, despite above-average precipitation in 7 years of the study. Broenniman et al. (2007) also demonstrated that *C. stoebe* is capable of niche shifts, enabling it to adapt to drier, warmer North American environments. Blumenthal et al. (2008) analyzed the effects of moisture on *C. stoebe* seeded into experimental plots of established native rangeland. Establishment was favoured more by added winter snowfall than by added summer irrigation.

Alien species invasion into rangelands is affected both by livestock and wildlife through preferential grazing on the native plant community, animal transport, and soil disturbance. Vigorous native plant communities can impose competitive stresses on invasive plant populations (Maron & Marler 2007), and plant vigour is affected by grazing by livestock and wildlife. Crown grazing management improved through the 1970s and 1980s, with cross-fencing, pasture rotations, and water developments. These activities could, after a lag period, be responsible for enhanced range condition and resulting knapweed suppression. Our metadata analysis fortunately included three adjacent grazed/ungrazed comparison sites. All three are subject to permitted livestock grazing plus deer use; the Johnstone Creek and Murray Gulch sites are also subject to elk grazing. The Fairview Meadow and Johnstone Creek ungrazed treatments excluded livestock only; the Murray Gulch RRA ungrazed site excluded all ungulates. Livestock stocking rates and rotations did not change significantly at any of the sites during the period of analysis. Based on these grazed/ungrazed comparisons, grazing appeared to retard but not eliminate the downward *C. diffusa* trend (see Figure 6).

Based on the above information, weather and grazing may have indirect effects but do not appear to be the primary drivers of the observed knapweed decline. This conclusion mirrors that of the more in-depth study conducted by Newman et al. (2011) in the Kamloops area.

**Biocontrol impacts on knapweed**

In this study, we were able to secure a limited amount of relevant biocontrol agent attack monitoring data that was collected close (< 500 m) to two of the knapweed monitoring sites (see Figure 7). Johnstone Creek and East Midway showed increasing insect attack rates in the years leading up to the period of knapweed decline; attack rates in East Midway declined simultaneous with reductions in knapweed cover (Table 3).
Several existing studies link insect biocontrol agents to knapweed decline (see, for example, Figure 8). In field cage treatments in the south Okanagan, Myers et al. (2009) showed decreased numbers of seedlings, rosettes, and bolted *C. diffusa* plants in cages with *Larinus minutus* added, compared to both caged and uncaged controls. They also reported a decline in *C. diffusa* flowering stems at three of four Southern Interior sites between 1978 and 2009. Stephens et al. (2009) reported annual declines in *C. diffusa* cover in the White Lake Basin (south Okanagan). Five different knapweed biocontrol insects were either seen or known to have been released in the Basin, beginning in the 1970s. Story et al. (2006) monitored spotted knapweed plant density over an 11-year period (1993–2004) at two sites in western Montana where *Cyphocleonus achates* was released. Spotted knapweed density declined significantly over time at both sites (99 and 77%, respectively), after *C. achates* numbers increased at both sites. Corn et al. (2006) found increasing mortality in *C. stoebe* with increasing numbers of *C. achates* in experimental plots.

Table 3: Years of *S. jugoslavica* release and rates of attack

<table>
<thead>
<tr>
<th>Site</th>
<th>Year of first release</th>
<th>Year (% attack)</th>
<th>Year (% attack)</th>
<th>Year (% attack)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Johnstone Creek</td>
<td>1986</td>
<td>1987 (0)</td>
<td>1990 (63)</td>
<td>—</td>
</tr>
<tr>
<td>West Midway</td>
<td>1985</td>
<td>1987 (10)</td>
<td>1990 (35)</td>
<td>2010 (no knapweed)</td>
</tr>
<tr>
<td>East Midway</td>
<td>1985</td>
<td>1988 (98)</td>
<td>1990 (41)</td>
<td>2010 (no knapweed)</td>
</tr>
</tbody>
</table>
Conclusions
The preponderance of descriptive evidence in this study points to the biocontrol program as the most plausible explanation for a decline in *C. diffusa* and *C. stoebe* cover values at representative sites in British Columbia’s Southern Interior, a conclusion supported by the studies cited above. We think a key turning point was the release and dispersal of root-feeding insects in the 1990s. The additive effect of root feeders combined with seed feeders offers a plausible explanation for the rapid knapweed collapse, and conforms to the logic of the cumulative stress hypothesis of Knochel et al. (2010). *Centaurea diffusa* appears to be more susceptible to current biocontrol agents than *C. stoebe*, but there was not enough data for a full comparison.

Frid et al. (2009) estimated the return on biocontrol investment for *C. diffusa* in British Columbia at $17 for each dollar spent. In addition to the economic value of low-elevation bunchgrass and open ponderosa pine ecosystem types in the province’s Southern Interior, these ecosystems support very high biodiversity and concentrations of species at risk (Austin et al. 2008). Even though direct negative impacts of invasive plants on biodiversity and species at risk are difficult to prove (Davis 2003), we should invoke the precautionary principle and assume the knapweeds and other invasive plant species have negative ecological impacts on these biodiverse, spatially limited ecosystems, and continue the use of biological control as a component of a proactive, integrated invasive plant control effort.

Notes


References


### Appendix: Site description and data for knapweed study sites

<table>
<thead>
<tr>
<th>Location/species/site description</th>
<th>Graph reference</th>
<th>No. of observations</th>
<th>Year of monitoring/cover values (SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>McLellan RRA Gully (C. diffusa)</strong></td>
<td>PPxh1a, 600 m, ungrazed</td>
<td>14</td>
<td>1998/0.7 (0.1) 2010/0.1 (0.02)</td>
</tr>
<tr>
<td><strong>Fairview RRA Meadow (C. diffusa)</strong></td>
<td>PPxh1a, 565 m, ungrazed</td>
<td>12</td>
<td>1998/1.4 (0.2) 2010/0</td>
</tr>
<tr>
<td><strong>Fairview RRA Meadow (C. diffusa)</strong></td>
<td>PPxh1a, 565 m, grazed</td>
<td>10</td>
<td>1998/1.9 (0.2) 2010/0</td>
</tr>
<tr>
<td><strong>Osoyoos Desert Centre (C. diffusa)</strong></td>
<td>BG, 355 m, ungrazed</td>
<td>4</td>
<td>1998/36.0 2000/9.30 2001/1.00 2002/0.50 2009/0</td>
</tr>
<tr>
<td><strong>Johnstone Creek RRA (C. diffusa)</strong></td>
<td>IDFxh4, 950 m, ungrazed</td>
<td>11</td>
<td>1997/1.5 (0.4) 2010/0</td>
</tr>
<tr>
<td><strong>Johnstone Creek RRA (C. diffusa)</strong></td>
<td>IDFxh4, 950 m, grazed</td>
<td>13</td>
<td>1997/1.1 (0.3) 2010/0.7 (0.3)</td>
</tr>
<tr>
<td><strong>Johnstone Creek Weed Transects (C. diffusa)</strong></td>
<td>IDFdm1, 800 m, grazed</td>
<td>7</td>
<td>1995/3.6 (0.9) 2000/12.1 (2.4) 2010/1.1 (0.6)</td>
</tr>
<tr>
<td><strong>East Midway Sphenoptera Release (C. diffusa)</strong></td>
<td>PPxh3, 650 m lightly grazed</td>
<td>2</td>
<td>1986/38.7 (3.6) 1997/17.2 (2.7) 2005/1.21 (0.6)</td>
</tr>
<tr>
<td><strong>Erickson Transect (C. diffusa)</strong></td>
<td>PPxh3, 950 m, grazed</td>
<td>6</td>
<td>1983/0 1998/16.1 (1.0) 2010/0</td>
</tr>
<tr>
<td><strong>Murray Gulch RRA (C. diffusa)</strong></td>
<td>PPxh3, 910 m, ungrazed</td>
<td>15</td>
<td>1996/0.4 2002/0.2 2009/0</td>
</tr>
<tr>
<td><strong>Murray Gulch RRA (C. diffusa)</strong></td>
<td>PPxh3, 910 m, grazed</td>
<td>8</td>
<td>1996/2.9 2002/4.4 2009/0.4</td>
</tr>
<tr>
<td><strong>West Midway Sphenoptera Release (C. diffusa)</strong></td>
<td>PPxh3, 585 m, lightly grazed</td>
<td>1</td>
<td>1986/34.8 (3.6) 1990/72.8 (7.4) 1998/38.5 2010/0</td>
</tr>
<tr>
<td><strong>Bunchgrass Hill Weed Transects (C. diffusa)</strong></td>
<td>IDFdm1, 800 m, grazed</td>
<td>7</td>
<td>1995/3.6 (0.9) 2000/12.1 (2.4) 2010/1.1 (0.6)</td>
</tr>
<tr>
<td><strong>Overton Moody Transect (C. diffusa)</strong></td>
<td>PPxh3, 585 m, grazed</td>
<td>5</td>
<td>1983/0.15 (0.08) 1998/17.2 (2.7) 2005/1.21 (0.6) 2010/0</td>
</tr>
<tr>
<td><strong>Pickering Hills RRA (C. diffusa)</strong></td>
<td>IDFdm2, 1010 m, ungrazed</td>
<td>9</td>
<td>1992/3.0 1993/4.0 1994/3.50 2007/0.90 2009/1.70</td>
</tr>
<tr>
<td><strong>Coldwater (C. stoebe)</strong></td>
<td>PPxh2, 705 m, grazed</td>
<td>a</td>
<td>1993/16.4 1997/38.3 2008/2.66</td>
</tr>
<tr>
<td><strong>Wallachin (C. stoebe)</strong></td>
<td>PPxh2a, 600 m, grazed</td>
<td>d</td>
<td>1993/4.4 1995/3.2 1997/9.6 2001/10.4 2008/1.09</td>
</tr>
<tr>
<td><strong>Promontory (C. stoebe)</strong></td>
<td>PPxh2, 820 m, ungrazed</td>
<td>c</td>
<td>1993/0.6 1995/6 1997/17.2 2001/11.4 2008/0</td>
</tr>
<tr>
<td><strong>Westwold Station (C. stoebe)</strong></td>
<td>IDFxh2a, 690 m, ungrazed</td>
<td>b</td>
<td>1996/17.5 2001/36.6 2008/37</td>
</tr>
</tbody>
</table>

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**Notes:**

- **a:** Biogeoclimatic zone abbreviations: BG = Bunchgrass; IDF = Interior Douglas-fir; PP = Ponderosa Pine.
- **b:** Numbers refer to site references in Figure 3; letters refer to site references in Figure 4.
- **c:** Standard error appears in parentheses.
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Test Your Knowledge

How well can you recall the main messages in the preceding article? Test your knowledge by answering the following questions.

Impact of Biological Control on Two Knapweed Species in British Columbia

1. Spotted knapweed (Centaurea stoebe) was first identified in British Columbia in:
   a) 1893
   b) 1925
   c) 1972

2. The most effective type of biocontrol insect on knapweed appears to be:
   a) Stem miner
   b) Root feeder
   c) Leaf feeder

3. Knapweed populations are affected by biological control insects, but they can also be affected by:
   a) Native insect attacks
   b) Plant diseases
   c) Weather variations

ANSWERS: 1=a; 2=b; 3=c.