

# A review of the biology of the weedy Siberian peashrub, *Caragana arborescens*, with an emphasis on its potential effects in North America

Katelyn B. SHORTT and Steven M. VAMOSI\*

*Department of Biological Sciences, University of Calgary, Calgary, Canada T2N 1N4*

(Received June 9, 2010; Accepted December 29, 2011)

**ABSTRACT.** The introduction and establishment of non-native species has been recognized as one of the most significant threats to the maintenance of native biodiversity in most taxa, including angiosperms. The Siberian peashrub, *Caragana arborescens* Lam. (Fabaceae), is native to Eurasia, but was introduced to North America in the mid-1700s. In the past 250 years, the species has become established in almost all of Canada, and approximately half of the states in the USA. However, the literature on its potential effects on native ecosystems is relatively sparse and scattered. To complement the *Caragana* Control Trials Project initiated by the City of Calgary (Alberta, Canada) in 2009, we review the biology, ethnobotany, ecosystem effects, and candidate control methods of *C. arborescens*. Perhaps unsurprisingly, we find evidence for both positive and negative effects and uses of *C. arborescens*. We caution that continued habitat degradation and climate change may facilitate *C. arborescens* becoming an invasive or noxious species in more areas with time. Finally, we advocate that more attention be paid to *C. arborescens* throughout its range, with special focus on habitat fragments, recently deforested areas, and wetlands impacted by human activities.

**Keywords:** Biological control; *Caragana arborescens*; Ecosystem; Fabaceae; Invasive species.

## CONTENTS

INTRODUCTION .....	2
METHODS .....	2
SPECIES BIOLOGY .....	2
Evolutionary history .....	2
Phenotypic characteristics .....	3
Chemical characteristics .....	3
Enemies .....	4
ETHNOBOTANY .....	4
Medicinal applications .....	4
Cultural uses .....	4
EFFECTS .....	5
Colonization and spread in exotic habitats .....	5
Potential invasiveness .....	5
CONTROL METHODS .....	5
Physical control .....	5
Chemical control .....	6
Biological control .....	6
CONCLUSIONS .....	6
LITERATURE CITED .....	6

\*Corresponding author: E-mail: smvamosi@ucalgary.ca; Tel: +1-403-210-8508; Fax: +1-403-289-9311.

## INTRODUCTION

The introduction of non-native species is one of the leading threats to biodiversity and natural ecosystems, with numerous and sometimes irreversible effects (Wittenberg and Cock, 2001). *Caragana arborescens* Lam. is native to Russia and China, and was introduced to North America in 1752, where it is considered exotic, but largely not noxious (AKEPIC, 2005; Dietz et al., 2008). However, in localized areas, such as the Weaselhead Natural Environment Area, a 620 ha wilderness area in the heart of the City of Calgary, it is deemed of potential concern to the ecological integrity of local ecosystems. The purpose of this review is to determine the potential for *C. arborescens* to become invasive in North America and to assess candidate control methods. We focus on four main topics, namely: (1) species biology, (2) ethnobotany, (3) effects, and (4) control methods.

## METHODS

We collated information on *C. arborescens* by searching the ISI Web of Science research database and the Natural Resources Conservation Service database of the United States Department of Agriculture (hereafter, USDA). Our efforts revealed that much of the research concerning *C. arborescens* has been conducted in its home range (especially China and Russia), which limited the number of articles available in English. Therefore, some of the information presented in this review has been taken from secondary sources, which have their own interpretations of the primary sources. Because very little published research has been conducted in North America regarding its invasiveness potential, our limited coverage of this topic relies on relatively few sources and inferences made from the biology of *C. arborescens* in its native range.

## SPECIES BIOLOGY

### Evolutionary history

Fabaceae (Leguminosae) is the third largest family of flowering plants, with approximately 19,400 species (Stevens, 2001 onwards). Traditionally, the family has been divided into three major subfamilies: Caesalpinioideae, Mimosoideae and Papilinoideae (Faboideae) (Wojciechowski et al., 2004). Papilinoideae is considered the most diverse and widespread, with 476 genera and 13,860 species, containing all familiar domesticated foods and crops that are found globally (Gepts et al., 2005). *Caragana* Fabr., a genus in the subfamily, is composed of approximately 100 species distributed within northern Eurasia from the Black Sea to southeast Siberia, and southward to eastern and south-western China, Nepal, Afghanistan and Turkmenistan (Zhang et al., 2009). *Caragana* has a temperate Asian distribution and commonly occurs in arid regions that can reach extremely cold temperatures (Zhang, 2004, 2005; Zhang et al., 2009). Species also occur in forests, grasslands, deserts and alpine mead-

ows (Zhang, 2005; Zhang et al., 2009).

The relationships among the species in the genus *Caragana*, as well as their origin and spread, have been the subject of some debate since the beginning of the last century. Komarov (1908) established the first classification of the genus in a monograph (Zhang, 2005; Zhang et al., 2009). The genus was proposed to have originated in East Asia. Furthermore, *C. sinica* (Buc'hoz) Rehd. was proposed to be the ancestral species of the group. By examining the leaf morphology of *C. sinica*, characterized by its pinnate leaves that contain two pairs of leaflets, Komarov (1908) determined that two distinct groups of species evolved from *C. sinica*. The radiation of species with pinnate leaves and many pairs of leaflets was accompanied by dispersal into North China, whereas the radiation of species with palmate leaves and two pairs of leaflets was accompanied by dispersal into Central Asia (Zhang, 2005). From this evidence, as well as the distribution range of *C. sinica*, Komarov (1908) proposed the 'East Asian Mongolian floristic migration hypothesis', suggesting that the genus dispersed northwards and westwards (Komarov, 1908; cited in Moore, 1968; Zhang, 2004, 2005; Zhang et al., 2009).

Moore (1968) adopted a different approach in characterizing the ancestral species of *Caragana*. Specifically, he questioned the basal position of *C. sinica* within the group. Chromosome counts for 17 species of *Caragana* were obtained and used to produce the first estimate of phylogenetic relationships among *Caragana* species, also incorporating rachis development (deciduous to persistent) and foliage condition (pinnate to variable to palmate). *Caragana sinica* was found to be a triploid hybrid, and the species group containing pinnate leaves with many pairs of leaflets were mostly diploid. Moore (1968) inferred that the species group with a diploid chromosome number of  $2n = 16$  was basal. By examining the distribution of species with different chromosome numbers, Moore (1968) proposed that Lake Balkhash (Kazakhstan) was the centre of origin for the genus. From this origin, the species were then thought to have dispersed eastwards towards the Pacific Ocean and westwards to southern Europe and Russia (Moore, 1968).

More recently, chromosome counts were obtained for 11 additional *Caragana* species, as well as descriptions of the pollen morphology for 34 species (Zhang et al., 1996; Zhang, 1998; see also Zhou et al., 2002). From these new data, these authors regarded eastern Siberia as the origin of the genus and *C. arborescens* as the basal species (Zhang, 2004, 2005; Zhang et al., 2009). Zhang (2004, 2005) additionally provided evidence that vicariance, rather than dispersal, was the main driver of the speciation patterns observed.

Given the lack of a fossil record for *Caragana* (Zhang, 2005), there is some uncertainty about when it first originated. Because *Caragana* is naturally isolated to temperate Asia, it has been proposed to be a comparatively young genus, possibly having originated after the Miocene (Zhang, 2004, 2005). Zhang (2004, 2005) based this infer-

ence on the observation that no species of *Caragana* are native to North America, hypothesizing that some species would have dispersed to North America if the genus had originated prior the existence of the Bering Land Bridge. However, given evidence that the land bridge was present during the Pleistocene, and may have even persisted into the Holocene (Ager, 2003), this hypothesis would require origination rates (i.e., ~100 species in <15,000 yr) that are orders of magnitude greater than are characteristic of famous adaptive radiations. For example, it is estimated that the 33 species constituting the Hawaiian silversword alliance diversified over the last 5-6 million years (Baldwin and Wagner, 2010). Similarly, ecological character displacement has led to only two species of threespine stickleback fish in several southwestern British Columbia lakes since the retreat of glaciers (i.e., ~13,000 yr; Vamosi, 2003). It was also suggested that *Caragana* diversified into two phylogenetically distinct “directions” influenced by the paleogeographical and paleoecological histories of the Tibetan Plateau and Central Asia: species inhabiting the Tibetan Plateau being characterized by pinnate leaves and adaptations against cold temperatures, and those found within Central Asia being characterized by palmate leaves and adaptations against drought (Zhang, 2005). Some major events in the Earth’s history hypothesized to have contributed to the evolution of the group include: the uplifting of the Tibetan Plateau, Pleistocene glaciations and increasing aridification of Central Asia (Zhang, 2005).

Although the aforementioned events likely have contributed to the history of this group, we caution that these interpretations relied partly on the notion that *Caragana* is a very young group and on a phylogenetic hypothesis that posited *C. arborescens* as the basal species (Zhang, 2005). Subsequent molecular phylogenies (Zhang et al., 2009; Zhang and Fritsch, 2010) reveal the latter species to be nested well within the crown group of section *Caragana*, which itself is not recovered as a basal group. Further phylogenetic and phylogeographic work is needed, which may yield interesting insights into the origins and spread of the genus and its member species.

### Phenotypic characteristics

*Caragana arborescens* is a deciduous perennial shrub or small tree that can reach heights of 3-5 m when fully mature (USDA NRCS, 2010). It takes approximately 10 years to mature and has a very rapid growth rate (Henderson and Chapman, 2006; USDA NRCS, 2010). A curvilinear relationship exists between height and age (Henderson and Chapman, 2006). Additionally, *C. arborescens* has the ability to resprout if damaged (USDA NRCS, 2010).

When young, the bark is smooth and olive green in colour, which gradually fades with age (USDA NRCS, 2010). The foliage is green and has alternate pinnate leaves, each being 5-10 cm long. Each leaf has eight to twelve paripinnate leaflets that end in a spine or bristle (Zhang et al., 2009; USDA NRCS, 2010). When forming nodules on its roots, *C. arborescens* establishes symbioses

with a limited number of rhizobial strains (Gregory and Allen, 1953).

The flowers of *C. arborescens* are bisexual and self-compatible, emerging from April to late June (Gregory and Allen, 1953; Dietz et al., 2008). The flowers form linear pods during June and July. *Caragana arborescens* is well known for its prolific seed production (Martine et al., 2008). A sigmoidal relationship exists between seed pod production and age (Henderson and Chapman, 2006). Seed pods are 2-5 cm in length and each contain around six seeds that vary in shape from oblong to spherical (Dietz et al., 2008). While ripening, the pods change from yellow to an amber or brown colour. When fully grown, the seed pods crack and burst, releasing the seeds. Seed dispersal of *C. arborescens* begins in July and is typically completed by mid-August (Dietz et al., 2008).

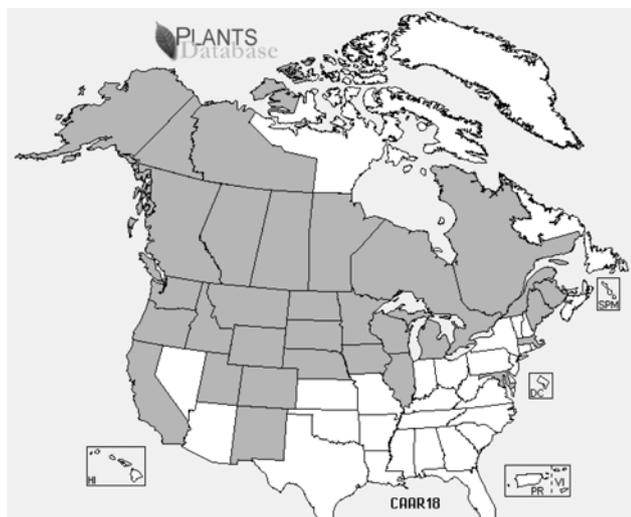
*Caragana arborescens* is known for its tolerance of many environmental conditions including droughts, temperatures to -38°C, infertile soils, sunny sites, high winds, alkaline soils and saline conditions (Henderson and Chapman, 2006; Dietz et al., 2008; Martine et al., 2008; USDA NRCS, 2010). This tolerance for cold and dry sites is almost certainly associated with its much greater spread through North America compared to other exotic legumes, such as Scotch broom (*Cytisus scoparius* L.) and common gorse (*Ulex europaeus* L.). Gorse, for example, is currently restricted to nine states and one province that are all either coastal (US: Hawaii, Washington, Oregon, California, Massachusetts, New York, Virginia; Canada: British Columbia), or adjacent to coastal states (Pennsylvania, West Virginia) (USDA NRCS, 2010).

### Chemical characteristics

*Caragana* species contain many chemical compounds that may prolong its lifespan and increase dispersal. At least ten species of *Caragana* contain esters, cardiac glycosides, steroids, terpenoids and phenolic compounds, but almost no traces of alkaloids (Wang et al., 2005). Phenolic compounds have been found in the water of drainage basins near *C. arborescens* populations. The compounds, due to their inhibitory properties, may disturb vital functions in plants such as *Agropyron repens*, supporting evidence that *C. arborescens* is detrimental to the growth of many grass species (Zolotukhin, 1980).

As noted above, *C. arborescens* is tolerant of alkaline soils and saline environments. It is especially tolerant to potassium chloride (KCl) and potassium sulfate (K<sub>2</sub>SO<sub>4</sub>) in soil (Redmann, 1986). Soils in prairie regions are often naturally rich in potassium, which may serve as a partial barrier to successful colonization of intolerant species. The current range of *C. arborescens* in North America (Figure 1) corroborates Redmann’s (1986) finding that this species is not noticeably limited by soil potassium concentrations.

*Caragana arborescens* is a nitrogen-fixing plant and, furthermore, it initiates nitrogen fixation at temperatures of 3-5°C, which is considerably lower than in many other species (Hensley and Carpenter, 1979). With the ability



**Figure 1.** Distribution of the introduced species, *C. arborescens*, in North America; areas (states, provinces, territories) confirmed to contain *C. arborescens* are shown in gray, whereas areas from which it is not known to occur are shown in white (USDA NRCS, 2010).

to initiate nitrogen fixation at such low temperatures, *C. arborescens* has a greater northern hardiness limit than most other studied species (Hensley and Carpenter, 1979).

Finally, *C. arborescens* is a prolific producer of the toxic non-protein amino acid, L-Canavanine (Rosenthal, 2001), which is an allelochemical that provides a barrier to herbivore predation and pathogen uptake. L-Canavanine is structurally similar to L-Arginine and is taken up by insects that cannot differentiate between the two amino acids (Rosenthal, 2001).

## Enemies

Despite being tolerant of harsh environmental conditions, *C. arborescens* is susceptible to various herbivores, allelopathic chemicals, pathogens and fungi. Grasshoppers, birds, beetles, moths and deer are known herbivores of *C. arborescens* (Rosenthal, 2001; Henderson and Chapman, 2006). Two species of aphids, *Therioaphis tenera* and *Aphis craccivora*, have been found living on many species of *Caragana*, and have previously been recorded with *C. arborescens* (Ripka, 2004). An energy trade-off has been identified for *C. arborescens* between growth of defensive spines and reproduction, which may initiate the growth of grazing-resistant individuals that are shorter, have smaller leaves, and produce fewer seed pods (Zhang et al., 2006).

Under short-term lab conditions, *C. arborescens* was susceptible to the allelopathic chemicals of the black walnut tree, *Julans nigra* (Rietveld, 1983). Seed germination of *C. arborescens* was inhibited by juglone, an allelopathic chemical released by the black walnut tree. However, these results were based on high concentrations of juglone, which may not be attained in nature.

*Caragana arborescens* is susceptible to various pathogens. Spot-forming pathogens that have been identified

include: *Alternaria alternate*, *Cladosporium herbarum*, *Leptoxyphium fumagu*, *Oidium* spp. and *Phyllosticta caraganae* (Tomoshevich, 2009). If infected on the roots, the nodules create a cylindrically-shaped infection zone, and the plant will restrict gas and liquid exchange to that area (Allen et al., 1955).

Finally, *C. arborescens* is also susceptible to several fungi, including *Erysiphe palczewskii*, a powdery mildew species found in Asia, Europe, Canada and the USA (Vajna, 2006; Lebeda et al., 2008a,b; Tomoshevich, 2009). Powdery mildew severely affects the leaves and shoots of *C. arborescens* (Vajna, 2006). Other fungal species commonly found on *C. arborescens* leaves include: *Microspora trifolii*, *Uromyces cytisi* and *Ascochyta borjomi* (Lebeda et al., 2008b; Tomoshevich, 2009).

## ETHNOBOTANY

### Medicinal applications

There is a long history of using *Caragana* species to treat ailments such as headaches, asthma, cough, nosebleeds and strain-induced fatigue in East Asian folk medicine (Meng et al., 2009). *Caragana arborescens* has also been used to treat menoxia, fatigue, rheumatoid arthritis, asthenia and uterine, cervical and breast cancer. The USDA describes *C. arborescens* as being used medicinally for breast and uterine cancer and other female anatomy problems (Meng et al., 2009). The two main chemical classes thought to contribute to the medicinal properties of *C. arborescens* are flavonoids and lectins (Wang et al., 2005; Meng et al., 2009).

Flavonoids are phenolic compounds that protect plants from UV radiation and play a part in sexual reproduction (Koes et al., 2005). They are beneficial to humans because they can act as anti-oxidant, anti-inflammatory, anti-cancer, anti-viral and anti-bacterial chemical compounds (Deng et al., 1997; Meng et al., 2009). The flavonoid found in *C. arborescens* is isoquercetin, which possesses hypoglycemic properties *in vitro* and has potential as an anti-diabetic agent (Meng et al., 2009).

Two types of lectins, which function to bind nitrogen-fixing bacteria to their root systems (Barondes, 1981), have been identified in *C. arborescens*. These lectins can be used as contraception and prophylaxis against sexually transmitted infections (STI) (Meng et al., 2009). *C. arborescens* lectins *in vitro* selectively eliminated cells infected with the *human immunodeficiency virus* (HIV) (Meng et al., 2009), suggesting their potential use in the fight against HIV and other sexually transmitted infections. Evidence to date demonstrates the potential of *C. arborescens* as a medicinal plant; however, more research on its efficacy in treating and eliminating specific conditions is needed.

### Cultural uses

*Caragana arborescens* has been globally cultivated for soil stabilization and mine and construction site improvement through nitrogen fixation (Wills, 1982; Meng et al.,

2009). In North America, it has been planted extensively as shrub buffer strips and shelterbelts on farms (Henderson and Chapman, 2006; Dietz et al., 2008). More recently, it has been used in residential areas for outdoor screening and ornamental hedges (Duke, 1983; Dietz et al., 2008; S. Vamosi, pers. obs.). Although the federal government of Canada planted *C. arborescens* primarily for windbreaks on farms during the 1930's, it was also used for wildlife and erosion control (Henderson and Chapman, 2006). *Caragana arborescens* has also been implemented in revegetation programs to control weed growth in forest plantings (Zolotukhin, 1980; Dietz et al., 2008).

The pods and seeds of *Caragana arborescens* are edible and are cultivated as a vegetable (Meng et al., 2009). The plant is used as nutritional livestock forage and in the arctic/subarctic it is used as fodder for reindeer herds (Duke, 1983). Other uses include fuel for burning, fibre production and the production of an azure dye (Meng et al., 2009; USDA NRCS, 2010).

## EFFECTS

### Colonization and spread in exotic habitats

In its native range, *Caragana arborescens* is distributed from China to southern Russia (Zhang, 2005; Dietz et al., 2008; USDA NRCS, 2010). It was first introduced into Europe during the mid-eighteenth century where it was cultivated for ornamental and hedgerow purposes (Moore, 1968). *Caragana arborescens* has spread extensively in North America since its introduction in 1752, and now occupies 21 states in the United States of America, and nine provinces and territories in Canada (Figure 1). Since its introduction, it has been able to spread from shelterbelt plantings on farms to natural areas adjacent to it, invading the natural forests of North America (Henderson and Chapman, 2006). Records show that 50 planted individuals were able to grow to a population of approximately 60,000 plants over 75 years in the Great Plains of Canada, indicating a rapid growth rate and the risk of extensive colonization and displacement of native species in North America (Henderson and Chapman, 2006).

### Potential invasiveness

Is *C. arborescens* a problem species in North America? At present, it is considered invasive only in three locations: Minnesota, Manitoba and Alberta (Martine et al., 2008; USDA NRCS, 2010). According to Rice (2010), however, *C. arborescens* is not presently considered noxious anywhere within North America.

In what appears to be a unique study of invasiveness potential, Henderson and Chapman (2006) studied the effects of a non-native *C. arborescens* population on native shrub species in Elk Island National Park, Canada. Native shrub diversity, but not species richness, was affected by *C. arborescens* density. The diversity of native shrubs was highest at intermediate *C. arborescens* density, which was correlated with a displacement of *Corylus cornuta*, a dom-

inant native species in its absence. Of the sixteen species considered, only four displayed significant neighbour associations with *C. arborescens*, suggesting the difficulty of making sweeping generalization about its effects on native plants. However, several aspects of its biology show its considerable potential to negatively impact ecosystems.

Because the adult plants reach heights of 3-5 m, they may decrease light availability to native plants (Henderson and Chapman, 2006). *Caragana arborescens* has a long life history strategy, maturing at 10 years of age and living up to 90 years of age as a canopy dominant (Henderson and Chapman, 2006). Populations have large numbers of recruits per year, taking advantage of forest canopy gaps. Henderson and Chapman (2006) noted that *C. arborescens* may reach these gaps before many native canopy dominant plants (e.g., *Populus tremuloides*, *Populus balsamifera*, *Salix* spp.). Finally, its long leaf-out period may lead to high recruitment rates and increased survival through increased intake of solar energy compared to many native species (Henderson and Chapman, 2006).

Additionally, *Caragana arborescens* secretes phenolic compounds into the soil, which inhibit the growth and germination of native plants and are highly toxic to microorganisms (Zolotukhin, 1980; Whitehead et al., 1982). Phenolic compounds influence many physiological processes, including nutrient uptake, protein synthesis, respiration, photosynthesis, and membrane permeability (Reigosa et al., 1999). Nitrogen fixation also alters local soil characteristics, potentially altering normal successional pathways.

Perhaps not surprisingly, some animals have already altered their behaviour in the presence of *C. arborescens*. For example, *C. arborescens* is visited by various bumblebee species for food and is an especially good plant for queens initiating nest building (Alanen, 2008). In the Northern Great Plains of Canada, *C. arborescens* shelterbelts have become an important nesting site for the Common Grackle (*Quiscalus quiscula*) (Yahner, 1982; Homan et al., 1996). Whether such activities by these and other species will help or hinder the spread of *C. arborescens* over time remains an open question.

## CONTROL METHODS

### Physical control

Physical removal can involve: mowing, hand-pulling, stabbing, soil solarisation, burning, bull-dozing surface material to remove root crowns from the soil, cutting, girdling, flooding or mulching (Hobbs and Humphries, 1995; Heiligmann, 1997; Tu et al., 2001; Shafroth et al., 2005; Meloche and Murphy, 2006; Delanoy and Archibold, 2007; White, 2007). Physical removal is likely the most environmentally friendly method, but it is labour intensive (Hobbs and Humphries, 1995). Burning is effective for killing seedlings and can also top-kill adult shrubs. However, it must be repeated annually or biennially over several years (Delanoy and Archibold, 2007). There have been combinations of hand pulling and mulching, which results

in a reduced juvenile population because light penetration to the seedlings is reduced (Meloche and Murphy, 2006; Tu et al., 2001). This control technique is only effective over a one-year span because the mulch eventually gets dispersed (Meloche and Murphy, 2006). If implemented, hand-pulling and mulching need to be repeated each year to be effective (Meloche and Murphy, 2006). In addition, there are problems with the effect of mulching stunting the growth of native plant species (Tu et al., 2001). The least effective physical control method is the cut-stump method with no application of herbicide (Meloche and Murphy, 2006). On its own, this method leaves open canopy areas, which may promote regrowth and seed germination, increasing the overall number of juveniles present and worsening the problem (Meloche and Murphy, 2006; Delaney and Archibold, 2007).

### Chemical control

Chemical control treatments involve herbicide application and are the most common form of invasive and noxious plant control (Hobbs and Humphries, 1995). Herbicides vary by effectiveness and application methods, but can typically be applied more easily to larger areas than can physical control treatments (Hobbs and Humphries, 1995). A variety of commercial (e.g., Garlon™ 4) and traditional (e.g., vinegar- and clove oil-based) herbicides have been applied in shrub control programs (e.g., Shafroth et al., 2005; Meloche and Murphy, 2006; Tyler et al., 2006; Delaney and Archibold, 2007; Heiligmann, 1997; Chirillo, 2008). Although herbicides have largely been applied to other invasive plant species to date (e.g., buckthorn, *Rhamnus cathartica* L.), one potentially effective strategy is a combination of stump cutting or girdling followed by the immediate application of herbicides. Unfortunately, there are challenges to using environmentally friendly traditional methods as alternatives to commercial herbicides because of safety concerns for people working with vinegar and clove oil (Chirillo, 2008). We do note that Captan and Thiram should not be used on *C. arborescens* because they have been found to increase germination by inhibiting seed-borne diseases (Dietz et al., 2008).

### Biological control

Biological control treatments involve identifying herbivores, seed predators and/or pathogens that appear to control the exotic plant population in its native range, and introducing them to the invaded range the exotic plant now occupies (Shafroth et al., 2005; Hobbs and Humphries, 1995). Biological control treatments are a lengthy and complicated process requiring extensive research on the impact the predator or pathogen will have on the environment it is introduced to (Hobbs and Humphries, 1995). We are unaware of any effective biological control methods for *C. arborescens*. Although they may sound preferable to other control methods, especially chemical control, they can be risky in terms of becoming harmful to native species. Additionally, they have historically had a low success rate, with Hobbs and Humphries (1995) estimating

the success of only one for every six biological treatments worldwide.

## CONCLUSIONS

*Caragana arborescens* is a prolific seed disperser with a long life history strategy (Martine et al., 2008). Furthermore, *C. arborescens* is protected by tolerance to drought, cold, salinity and infertile soils (Zolotukhin, 1980; Dietz et al., 2008; USDA NRCS, 2010). Together, these characteristics result in the potential for high recruitment rates and spread across landscapes, including habitats marginal or inhospitable to native plant species. Therefore, the potential exists for various forests of Canada and the USA to be rapidly invaded by *C. arborescens* once small populations have established (e.g., Henderson and Chapman, 2006).

Our literature review reveals that *C. arborescens* has various positive characteristics and applications, including some directly related to human welfare, although the intentional farming of this species for such purposes should likely be restricted to its native range. *Caragana arborescens* may have the ability to severely impact forests; however, very little research addressing these issues has been conducted in North America. Future studies should focus on (i) the potential of *C. arborescens* to invade and/or alter forests of North America, (ii) whether their phenolic compounds affect native flora, and (iii) how to effectively control populations of *C. arborescens* in North America if it becomes invasive. Thus far, herbicides appear to be more effective and carry a lower financial cost than physical removal. However, many native species are susceptible to herbicides; thus, their environmental costs should be taken into account (Henderson and Chapman, 2006). Overall, much remains to be learned about the effects, both positive and negative, of this exotic member of North America's flora.

**Acknowledgements.** We thank Jill Luka and the City of Calgary for the opportunity to review the biology of *C. arborescens* and to be involved with the *Caragana* Control Trials Project. Research in the laboratory of SMV is supported by grants from the Natural Sciences and Engineering Research Council of Canada (NSERC).

## LITERATURE CITED

- Ager, T.A. 2003. Late Quaternary vegetation and climate history of the central Bering land bridge from St. Michael Island, western Alaska. *Quatern. Res.* **60**: 19-32.
- AKEPIC-Alaska Exotic Plant Information Clearinghouse. 2005. Invasive plants of Alaska. Alaska Association of Conservation Districts Publication. Anchorage, Alaska.
- Alanen, E. 2008. Habitats and food plants of the bumblebee queens in an agricultural landscape. *Proc. Neth. Entomol. Soc. Meet.* **19**: 59-65.
- Allen, E.K., K.F. Gregory, and O.N. Allen. 1955. Morphological development of nodules on *Caragana arborescens* Lam.

- Can. J. Bot. **33**: 139-148.
- Baldwin, B.G. and W.L. Wagner. 2010. Hawaiian angiosperm radiations of North American origin. *Ann. Bot.* **105**: 849-879.
- Barondes, S.H. 1981. Lectins: their multiple endogenous cellular functions. *Ann. Rev. Biochem.* **50**: 207-231.
- Chirillo, S. 2008. Non-herbicide weed control strategies implemented by City Parks staff in the northwest: maintaining shrub beds and landscaped areas. Northwest Coalition for Alternatives to Pesticides, Eugene, Oregon.
- Delanoy, L. and O.W. Archibold. 2007. Efficacy of control measures for European Buckthorn (*Rhamnus cathartica* L.) in Saskatchewan. *Environ. Manage.* **40**: 709-718.
- Deng, W., X. Fang, and J. Wu. 1997. Flavonoids function as antioxidants: by scavenging reactive oxygen species or by chelating iron? *Radiat. Phys. Chem.* **50**: 271-276.
- Dietz, D.R., P.E. Slabaugh, and F.T. Bonner. 2008. *Caragana arborescens* Lam.: Siberian peashrub. In F.T. Bonner and R.P. Karrfalt (eds.), *The Woody Plant Seed Manual*. Agric. Handbook No. 727. Washington, DC. US Department of Agriculture, Forest Service, pp. 321-323.
- Duke, J.A. 1983. Handbook of energy crops. Unpublished. Available: Center for New Crops and Plants Products (<http://www.hort.purdue.edu/newcrop/default.html>). Purdue University. Department of Horticulture and Landscape Architecture. West Lafayette, IN. (Accessed March 30, 2010).
- Gepts, P., W.D. Beavis, E.C. Brummer, R.C. Shoemaker, H.T. Stalker, N.F. Weeden, and N.D. Young. 2005. Legumes as a model plant family. Genomics for food and feed report of the cross-legume advances through genomics conference. *Plant Physiol.* **137**: 1228-1235.
- Gregory, K.F. and O.N. Allen. 1953. Physiological variations and host plant specificities of rhizobia isolated from *Caragana arborescens* L. *Can. J. Bot.* **31**: 731-738.
- Heiligmann, R.B. 1997. Controlling undesirable trees, shrubs, and vines in your woodland. Ohio State University Extension Fact Sheet **45**: 1-3.
- Henderson, D.C. and R. Chapman. 2006. *Caragana arborescens* invasion in Elk Island National Park, Canada. *Nat. Areas J.* **26**: 261-266.
- Hensley, D.L. and P.L. Carpenter. 1979. The effect of temperature on N<sub>2</sub> fixation (C<sub>2</sub>H<sub>2</sub> reduction) by nodules of legume and actinomycete-nodulated woody species. *Bot. Gaz.* **140**: S58-S64.
- Hobbs, R.J. and S.E. Humphries. 1995. An integrated approach to the ecology and management of plant invasions. *Cons. Biol.* **9**: 761-770.
- Homan, H.J., G.M. Linz, W.J. Bleier, and R.B. Carlson. 1996. Colony-site and nest-site use by common grackles in North Dakota. *Wilson Bull.* **108**: 104-114.
- Koes, R.E., F. Quattrocchio, and J.N.M. Mol. 1994. The flavonoid biosynthetic pathway in plants: function and evolution. *BioEssays* **16**: 123-132.
- Komarov, V.L. 1908. Generis *Caragana* monographia. *Acta. Horti. Petrop.* **29**: 377-388.
- Lebeda, A., B. Mieslerová, and M. Sedlářová. 2008a. First report of *Erysiphe palczewskii* on *Caragana arborescens* in the Czech Republic. *Plant Pathol.* **57**: 779.
- Lebeda, A., B. Mieslerová, M. Sedlářová, and M. Pejchal. 2008b. Occurrence of anamorphic and teleomorphic stage of *Erysiphe palczewskii* (syn. *Microsphaera palczewskii*) on *Caragana arborescens* in the Czech Republic and Austria and its morphological characterisation. *Plant Prot. Sci.* **44**: 41-48.
- Martine, C.T., S. Leicht-Young, P. Herron, and A. Latimer. 2008. Fifteen woody species with potential for invasiveness in New England. *New England Bot. Club* **110**: 345-353.
- Meloche, C. and S.D. Murphy. 2006. Managing Tree-of-Heaven (*Ailanthus altissima*) in parks and protected areas: a case study of Rondeau Provincial Park (Ontario, Canada). *Environ. Manage.* **37**: 764-772.
- Meng, Q., Y. Niu, X. Niu, R.H. Roubin, and J.R. Hanrahan. 2009. Ethnobotany, phytochemistry and pharmacology of the genus *Caragana* used in traditional Chinese medicine. *J. Ethnopharmacol.* **124**: 350-368.
- Moore, R.J. 1968. Chromosome numbers and phylogeny in *Caragana* (Leguminosae). *Can. J. Bot.* **46**: 1513-1522.
- Redmann, R.E., J. Haraldson, and L.V. Gusta. 1986. Leakage of UV-absorbing substances as a measure of salt injury in leaf tissue of woody species. *Physiol. Plant.* **67**: 87-91.
- Reigosa, M.J., X.C. Souto, and L. González. 1999. Effect of phenolic compounds on the germination of six weeds species. *Plant Growth Regul.* **28**: 83-88.
- Rietveld, W.J. 1983. Allelopathic effects of juglone on germination and growth of several herbaceous and woody species. *J. Chem. Ecol.* **9**: 295-308.
- Rice, P.M. 2010. Invaders Database System (<http://invader.dbs.umt.edu>). Division of Biological Sciences, University of Montana, Missoula. (Accessed March 30, 2010).
- Ripka, G. 2004. Recent data to the knowledge of the aphid fauna of Hungary (Homoptera: Aphidoidea). *Acta Phytopathol. Entomol. Hung.* **39**: 91-97.
- Rosenthal, G.A. 2001. L-Canavanine: a higher plant insecticidal allelochemical. *Amino Acids* **21**: 319-330.
- Sanchir, C. 1979. Genus *Caragana* Lam., systematics, geography, phylogeny and economic significance in study on flora and vegetation of P. R. Mongolia, Vol. 1. Academic Press, Ulan Bator.
- Shafroth, P.B., J.R. Cleverly, T.L. Dudley, J.P. Taylor, C. Van Riper III, E.P. Weeks, and J.N. Stuart. 2005. Control of *Tamarix* in the Western United States: implications for water salvage, wildlife use, and riparian restoration. *Environ. Manage.* **35**: 231-246.
- Stevens, P.F. 2001. Onwards. Angiosperm Phylogeny Website. Version 9, June 2008 [and more or less continuously updated since]. Accessed June 7, 2010.
- Tomoshevich, M.A. 2009. Pathogenic mycobiota on trees in

- Novosibirsk plantations. *Contemp. Probl. Ecol.* **2**: 382-387.
- Tu, M., C. Hurd, and J.M. Randall. 2001. *Weed Control Methods Handbook*, The Nature Conservancy, <http://tncinvasives.ucdavis.edu>, Version: April 2001.
- Tyler, C., A.S. Pullin, and G.B. Stewart. 2006. Effectiveness of management interventions to control invasion by *Rhododendron ponticum*. *Environ. Manage.* **37**: 513-522.
- USDA NRCS. 2010. PLANTS Database (<http://plants.usda.gov>). National Plant Data Center, Baton Rouge, LA. (Accessed March 30, 2010).
- Vajna, L. 2006. First report of powdery mildew on *Caragana arborescens* in Hungary caused by *Erysiphe palczewskii*. *Plant Pathol.* **55**: 814.
- Vamosi, S.M. 2003. The presence of other fish species affects speciation in threespine sticklebacks. *Evol. Ecol. Res.* **5**: 717-730.
- Wang, J.-R., L. Ding, Y.-Y. Zhang, Z.-Y. Chang, and Z.-W. Li. 2005. Testing of active constituents in the stems and leaves of ten *Caragana* plants. *Acta Bot. Boreali-Occidentalia Sin.* **25**: 2549-2552.
- White, T.C.R. 2007. Flooded forests: death by drowning, not herbivory. *J. Veg. Sci.* **18**: 147-148.
- Wills, B.J. 1982. Rhizobial inoculation of Siberian pea-shrub (*Caragana arborescens* Lamb.) for semi-arid revegetation. *New Zeal. J. Exp. Agr.* **10**: 353-354.
- Wittenberg, R. and M.J.W. Cock. (eds.). 2001. *Invasive Alien Species: A Toolkit of Best Prevention and Management Practices*. CAB International, Wallingford, Oxon, UK, pp. xvii-228.
- Wojciechowski, M.F., M. Lavin, and M.J. Sanderson. 2004. A phylogeny of legumes (Leguminosae) based on analysis of the plastid matK gene resolves many well-supported subclades within the family. *Am. J. Bot.* **91**: 1846-1862.
- Yahner, R.H. 1982. Avian nest densities and nest-site selection in farmstead shelterbelts. *Wilson Bull.* **94**: 156-175.
- Zhang, M.L. 1998. A preliminary analytical biogeography in *Caragana* (Fabaceae). *Acta Bot. Yunnan.* **21**: 1-11.
- Zhang, M.L. 2004. Ancestral area analysis of the genus *Caragana* (Leguminosae). *Acta Bot. Sin.* **46**: 253-258.
- Zhang, M.L. 2005. A dispersal and vicariance analysis of the genus *Caragana* Fabr. *J. Integr. Plant Biol.* **47**: 897-904.
- Zhang, M.L. and P.W. Fritsch. 2010. Evolutionary response of *Caragana* (Fabaceae) to Qinghai-Tibetan Plateau uplift and Asian interior acidification. *Plant Syst. Evol.* **288**: 191-199.
- Zhang, M.L., X.Y. Tian, and J.C. Ning. 1996. Pollen morphology and its taxonomic significance of *Caragana* Fabr. (Fabaceae) from China. *Acta Phytotax. Sin.* **34**: 397-409.
- Zhang, M.L., P.W. Fritsch, and B.C. Cruz. 2009. Phylogeny of *Caragana* (Fabaceae) based on DNA sequence data from *rbcl*, *trnS-trnG*, and ITS. *Mol. Phylogenet. Evol.* **50**: 547-559.
- Zhang, Z., S.P. Wang, P. Nyren, and G.M. Jiang. 2006. Morphological and reproductive response of *Caragana microphylla* to different stocking rates. *J. Arid Environ.* **67**: 671-677.
- Zhao, Y.Z. 1993. Taxonomic study of the genus *Caragana* from China. *Acta. Sci. Nat. Univ. Intramongolicae.* **24**: 631-653.
- Zhou, Q.X., Y.P. Yang, and M.L. Zhang. 2002. Karyotypes of fourteen species in *Caragana*. *Bull. Bot. Res.* **22**: 492-496.
- Zolotukhin, A.I. 1980. Allelopathic effect of shrubs used in steppe forestation on quack grass. *Sov. J. Ecol.* **11**: 203-207.

## 雜草型樹錦雞兒 (*Caragana arborescens*) 之生物學綜論，特別著重其在北美洲的潛在影響

Katelyn B. SHORR and Steven M. VAMOSI

Department of Biological Sciences, University of Calgary, Calgary, Canada T2N 1N4

引進外來物種及其定居被認為是包括被子植物在內的原生生物多樣性的一大威脅。原產歐亞大陸的豆科植物「樹錦雞兒」於 1700 年代中葉引進北美洲，歷經 250 年這種植物幾乎已定居於加拿大全國和美國半數的州；但有關它對於原生生態系潛在影響的文獻卻不多見。為呼應加拿大卡加利市 2009 年倡導的控制樹錦雞兒試驗計劃，我們就樹錦雞兒的生物學、民族植物學、對生態系之影響、與可能的控制的方法進行綜論，並提供證據表明樹錦雞兒對於生態的正面及負面影響及其利用。值得注意的是，持續的棲地退化與氣候變遷將促進樹錦雞兒在更多的地區成為入侵性的惡劣雜草。我們必需特別關注樹錦雞兒的全部分布區域，尤其是受到人為活動干擾的破碎棲地、新近毀林地區以及濕地。

**關鍵詞：**生物控制；樹錦雞兒；生態系；入侵種。