Predicting weed invasion in Canada under climate change: Evaluating evolutionary potential

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Many efforts are underway to predict changes in the distribution of invasive plants under climate change (Kriticos et al. 2004; Hickling et al. 2006; Jarnevi and Van Hezewijk 2010; Bradley et al. 2010), but relatively few of these account for weed evolution (Clements and Stohlgren 2009; McDonald et al. 2009; Bourchier and Van Hezewijk 2010; Bradley et al. 2010).
DiTommaso 2011). Approaches to predictive modeling, such as CLIMEX models (Kriticos et al. 2004) utilize climate data for an invasive plant in its home range or known range, and map these parameters on to new potential ranges. These models can predict changes in weed distribution under climate change by developing scenarios based on increased temperatures and/or other climatic parameters (McDonald et al. 2009). CLIMEX models have provided numerous useful predictions on the spread of invasive plants, including attempts to predict changes in weed distribution due to warmer temperatures and other climatic alterations predicted by climate change models (e.g., Kriticos et al. 2004; Pattison and Mack 2008; Potter et al. 2009; Watt et al. 2009; Chejara et al. 2010).

The default methodology when undertaking these predictive exercises is to assume the plants themselves are static entities. However, changes in weed distributions may often reflect evolutionary change in the plants themselves, and frequently correspond to anthropogenic influences such as cropping practices (Clements et al. 2004). Many of these recent changes in plant distribution represent northward movement of weeds within North America (Clements et al. 2004). In the face of climate change leading to warmer conditions in parts of Canada, this northward movement may be accelerating in North America. The objectives of this review are to examine this evolutionary potential of invasive plants more closely to determine (1) whether particular traits of invasive plants have a strong and predictable predilection for adaptation to changing climate, and (2) whether this evolutionary potential could or should be incorporated into predictive models of changing weed distribution under climate change.

**POTENTIAL EVOLUTION OF WEED TRAITS**

For many years, weed scientists thought weeds would not develop herbicide resistance on a comparable scale to the insecticide resistance concerns emerging in the 1950s and 1960s (Gressel and Segel 1978). Now, however, herbicide resistance is widespread (Heap 2012), showing weeds to have a strong potential to evolve in the presence of such an intense and widely imposed selection pressure. Similarly, Baker’s (1965) contention that weed success was primarily due to possession of an “all-purpose genotype” emphasized plasticity of weed genotypes over potential for actual changes in genetic traits. Yet there are many examples of weed success due largely to genetic change (Clements et al. 2004). The mechanisms of such alterations are often subtle because a large proportion of weeds are predominantly selfing. Some of these mechanisms include occasional outcrossing within selfing populations, storage of genetic variation in seed banks, and evolution of phenotypic plasticity (Clements et al. 2004).

When predicting the potential of invasive species to evolve rapidly, it is useful to consider particular traits that would likely make such species successful in novel environments (Whitney and Gabler 2008). Although there are numerous potential traits that could be selected for, Whitney and Gabler (2008) highlighted 10 of particular interest for invasive species in general, which we modified for invasive plants (Clements and DiTommaso 2011). These plant traits include: (1) high growth rate, (2) wide climatic or environmental tolerance, (3) short generation time, (4) prolific or consistent reproduction, (5) modified seed size, (6) effective dispersal, (7) uniparental reproduction capacity, (8) no specialized germination requirements, (9) high competitive ability, and (10) effective defenses against natural enemies (Table 1).

Because of life history constraints, it is highly unlikely for any particular invasive species to undergo directional selection for all 10 of these traits simultaneously, but it is possible for selection pressures to operate on several traits in a given species synergistically. In the following case studies of four invasive plant species of interest in Canada, we focused on at least three of these traits.

Table 1. Invasive plant character traits targeted for natural selection under climate change evaluated for the four species highlighted in this analysis: Himalayan balsam (HB), velvetleaf (V), Japanese knotweed (JK), and johnsongrass (J). The 10 character traits are from Clements and DiTommaso (2011), based on Whitney and Gabler (2008), and evaluations were made according to literature sources and personal observations by the authors.

<table>
<thead>
<tr>
<th>Character trait</th>
<th>HB</th>
<th>V</th>
<th>JK</th>
<th>J</th>
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<tbody>
<tr>
<td>(1) High growth rate</td>
<td>++</td>
<td>+</td>
<td>++</td>
<td>+</td>
</tr>
<tr>
<td>(2) Wide climatic or environmental tolerance</td>
<td>++</td>
<td>++</td>
<td>++</td>
<td>++</td>
</tr>
<tr>
<td>(3) Short generation time</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
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<tr>
<td>(4) Prolific or consistent reproduction</td>
<td>++</td>
<td>++</td>
<td>++</td>
<td>+</td>
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<tr>
<td>(5) Modified seed size</td>
<td>++</td>
<td>++</td>
<td>+</td>
<td>+</td>
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<tr>
<td>(6) Effective dispersal</td>
<td>++</td>
<td>–</td>
<td>++</td>
<td>+</td>
</tr>
<tr>
<td>(7) Uniparental reproduction capacity</td>
<td>–</td>
<td>+</td>
<td>+/−</td>
<td>+</td>
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<tr>
<td>(8) No specialized germination requirements</td>
<td>+</td>
<td>–</td>
<td>+/−</td>
<td>+</td>
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<tr>
<td>(9) High competitive ability</td>
<td>+</td>
<td>+</td>
<td>++</td>
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<td>(10) Effective defenses against natural enemies</td>
<td>?</td>
<td>+</td>
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</tr>
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*Key: ++ strong evidence the trait is important, + some evidence the trait is important, − evidence the trait is unimportant, ? not enough evidence to judge.*
that could influence the evolution of these species. The goal was to determine whether such evolutionary potential could be considered when attempting to predict distributional changes, namely, is there enough information known about a particular trait to assess whether such adaptations could affect predictions on changes in the distribution for these species?

**HIMALAYAN BALSAM (IMPATIENS GLANDULIFERA ROYLE)**

Himalayan balsam (Impatiens glandulifera) (Balsaminaceae) is an invasive annual herb native to Asia that can attain 3 m in height (Clements et al. 2008). Adding to its relatively tall stature, its showy pink or purple flowers make it a highly visible and competitive invader, particularly in riparian areas where monocultures of Himalayan balsam can reduce bank stability and reduce native biodiversity. The plant has created environmental problems in sensitive riparian areas in the United Kingdom since 1855, in Eastern Europe since 1896 and in Canada since 1901 (Clements et al. 2008). Although it is fairly widespread in somewhat isolated regions of coastal British Columbia, Ontario and the Maritimes, Himalayan balsam has the potential to expand its range much further in Canada, including many regions north of its current distribution, especially if climate change predictions of warming in some parts of Canada are realized (Motha and Baier 2005). Such range expansion could be predicted utilizing CLIMEX modeling based on its native range in Asia, but there is evidence to suggest that evolutionary adaptation should also be considered.

The competitiveness of Himalayan balsam in riparian zones is surprising considering its life history as an annual plant germinating in the spring. Thus, growth rate, the first characteristic among the 10 potential traits (Table 1) is a significant attribute for this species. Himalayan balsam is generally not shade tolerant, e.g., it is generally not expected to grow rapidly at less than 30% full daylight (Andrews et al. 2005). This tends to restrict its occurrence to recently disturbed or cleared areas along streams or rivers. However, similar growth rates to those measured in open areas were also observed in woodlands of the United Kingdom (Andrews et al. 2005). Likewise, within its Canadian range, there are some populations that thrive under closed canopies, although most populations are found in more open environments (Clements, unpublished observation).

Andrews et al. (2005) found that these relatively high growth rates in shaded conditions could be explained by Himalayan balsam employing KNO₃ as an osmoticum under low light conditions. Thus, these woodland populations of Himalayan balsam have a physiological mechanism which enables plants to switch from the normal osmoticum molecules used such as organic acids and sugars to nitrates when growing under low irradiance. This is clearly a beneficial adaptation in United Kingdom populations; whether or not this mechanism or its efficiency could be selected for to allow greater range expansion is not clear without examining its heritability. Certainly in any case where an invasive plant is able to adapt and colonize adventive habitats, management becomes more difficult.

The trait listed by Whitney and Gabler (2008) as “wide climatic or environmental tolerance” is a key attribute to examine when considering potential range expansion due to climate change. A well-known method of assessing the genetic underpinning for this attribute in plants is via “common garden” experiments whereby seed from populations occurring in different geographic regions is planted under identical growing conditions (or conversely, seed from a single site could be planted under a variety of growing conditions to test the adaptability of the population). Such a common garden experiment was performed on Himalayan balsam using 26 populations from nine European regions in a common garden in Denmark to determine variation in flowering times and other traits (Kollmann and Bañuellos 2004).

Kollmann and Bañuellos (2004) found that northern populations flowered first and that the above-ground biomass, height and basal diameter of plants were lower than more southern populations. Seed size was also smaller in northern populations, but it was impossible to identify from the experiment whether the seed size difference was genetically based or due to maternal effects. Furthermore, growing northern population plants under different photoperiod regimes may result in plants flowering earlier and therefore producing smaller seeds. Still, given the range of ecotypes across a north–south gradient identified by Kollmann and Bañuellos (2004), it is clear that Himalayan balsam is capable of adapting to more northerly environments via natural selection. The implication for climate change prediction is that the plant could extend its range beyond that which would be predicted from modeling its spread based on a warm-climate genotype. Perhaps this climatic adaptability is consistent with the geographic origin of the plant in the mountainous Himalayan region, where climate varies widely over relatively short distances (Rau 1974).

Although not necessarily a genetic trait, small seed size could be selected for in northern populations. A more important seed trait for Himalayan balsam is the ability to float; in fact the ability of its seeds to float and to germinate rapidly compared with other Impatiens species may be critical to its successful establishment (Perglová et al. 2009). Wadsworth et al. (2000) estimated the maximum waterborne dispersal distance for Himalayan balsam seeds to be 20 km. If floating ability is variable and under selective pressure, it could have a major impact on capacity for spread since the principal means of dispersal is generally via floating seeds along waterways. It may be that larger seeds have greater longevity in water, as Mannesse (1990) observed for the herbaceous perennial swamp lily.
VELVETLEAF (ABUTILON THEOPHRASTII MEDIC.)

Like Himalayan balsam, velvetleaf (*Abutilon theophrasti* Medic.) is an invasive summer annual native to Asia and specifically China and India (Warwick and Black 1988). Its common name arises from its large, heart-shaped hairy leaves. Plants produce numerous 2-cm-diameter yellow flowers, with each plant producing as many as 8000 seeds, which can survive more than 50 yr in soil (Spencer 1984; Warwick and Black 1988). Unlike Himalayan balsam, velvetleaf is primarily selfing.

Velvetleaf is a serious crop pest causing millions of dollars in crop damage annually in North America and is advancing northward. Currently, it occurs widely in Ontario and Quebec and was observed in British Columbia in 1990 (Warwick and Black 1988; Warwick 1990; Washington State Noxious Weed Control Board 2000). In the course of its northward spread velvetleaf has colonized areas with climates cooler than its native range. In Ontario, it colonized all but three counties from 1950 to 1985, but there is a limit to its northward expansion given its inability to reproduce during the short Alaskan growing season (Anderson et al. 1985). Thus, in terms of Whitney and Gabler’s (2008) category of selection for wide climatic tolerance, it seems likely that the ability of North American velvetleaf populations to survive in more northern climates may be a genetic adaptation, although this has not been directly tested.

A second adaptive trait that could be selected for in velvetleaf is “prolific or consistent reproduction”. The plant produces relatively large seeds, with a high degree of dormancy. The maternal environment most affects seed coat thickness, which in turn directly determines the dormancy status of seeds (Schutte et al. 2008). Interestingly, velvetleaf seed and seed coat weights decreased when grown with corn relative to plants grown in pure stand (Nurse and DiTommaso 2005) showing that this trait could be modified by environmental factors. Thus, seed coat thickness could potentially be a target for natural selection, although genetic research is required to determine whether changes in this trait may be due to phenotypic plasticity rather than genetic differences.

A third trait in Whitney and Gabler’s (2008) list pertinent to velvetleaf is competitiveness, as the plant is highly competitive in many important cropping systems (e.g., corn, soybean). Schmidt et al. (2011) observed greater tolerance of velvetleaf compared with corn to drought, because unlike corn velvetleaf can physiologically adjust to drought conditions through stomatal closure and senescence of older leaves. If the level of response can be selected for, this is a powerful adaptive trait that could allow substantial expansion of its current range in Canada, including more northerly regions, if climate change results in warmer and drier conditions.

As with Himalayan balsam, it is important to understand the population genetics of velvetleaf and how variable its traits may be under natural selection in order to accurately evaluate the significance of any trait for predicting range expansion. Because velvetleaf is primarily selfing, relatively uniform genotypes are produced within populations (Warwick et al. 1984). Despite this relative uniformity, mean seed weight declines and reproductive allocation and seed dormancy increase with a shorter growing season (Warwick and Black 1986). One might expect that these differences may simply be phenotypic differences, but Anderson et al. (1985) demonstrated genetic differentiation in response to local climate among 14 North American populations. Although the general appearance of the plant was similar among the populations, more southerly populations initiated capsule formation earlier and continued to produce capsules longer than more northerly populations (Anderson et al. 1985). The plant could reproduce well at the northern limits of its known range, even when subject to frost, highlighting the potential to extend its range further north (Anderson et al. 1985).

In light of the potential for genetic change exhibited by velvetleaf, it is interesting to consider a specific example where the CLIMEX model was employed. Using this model, Holt and Boose (2000) found that velvetleaf was already distributed according to its climatic niche within California, thus predicting no further spread in California. Yet if velvetleaf populations could adapt to different climatic conditions as suggested by Anderson et al. (1985), then it would be more difficult to determine whether or not velvetleaf is capable of further expansion in California – or elsewhere. To specifically evaluate this potential one might...
need to examine some of the traits listed previously (Table 1) in more detail such as competitiveness and seed coat thickness from a genetic perspective, to determine whether velvetleaf could produce ecotypes better adapted to the northern fringe of its range.

**JAPANESE KNOTWEED [FALlopia japonica (Houttt.) Ronse Decr.]**

Japanese knotweed [Fallopia japonica (Houtt.) Ronse Decr.] is a perennial geophyte native to Asia. It is most problematic on riparian corridors and road and railroad rights-of-way, impacting biodiversity and altering hydrologic processes (Barney et al. 2006). Initially, it was thought to spread primarily by clonal means in North America, via stems and/or rhizomes but now hybridization with other Fallopia spp. is rendering reproduction by seed more common (Bourchier and Van Hezewikj 2010).

Like Himalayan balsam and velvetleaf, Japanese knotweed exhibits a fairly broad climatic tolerance, which appears to be increasing in North America. At present, Japanese knotweed has a more southerly range in North America than Europe, primarily between 33° and 48° N, but its range has been increasing steadily northward. Barney (2006) identified only one population north of the 50°N latitude (in Alaska) and found it present in only 93 Canadian municipalities as of 2006, thus having potential for much greater range expansion (Bourchier and Van Hezewikj 2010). There is considerable evidence of its adaptability to a wide variety of conditions despite its apparent preference for riparian areas or other transport corridors such as roadways. It can tolerate extreme pH, salt and high sulfur dioxide conditions, high shade, high temperatures, drought, waterlogging, burning, and varied soil types (Beerling et al. 1994; Barney et al. 2006). Japanese knotweed can be frost sensitive but a Japanese study found that although sensitive to frost earlier in the season, some seedlings survived temperatures of −15°C in November due to acquisition of winter hardness (Maruta 1983). Thus, despite the presumed origin of Japanese knotweed in relatively warm regions of Asia, it has some capability to tolerate frost and spread northward of its current distribution, particularly if frost occurrence is reduced in Canada with climate change as has been predicted (Motha and Baier 2005). These traits could be selected for if northward movement was facilitated by warming climate in combination with anthropogenic assistance (e.g., through transport of soil containing rhizomes and/or stem pieces).

The capacity of Japanese knotweed to reproduce from its extensive rhizomes (5–6 m in length) is legendary (Beerling et al. 1994; Barney et al. 2006). Just a small section of stem or rhizome (e.g., several centimeters or 0.7 g) is needed to produce tillers (Beerling et al. 1994). Vegetative fragments in this species can spread by water, wind, and earthmoving activities (Barney et al. 2006). Downstream dispersal in watercourses provides a particularly effective pathway for spread with seeds even able to disperse by seawater (Beerling et al. 1994). Meanwhile, panicles can produce ~200,000 seeds per stem if all flowers are pollinated (Bram and McNair 2004). As the frequency of hybridization among Fallopia species in North America increases, this could be a selective force that leads to substantial increases in seed production.

Bourchier and Van Hezewikj (2010) examined the potential spread of Fallopia species in Canada under climate warming scenarios and reported that existing Fallopia sites occupied less than 50% of suitable habitats in British Columbia. Warmer temperatures from 2000 to 2008 resulted in 53% of southern Ontario habitats being suitable for Fallopia colonization compared with 35% colonization when 1971–2000 climate data were used (Bourchier and Van Hezewikj 2010). Bourchier and Van Hezewikj (2010) suggested that different invasive Japanese knotweed genotypes might be selected for in different Canadian regions, which could influence the relative success of biological control agents considered for release.

**JOHNSONGRASS [Sorghum halapense (L.) Pers.]**

Johnsongrass [Sorghum halapense (L.) Pers.] is a perennial C₄ grass native to Eurasia that reproduces via rhizomes and seeds (Warwick and Black 1983). It was introduced as a forage crop in the southern United States of America in the 1800s and did not reach Canada until 1959, but has since continued to spread northward (Warwick and Black 1983). For example, in 1926 this species was rarely reported to overwinter north of 38° N latitude but more recently has been reported overwintering at 43°N latitude in Ontario and New York, USA (Warwick et al. 1986).

In general, johnsongrass is best adapted to warm, humid conditions in the subtropics, but new ecotypes have emerged enabling range expansion in North America. Adaptations for a wider climatic tolerance among these new ecotypes include increasing cold tolerance in rhizomes (Warwick et al. 1986). Another remarkable adaptation observed in North America is the annual life history of northern populations compared with perenniality in southern populations (Warwick et al. 1986). Both the cold tolerance of rhizomes and the annual life history in northern populations clearly represent genetic differences influenced by climatic selection pressures. There is actually an array of differences between annual and perennial populations, including increased seed weight and percentage seedling emergence, more rapid seedling growth, earlier flowering, greater resource allocation to reproduction, and fewer rhizomes in northern populations (Warwick et al. 1984).

As in the case of velvetleaf, the potential for genetic diversity in johnsongrass is limited by its largely selfing breeding system. Interestingly, selfing does reflect uniparental reproductive capacity, which is adaptive
when spreading to recently disturbed areas where the availability of conspecific pollen may be limited. In the case of velvetleaf, enough variation has occurred to establish a north–south gradient of genotypes, a gradient which has implications for rapid selection to changing climate patterns. Warwick et al. (1984) suggested that genetic variation needed for this large shift in the ecology of northward-invading johnsongrass populations was likely provided by introgression from domesticated sorghum [Sorghum bicolor (L.) Moench], illustrating yet another mechanism by which weed species can gain selective advantages in association with agriculture.

**PREDICTION OF WEED EVOLUTION UNDER CLIMATE CHANGE: PROGNOSIS**

To consider the value of weed evolution in the development of predictive models of invasive species spread in a changing climate, it was useful to examine how the population dynamics of four very different species would be affected. As such, we selected four fairly distinct plant types—an obligatory outcrossing annual dicot, Himalayan balsam, a mostly selfing annual dicot, velvetleaf, a perennial dicot that reproduces via rhizomes but forms fertile hybrids, Japanese knotweed, and finally a perennial grass that is mostly selfing, johnsongrass. Predictably, these weeds rate somewhat differently across a list of 10 traits that could be significant targets for natural selection under climate change (Table 1). Fairly robust information is available on most of these traits, with the exception of “effective defenses against natural enemies,” although some information is available on velvetleaf in the context of biological control (Warwick and Black 1988). Because some of these traits are important for each of these four species, weed evolution is an important consideration in developing predictions of range expansion under climate change (Broennimann et al. 2007; Hulme 2009; Clements and DiTommaso 2011). However, potential mechanisms of weed evolution involve many different traits so predicting the exact course of evolution is very difficult. Perhaps CLIMEX-type models could just incorporate a “fudge factor,” based on the prediction that evolutionary change in invasive plant species like this will likely lead to greater range expansion that expected. However, in effect CLIMEX models already incorporate a degree of uncertainty in terms of the presentation of model results. Furthermore, Petitpierre et al. (2012) compared native and invasive ranges for 50 terrestrial plant species and found that less than 15% of invading species exhibited climate niche shifts beyond their native ranges. Their analysis did not include the four species examined in the present paper and was a statistical analysis of shifts in range not accounting for specific aspects of biology such as evolution, but nevertheless indicates that CLIMEX-type models should be able to predict introduced ranges most of the time (Petitpierre et al. 2012). Similarly, Alexander et al. (2012) concluded that ribwort plantain (Plantago lanceolata) exhibited niche conservatism in its introduced range.

Perhaps what is more important is that specific traits for a given weed species of interest must be carefully evaluated, and possibly incorporated into the models. Thus, in the case of Himalayan balsam, the nature of its highly effective dispersal through hydrochory along river systems needs to be better studied, in conjunction with its relatively labile genome promoted by outcrossing. By contrast, velvetleaf does not have particularly effective long-distance dispersal to be targeted by evolution, but its dispersal through time via seed dormancy and the particular relationship this has to climatic factors warrants more in-depth study. With Japanese knotweed, there are many factors to consider in assessing how adaptable this plant is to climate change, both because of its reproduction by seed and by vegetative means, although reproduction by seed is complicated by its being a member in a complex of Fallopia species capable of interbreeding and thereby producing unpredictable new forms from genetic recombination (Bourchier and Van Hezewijk 2010). Finally in the case of johnsongrass, it would be interesting to perform more in-depth work to better understand how differences observed between northern annual populations and southern perennial populations in North America might relate to the dynamics of climate change, i.e., could this plant expand its range even further north with the recent advent of annual forms in northern populations (Warwick et al. 1986)?

Another important consideration is how range expansion of a species’ northern edge concomitant with climate change influences selection pressures. Reed canary grass (Phalaris arundinacea L.) was shown to have greater genetic variation at the edges of its range, indicating greater potential for evolution in such areas (Lavergne and Molofsky 2007). Northern populations of saltcedar (Tamarix ramosissima Ledeb.) exhibited increased allocation to seedling roots relative to southern populations (Sexton et al. 2002). For the four species reviewed here, or any other species of concern, a concerted effort to compare populations along the northern edge of their ranges to more southerly populations would likely provide the best indicator of the potential for rapid evolution under climate change. For example, a common garden experiment such as the one carried out by Kollmann and Bañuelos (2004) in Europe for North American populations of Himalayan balsam would yield valuable insights into its population genetics on a continental scale. The study by Alexander et al. (2012) of ribwort plantain comparing latitudinal gradients in both introduced and native ranges also provides a good example of the needed research on population genetics. Alexander et al. (2012) found that the native populations followed a clearer trend in temperature tolerance, and that both types of populations failed to reproduce outside the normal range.
Many of the apparent differences among populations discussed in this paper may simply be phenotypic differences without a genetic basis. Although the genetic basis of many of the traits discussed is known, there is much work still to be done to understand the heritability of some of these traits. Not having an in-depth understanding of how these traits are controlled may have serious economic implications as a result of inaccuracies in predicting future distributions of invasive species in new regions of Canada. Furthermore, the information needed goes beyond simply knowing whether or not the differences are genetic, to questions of how rapidly these changes can take place, and what the characteristics and population dynamics of a given weed species are at the margins of its geographic range. We envision performing these types of investigations concomitantly with studies predicting the spread of plants using CLIMEX-type models that do not incorporate evolutionary change, but can provide a relatively rapid analysis of the general trend in range expansions of invasive plants.

ACKNOWLEDGEMENTS

We thank Shahrokh Khanizadeh, Editor-in-Chief, Canadian Journal of Plant Science, for the opportunity to participate in this special issue of CJPS, and also for his leadership role in the Plant Canada meeting as Plant Canada President. We also thank the many others who made Plant Canada 2011 a success, including the conference co-chairs Yousef Papadopoulos and David Percival. The excellent work of Christine Giles in searching out the literature on the four species profiled is gratefully acknowledged. We would also like to acknowledge Franz and Martha Steffan for lending DRC their cabin, which facilitated the timely drafting of the paper. Comments by three anonymous reviewers were very helpful in improving the manuscript.


