TAXONOMY, DISTRIBUTION, RARITY STATUS AND USES OF CANADIAN CACTI

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Summary. The cacti of Canada include four taxa: *Escobaria vivipara* var. *vivipara*, *Opuntia fragilis* var. *fragilis*, *O. humifusa*, and *O. polyacantha* var. *polyacantha*. These species are well adapted to survive the freezing temperatures prevalent during the long Canadian winters. Although they are widely distributed in the southern portion of the country, some species are rare or uncommon at the provincial level, e.g., *E. vivipara* var. *vivipara* in Saskatchewan and *O. polyacantha* var. *polyacantha* in British Columbia. *O. humifusa* is listed as rare at the national level but is common in the U.S. This paper presents an overview of the taxonomy, distribution, current status, and traditional aboriginal and modern uses of Canadian cacti. It also discusses the reproductive strategies and the correlation in the distribution of cacti at high latitudes with chromosome number variation (polyploidy).

Introduction

The cactus family includes remarkable plants with several morphological and physiological adaptations that enable them to survive the harsh Canadian winters. Unlike most flowering plant families that have fairly narrow ranges of distributions in terms of environment and latitude, the Cactaceae are distributed over a wide range of environments that include the humid, wet tropics, the tropical and temperate deserts, and the cold sub-arctic regions of Canada and Patagonia, where temperatures are often below -30°C. In spite of the severe winters with prevailing low temperatures that limit the distribution of many plant families, Canada's flora contains several succulent plants, including four species of cacti, which are the subject of this paper. Thus far, most literature on Canadian cacti has dealt mainly with the taxonomy, and few authors have discussed other aspects of their biology. Here I present an overview of the most relevant aspects regarding the natural history, taxonomy and uses of the native cacti of Canada based on literature review, herbarium specimens and personal observations.

Taxonomy

Although the taxonomic diversity of the Cactaceae in Canada is low, the family is distributed in the central and southern portions of the country, and its west to east range includes the provinces of British Columbia, Alberta, Saskatchewan, Manitoba, and Ontario. The Canadian flora includes four species in two genera: *Escobaria* Britton and Rose and *Opuntia* Mill. (Benson, 1982; Scoggan, 1979). These species have developed extreme resistance to cold and represent extreme examples in this typically xerophytic family.

The genus *Escobaria* includes small, globose cacti of the subfamily Cactoideae and is represented in Canada by only one species: *E. vivipara* (Nuttall) Buxbaum with its typical var. *vivipara*. *Coryphantha vivipara* (Nuttall) Britton and Rose is under the synonymy of *E. vivipara* (Anderson, 2001; Hunt, 1999). The second genus, *Opuntia*, belongs to the subfamily Opuntioideae and includes three species distributed in Canada. These species have been cited as *O. compressa* (Salisbury) Macbride, *O. fragilis* (Nuttall) Haw., and *O. polyacantha* Haw. (Scoggan, 1979); however, *O. compressa* is an invalid name (Benson, 1982) and is in synonymy. It is now recognized

as *O. humifusa* (Rafinesque) Rafinesque (Anderson, 2001; Hunt, 1999: McGregor et al., 1986). Because of this, the binomial *O. humifusa* is used in this paper. The names of the other two species (*O. fragilis* and *O. polyacantha*) are unchanged, but there are several varieties for each species. In Canada, we have only the typical variety of each species, i.e., *O. fragilis* var. *fragilis* and *O. polyacantha* (Harms, in press). For additional taxonomic and nomenclatural information a propos of these and other taxa, the reader is advised to consult Anderson (2001), Benson (1982), and McGregor et al. (1986) and references cited therein. Scientific names and taxonomic authorities for the species outside the Canadian range mentioned in this paper are maintained according to the original reference from which they were obtained.

Taxonomic Key to Native Cacti of Canada

The taxonomic key below is adapted from Anderson (2001), Harms (1983), and McGregor et al. (1986) and includes the major distinctive morphological characters useful in the identification of Canadian cacti.

- 3a. Stem segments usually less than 5 cm long to 2.5 cm wide, thick and not strongly flattened, terminal pads easily detached; areoles 3–6 mm apart; glochids brown to tan, conspicuous; spines 1–6, barbed, spreading straight, from 1–3 cm long. Flowers yellowish, sometimes greenish 3–4 cm long, up to 4 cm in diameter.



Fig. 1. *Escobaria vivipara* var. *vivipara* growing in the Qu'Appelle River Valley, Saskatchewan. A. plant. B. Flower detail. (Photos: G. Lee).

Distribution and Rarity Status of Canadian Native Cacti

Despite the widespread geographic distribution and the relative abundance of some species, overcollection and other human pressures, such as agricultural expansion, continue to threaten plant life. Habitat fragmentation and the removal of entire plants are major factors that deplete wild populations and lead to the loss of genetic diversity. Cacti, in general, are precious plants for collectors, and it appears that the rarer the plant, the more desirable the specimen. As a result of overcollection, the Cactaceae are listed in the appendices of the Convention on International Trade in Endangered Species (CITES).

Canadian native cacti are hardy species, which make them quite popular among horticulturists, collectors, and amateur gardeners, who commonly use them in rock gardens. Out of the four species found in Canada, only *Opuntia humifusa* is nationally rare and listed as an endangered species by the Committee of the Status of Endangered Wildlife in Canada (COSEWIC). In conjunction with the Canadian Conservation Data Centre (CCDC), COSEWIC compiles information about rare and endangered species of plants and animals in an effort to preserve Canadian biodiversity. To provide accurate information regarding the status of Canadian cacti in this paper, the data gathered from literature was checked against that of the CCDC's in Alberta, British Columbia, Manitoba, Ontario and Saskatchewan, as well as COSEWIC's database and species listing. The following summarizes the current status for each species.

Escobaria vivipara var. *vivipara* (Fig. 1) is found in the provinces of Alberta, Saskatchewan and Manitoba growing in dry plains and sandhills with gravelly, stony ground. *E. vivipara* is not threatened in Alberta, but it appears to be uncommon in Saskatchewan (Harms, in press), where the number of populations found is few and localized. In Manitoba, this species is listed as rare, and in the U.S. it is threatened in Colorado and rare in Minnesota (White and Johnson, 1980).

Opuntia fragilis var. fragilis (Fig. 3) is the most widespread cactus species throughout its range of distribution in Canada, occurring from British Columbia to Ontario. It is common in habitats with exposed bedrocks, in sandy and gravelly soils of prairie grasslands and in clay flats (Douglas et al., 1989; Moss, 1994; V. Harms, University of Saskatchewan, pers. com.), and has been seen in areas of light shade at edges of forested coulees and grasslands (Fig. 3A) (R. Olson, University of Saskatchewan, pers. com.). It is also distributed along the southern edge of the boreal forests of Saskatchewan, usually on sandy soils (Cota-Sánchez, pers. obs.). A similar distributional pattern has been observed in the boreal forest of Manitoba, where this species is found on southfacing outcrops (Frego and Staniforth, 1986). *O. fragilis* var. *fragilis* is excluded from the rare plant list in Canada. It is a widely distributed species in the Midwest of the U.S., but it is threatened in Iowa, Michigan, and Wisconsin (Klinkenberg, 1987).

Opuntia humifusa (Fig. 2) is the only cactus native to Ontario and is restricted to the southern part of the province, mainly Pelee Island and Point Pelee (Klinkenberg, 1987; Reznicek, 1982), and ranges south to the eastern states of the U.S. and to northern Mexico (McGregor et al., 1986). It is usually found in sand dunes, prairies (Fig. 2A), and open savannahs with dry, sandy soil. At the national level, *O. humifusa* was first included in the rare category by Argus and White (1977). More recently, the status of this species was reevaluated and is now listed as an endangered species in Canada (Klinkenberg, 1987; Klinkenberg and Klinkenberg, 1985). Although this species is rare in Canada, it is abundant just to the south in the U.S.

Opuntia polyacantha var. polyacantha (Fig. 4) is common in Canada. This species is distributed in the provinces of British Columbia, Alberta, Manitoba, and Saskatchewan (Douglas et al., 1989; Moss, 1994; Scoggan, 1957), and ranges into the western U.S. and northernmost part of Mexico (Anderson, 2001). *O. polyacantha* is found in prairie habitats with dry alkaline and sandy soils and banks of coulees (Fig. 4A), most frequently in open, exposed areas (Fig. 4B). With the exception of British Columbia, where this species is listed as rare with an R3 category or scattered

populations (Straley, Taylor and Douglas, 1985), it is not at risk throughout its range of distribution (COSEWIC, 2000; Harms, in press).

Doubtful Species. According to Scoggan (1979), reports of Coryphantha missouriensis (Sweet) Britton and Rose (currently accepted as Escobaria missouriensis (Sweet) D. R. Hunt) in Manitoba in the early 1900s remain obscure and require corroboration of their occurrence in Canada.



Fig. 2. *Opuntia humifusa*. A. Plant blooming in Point Pelee National Park, Ontario (Photo: M. J. Oldham). B. Stem detail and necrotic tissue (indicated by the arrow) possibly due to freezing damage (Photo: C. V. Boskirk). C. Flower detail of a plant growing in Sussex County, Delaware (Photo: C. Gracie).



Fig. 3. *Opuntia fragilis* var. *fragilis* in Saskatchewan. A. Habitat of *O. fragilis* var. *fragilis* in Saskatchewan Landing Provincial Park. This species is typically found in the edges of forested coulees and grasslands, often shaded by grasses and shrubs (Photo: R. Olson). B. Plant growing in Matador Ranch in SW Saskatchewan (Photo: G. Lee).



Fig. 4. *Opuntia polyacantha* var. *polyacantha* in Saskatchewan. **A.** The eroding sandy banks of coulee (seen in the distance), Saskatchewan Landing Provincial Park, are often good habitat for this species (Photo: R. Olson). B. A patch of *O. polyacantha* var. *polyacantha* growing on exposed, sandy washout at the base of coulee in Saskatchewan Landing Provincial Park (Photo: R. Olson). C. Plant growing in the Old Man On His Back conservation area located in the SW corner of Saskatchewan (Photo: G. Lee). D. Flower detail (Photo: G. Lee).

The Northernmost Distribution of the Cactaceae

It is evident that the specialized morphological features in the Cactaceae are directly related to the environment in which they are predominant, i.e., usually arid and semi-arid habitats. However, some species occur beyond what is considered the "normal" ecological environments for the family, such as humid tropical rain forests (where they often grow as epiphytes) and areas of high latitudes (and altitudes) characterized by freezing temperatures. Out of an estimated 20 cold-resistant genera of cacti listed by D'Arcangeli (2002) and Nobel and Bobich (2002), the Canadian cacti are most adapted to withstand cold, harsh winters.

Tolerance to low temperatures varies among cactus species. The most-cold resistant cacti in the Northern Hemisphere are *Escobaria vivipara* var. *vivipara*, *Opuntia fragilis* var. *fragilis*, *O. humifusa*, and *O. polyacantha* var. *polyacantha*. These exceptional species have evolved to withstand long and extended periods of freezing temperatures, which affect important physiological processes (photosynthesis and respiration) for the survival of the species. The extreme low temperatures that can be tolerated for these species varies from -48° C in *O. fragilis* -25^oC in *O. humifiusa*, -18^oC in *O. polyacantha*, and -22^oC in *E. vivipara* (Nobel and Bobich, 2002).

The mechanisms of how cacti cope with the effects of low temperature are not fully understood. Several physiological adaptations have been attributed to the ability of some cacti to survive in extremely low temperatures, namely cold-hardening, growth habit, and changes in water content and osmotic pressure (Gibson and Nobel, 1986; Nobel and Bobich, 2002). Super-cooling or the cold-hardening process is an inherent cold-acclimatization of plants as a response to the gradual decrease in temperatures from fall to winter and can increase the chances of survival during winter. This ability to harden is common in most plants. It has been reported in *E. vivipara* and *O. humifusa*, and it has been suggested that cold-hardening prevents damage from freezing by increasing protection of membrane proteins and tolerance to intracellular dehydration (Gibson and Nobel, 1986).

Low growth habit in cacti has been correlated with their distribution at higher latitudes and altitudes as an adaptation to avoid cold, windy conditions and to take advantage of thermal insulation from snowfalls. As a result, low-growing species of cacti are most likely to occur at higher latitudes in both the northern and southern hemispheres (Nobel and Bobich, 2002). For instance, *Eriosyce ceratistes* Britton and Rose (South America), and *Escobaria vivipara*, *Pediocactus simpsonii* (Engelm.) Britton and Rose (North America) are most likely to survive at higher latitudes than cacti with columnar or arborescent habit, such as *Carnegiea gigantea* (Engelm.) Britton and Rose and *Lophocereus schottii* (Engelm.) Britton and Rose (Nobel and Bobich, 2002).

On the other hand, the gradual loss of water content in cladodes of *Opuntia humifusa* is important for tolerance to lower temperatures (Nobel, 1988). According to this source, water loss in this species is up to 35% in winter. In Saskatchewan and Alberta, plants of *O. fragilis* var. *fragilis* and *O. polyacantha* var. *polyacantha* also experience water loss in winter. The plants start an apparent dehydration process as the temperatures drop in the fall. As a consequence of water loss, the cladodes wrinkle during winter and then rehydrate in spring when water becomes available (Cota-Sánchez, pers. obs.). A similar condition has been reported in *O. humifusa* in response to exposure to low temperatures (Nobel and Bobich, 2002). Their ability to survive in low temperatures for extended periods is also correlated with the ability of the plant to control a net CO_2 uptake (Nobel, 1988), which is greatly reduced as the photosynthetic rate decreases when plants enter an apparent latent stage.

Cellular death in cacti as a result of low temperature damage is due to shrinkage of protoplast and cell desiccation, which gradually cause death because of the affects on the structure and function of cellular membrane and enzymatic systems (Nobel and Bobich, 2002). Death by freezing reflects intracellular dehydration (Nobel, 1988) and is evidenced by necrotic tissue in areas of the plant exposed (Fig. 2B). In addition to the inherent physiological and morphological adaptations to low temperatures, the key to the success of these species in higher latitudes is correlated with the microhabitat and ecological conditions in which they occur, e.g., southern exposures and protected or sheltered areas which are relatively more favorable for their survival. Moreover, low growth habit along with the thermal insulation that snow cover provides are relevant for the survival of many plant species (Geiger, 1965), as the moisture of the microhabitat reduces stem water loss, preventing cellular damage due to desiccation (Nobel, 1988).

The four Canadian native cacti are far beyond the frost line to which most cacti are restricted. The following summary of the distribution of cacti in Canada is based on data compiled from the collections of major Canadian herbaria, namely the Royal British Columbia Museum Herbarium (V), the University of Alberta (ALTA), the University of Winnipeg (UWPG), L'Université de Montreal (MT), the University of Regina (USAS), and the University of Saskatchewan (SASK). The data indicate that *Opuntia fragilis* var. *fragilis* is the cactus that reaches the northernmost distribution. Several herbarium specimens collected in the Peace River area in Alberta support the distributional range of this species (Table 1). According to information obtained from herbarium specimens, the northernmost locality of this species is recorded from the Beatton River, SW of Cecile Lake at 56° 17' N latitude and 120° 39' W longitude (Table 1). The area of the Peace River system and the environs of the town includes a mixture of cropland, rangeland and pasture in which *O. fragilis* var. *fragilis* grows particularly well on hillsides and flat areas with sandy and/or clay soils (Moss, 1994).

Table 1. Label information of four herbarium specimens with the northernmost localities of *Opuntia fragilis* var. *fragilis*. Altitude information is given whenever it was obtained from labels. Abbreviations indicate the acronyms of the herbaria in which the specimens are deposited. ALTA = University of Alberta, SASK = University of Saskatchewan, V = British Columbia Museum Herbarium.

Locality	Coordinates	Collector name & no.	Herbarium
			& acc. no.
ALBERTA. Beaton River, SW Cecile Lake. 610 m alt.	56 [°] 17'N and 120 [°] 39'W	L. E. Pavlick & B. Taylor, 79-717. 7/16/1979	V - 98316
ALBERTA. Bear Flat Approx. 455-640 m alt.	56 [°] 16'N and 121 [°] 10'W	T. C. Brayshaw, 6092. 8/20/1976.	V - 92481
ALBERTA. Peace River Town	56 [°] 15'N and 117 [°] 17'W	E. H. Moss, 6107. 7/17/1941	ALTA – 12870
ALBERTA. E Peace River Town	56° 14'N and 117° 16'W	N. A. Skoglund, 934. 6/19/1973	SASK – 57111
ALBERTA. N Peace River System (see Scoggan, 1979)			

Factors Influencing Distribution

In addition to their morphological and physiological degrees of specialization, the colonization and survival success of cacti in Canada may be explained in part by their sexual and asexual reproductive versatility. Sexual reproduction is common in the family, but several species in the Opuntioideae rely almost entirely on vegetative reproduction. According to field observations by Vern Harms (University of Saskatchewan) in Saskatchewan over the last quarter century, in most years *Opuntia polyacantha* blooms quite prolifically (Fig. 4C) over a relatively short period of time in late spring–early summer. Insects, such as bees, visit these blossoms, implying entomophilous pollination and sexual reproduction. For *O. fragilis* in Saskatchewan, on the other hand, anthesis is very rare and Harms does not recall ever seeing this prickly-pear flowering in the field; however, some herbarium specimens do have flowers. One would assume frequent vegetative propagation simply due to the terminal pads detaching so readily and dispersing via animals. Perhaps in Saskatchewan, this may represent the species' main or almost only reproductive strategy.

Asexual reproduction, in the form of apomixis, in the many-branched *Opuntia* species represents a reproductive advantage for colonizing new habitats. Vegetative reproductive strategies coupled with high dispersal and establishment capabilities have played a major role in the wide distribution of some species of *Opuntia*. In fact, dispersal via apomixis is more efficient in plants with small detachable stem pads. Such is the case in O. fragilis, which exhibits one of the highest dispersal rates in the Cactaceae, ranging from Northern Mexico to south-central Canada. Frego and Staniforth (1986) explain that the distribution of O. fragilis in the boreal forests of southern Manitoba is related to the species' ability to disperse entirely by vegetative means. According to these authors, there is evidence for three dispersal mechanisms in this species: epizoochory, geochory, and hydrochory. Epizoochory involves the typical breakage of terminal pads that act as diasporas when the spines attach to the fur of animals, facilitating dispersal. This strategy is also a common spreading mechanism in other *Opuntia* species of southwestern U.S., Mexico and other areas of South America (Anderson, 2001; Cota-Sánchez, pers. obs.). In geochory the detached pads tend to roll downhill until the plant anchors in the substrate whenever the conditions are appropriate. Frego and Staniforth (1985) also provided evidence that pads of O. fragilis that roll down to the river can be dispersed via hydrochory, an unusual dispersal mechanism in the family. The pads float for a period of 40 days or more until the plants anchor along riverbanks. Finally, the edible fruits of Escobaria vivipara and Opuntia spp. provide other possibilities for dispersal in new environments when animals distribute seeds far away from the original sites. Overall, these strategies provide means to increase dispersal distance and colonization of other habitats.

Vivipary (the germination of seeds before they are shed from the parental plant) has been reported in *Escobaria vivipara* (Cota, 1993; Zimmerman, 1985), *Epiphyllum phyllanthus* (L.) Haw. (Conde, 1975) and *Rhipsalis pilocarpa* Löfgren (Lombardi, 1993). It appears that the specific epithet in *E. vivipara* refers to its prolific habit (Mitich, 1964). Thus far, this survival strategy is not documented in populations of the Canadian prairies; nevertheless, it would be of significance to investigate the occurrence of this survival mechanism in these latitudes with short growing season. Hence, vivipary may be favorable in areas with relatively fast photoperiod changes (the shortening of day length along with the changing of environmental conditions), as it confers advantages by providing shelter for young seedlings and protection from desiccation and low temperatures. Finally, although *Escobaria vivipara* is diploid in southern U.S. (Remski, 1955; Weeding and Powell, 1978), I predict that this species is polyploid in these latitudes and perhaps partially infertile (low seed-set). Hence, agamospermy (production of seeds without sexual fusion) is probably the only mechanism by which viable seeds are produced, but studies of the reproductive biology of this species are needed to test this hypothesis.

Johnson and Packer (1965) suggest that hybridization (the formation of offspring involving parents of two different species) and polyploidy (having more than twice the normal haploid number of chromosomes) are equally important in the evolution of plants in areas of high latitudes, especially in the arctic and sub-arctic regions. In the Cactaceae, particularly in *Opuntia*, natural hybridization is associated with polyploidy and/or asexual reproduction (Pinkava et al., 1985). Although hybridization has not been documented in the Canadian opuntias, the process is suspected to occur in nature, as indicated by the existence of populations with a morphology intermediate between *O. fragilis* var. *fragilis* and *O. polyacantha* var. *polyacantha* (V. Harms, University of Saskatchewan, pers. com).

Polyploidy has been important in the evolution of the Cactaceae (Gibson and Nobel, 1986), particularly in the genus *Opuntia* (Pinkava et al., 1985). It is quite likely that the same premise applies to Canadian species, as polyploidy has been reported in *O. compressa* (2n=4x=44) (Katagiri, 1953; Marcucci and Tornadore, 1997) and *O. fragilis* (2n=3x=66) (Pinkava et al., 1977). In addition, early reports of chromosome numbers in *O. polyacantha*, including populations from Alberta and

Saskatchewan, indicate that this taxon exhibits different ploidy levels throughout its range in the U.S. and Canada. Stockwell (1935), in a survey including North American cacti, reports the interesting trend of an increase in chromosome number (and thus ploidy level) with increase in latitude in *O. polyacantha*. According to his data, populations of this species in Colorado are diploid (2n=2x=22), plants from Saskatoon, Saskatchewan, and from southern Alberta are tetraploid (2n=4x=44), and specimens from the Peace River area in northern Alberta are hexaploid (2n=6x=66). In short, there is a tendency for increasing chromosome number at higher latitudes. A similar trend for the increase in ploidy level with increase in latitude in the Cactaceae has been reported in *Echinocereus* Engelm. (Cota and Philbrick, 1994). Additional data supporting lower ploidy levels (2n=2x=22) of *O. polyacantha* at lower latitudes have been reported in populations from Texas by Pinkava et al. (1992) and Weedin and Powell (1978). Overall, polyploidy has been important in the adaptation of these species to the long periods of freezing temperatures and in the colonization of high latitude environments.

Economic Uses

As in many regions of Central and South America, indigenous people in Canada have used cacti as an important source of food and medicine. The native cacti of Canada are also commonly used in horticulture. Following is a summarized account of the past and current uses of these plants.

Escobaria vivipara. Indigenous people in Saskatchewan eat the fleshy, juicy fruits as part of their diets (Harms, 1983). Similarly, the Blackfoot Indians, who occupy areas of the eastern part of the Rocky Mountains (southeastern corner of Alberta, the southwestern of Saskatchewan and central Montana), use the fruits as a drug and as food (Johnston, 1970). The fruits are eaten to treat diarrhea and are also consumed fresh or boiled to make candy (Moerman, 1988).

Opuntia fragilis. The flesh of this plant was used by the Okanagan-Colville to treat skin infections and was eaten for its diuretic properties. The stems were used as food by the Okanagan-Colville and Shuswap (Moerman, 1988). A novel use of this plant was that of the Okanagan-Colville, who used the spines as fishhooks (Moerman, 1988). This species is frequently used in landscaping by gardeners (Bernshaw and Bernshaw, 1984).

Opuntia humifusa. In the Plains regions of the U.S., the Dakota, Lakota, Nanticoke, and Pawnee tribes apply the peeled stems of *O. humifusa* to injured areas to treat various types of wounds, warts, and snakebites. This species was also used as a source of dyes (Moerman, 1988). Because of its hardiness, it is highly appreciated by gardeners (Klinkenberg, 1987).

Opuntia polyacantha. In Saskatchewan, the stem pads are used as food for humans and livestock (Harms, 1983). Various North American tribes have used the stems and fruits of this species for different purposes. As part of their diet, the Blackfoot Indians ate stems after removing the spines and cuticule, and fresh portions of the stem were used to treat wounds and warts (Johnston, 1970). Other uses of this plant include as an ointment for dermatitis by the Okanagan-Colville and as a dye (from the red fruits) by the Navajo (Moerman, 1988). Johnston (1970) also reports one of the most striking uses of this species: the Blackfoot used it to heal wounds by sticking spines into the affected part of the body and then igniting them. According to their beliefs, the spines that sparked and burned the brightest were the most effective in the healing process.

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Literature cited

Anderson, E. A. 2001. The Cactus Family, Timber Press, Portland, OR. 776 pp.

Argus, G. W., and D. J. White. 1977. *The Rare Vascular Plants of Ontario*. Syllogeus, No. 14. National Museums of Canada, Ottawa. 62 pp.

Benson, L. 1982. *The Cacti of the United States and Canada*. Stanford University Press, Stanford, CA. 1044 pp.

Bernshaw, E. & N. 1984. Cacti in Canada. Nature Canada 13: 22-27.

COSEWIC. 2000. Ontario Plants at Risk: http://www.rbg.ca/cbcn/en/atrisk/par_ont.html.

Conde, L. F. 1975. Vivipary in Epiphyllum. Cact. Suc. J. (U.S.) 47: 38-39.

Cota, J. H. 1993. Pollination syndromes in the genus Echinocereus: A review. Cact. Suc. J. (U.S.) 65: 19-26.

-----, and C. T. Philbrick. 1994. Chromosome number variation and polyploidy in the genus *Echinocereus* (Cactaceae). *Amer. J. Bot.* 81: 1054–1062.

D'Arcangeli, E. 2002. Cold Resistance of some cacti. Piante Grasse 4: 1-2.

Douglas, G. W., Gerald B. Straley, and D. Meidinger. 1989. Cactaceae. In: *Vascular Plants of British Columbia* Part 1, pp. 129. Special Report Series No. 2, 158 pp. Ministry of Forests, BC.

Frego, K. A., and R. J. Staniforth. 1986. Factors determining the distribution of *Opuntia fragilis* in the boreal forests of southeastern Manitoba. *Can. J. Bot.* 63: 2377–2382.

- Geiger, R. 1965. The Climate Near the Ground. Harvard University Press, Cambridge. 611 pp.
- Gibson, A. C., and P. S. Nobel. 1986. The Cactus Primer. Harvard University Press, Cambridge, MA. 286 pp.

Harms, V. L. 1983. Native Cacti of Saskatchewan. Blue Jay 41: 131-139.

- -----. 2003. Checklist of the vascular plants of Saskatchewan and the provincially and nationally rare native plants in Saskatchewan. Extension Division, University of Saskatchewan, Saskatoon, 328pp.
- Hunt, D. 1999. CITES. Cactaceae Checklist. 2nd. Ed., Royal Botanic Gardens Kew.
- Johnson, A. W., and J. G. Packer. 1965. Polyploidy and environment in arctic Alaska. Science 148: 237–239.

Johnston, A. 1970. Blackfoot Indian utilization of the Flora of the Northwestern Great Plains. *Econ. Bot.* 24: 301–324.

Katagiri, S. 1953. Chromosome numbers and polyploidy in certain Cactaceae. *Cact. Suc. J.* (U.S.) 25: 141–143.

Klinkenberg, B. 1987. Rare Species of Cactaceae. In: *Atlas of the Rare Vascular Plants of Ontario*. G. W. Argus, K. M. Pryer, and D. J. White (Eds.). National Museum of Canada, Ottawa.

-----, and Klinkenberg, R. 1985. Status report of the Eastern prickly pear cactus *Opuntia humifusa* in Canada. Committee on the Status of Endangered Wildlife in Canada. 43 pp.

Lombardi, J. A. 1993. Vivipary in Rhipsalis pilocarpa Löfgren (Cactaceae). Cienc. Cult. 45: 407.

Marcucci, R., and N. Tornadore. 1997. Mediterranean chromosome number reports. *Flora Mediterranea* 7: 262267.

McGregor, R. L., T. M. Barkley, R. E. Brooks, and E. K. Schofield. 1986. Cactaceae. In: *Flora of the Great Plains*. McGregor et al. (Eds.). pp. 153–160. University of Kansas Press, Lawrence.

Mitich, L. W. 1964. North Dakota native cacti. Cact. Suc. J. (U.S.) 36: 42-44.

Moerman, D. E. 1988. Native American Ethnobotany. Timber Press, Portland, OR.

Moss, E. H. 1994. Cactaceae. In: The Flora of Alberta. 2nd. Ed., pp. 409. University of Toronto Press. Toronto.

- Nobel, P. S. 1988. *Environmental Biology of Agaves and Cacti*. Cambridge University Press, Cambridge. 270 pp.
- ----- and Bobich, E. G. 2002. Environmental Biology. In: *Cacti: Biology and Uses*. Nobel, P. S. (Ed.), pp. 57–74. University of California Press, Berkeley.
- Pinkava, D. J., L. A. McGill, and T. Reeves. 1977. Chromosome numbers in some cacti of Western North America-III. *Bull. Torrey Bot. Club* 104: 105–110.

- -----, M. A. Baker, B. D. Parfitt, M. W. Mohlenbrock and R. D. Worthington. 1985. Chromosome numbers in some cacti of Western North America-IV. *Syst. Bot.* 10: 471–483.
- -----, B. D. Parfitt, M. A. Baker, and R. D. Worthington. 1992. Chromosome numbers in some cacti of Western North America-VI, with nomencaltural changes. *Madroño* 39: 98–113.
- Remski, M. F. 1955. Cytological investigations in *Mammillaria* and some associated genera. *Bot. Gazzete* 116: 163–171.
- Reznicek, A. A. 1982. The cactus in southwestern Ontario. Ont. Field Biol. 36: 35-38.
- Scoggan, H. J. 1957. Cactaceae. In: *The Flora of Manitoba*. Pp. 400–401. National Museum of Canada Bulletin No. 140, Biological Series 47. 618 pp.
- -----. 1979. Cactaceae. In: *The Flora of Canada* Part 4, pp. 1119–1120. National Museums of Canada, Ottawa.
- Stockwell, P. 1935. Chromosome numbers of some of the Cactaceae. Bot. Gazette 96: 56-570.
- Straley, G. B., R. L. Talor, and G. W. Douglas. 1985. *The Rare Vascular Plants of British Columbia*. Syllogeus No. 59. National Museums of Canada, Ottawa.165 pp.
- Weedin, J. F., and M. Powell. 1978. Chromosome numbers in Chihuahuan Desert Cactaceae. Trans-Pecos Texas. *Amer. J. Bot.* 65: 531–537.
- White, D. J., and K. L. Johnson. 1980. *The Rare Vascular Plants of Manitoba*. Syllogeus No. 27, National Museums of Canada, Ottawa. 76 pp.
- Zimmerman, A. D. 1985. Systematics of the genus *Coryphantha* (Cactaceae). Ph. D. Thesis. University of Texas, Austin.