Stewardship Account for
Clarkia purpurea ssp. quadrivulnera

Prepared for the
Garry Oak Ecosystems Recovery Team
March 2002
by

Brenda Costanzo,
BC Conservation Data Centre,
PO Box 9344
Station Provincial Government,
Victoria, BC
V8W 9M7

Funding provided by the Habitat Stewardship Program of the Government of Canada and the Nature Conservancy of Canada

STEWARDSHIP ACCOUNT

Clarkia purpurea ssp. quadrivulnera

Species information:

Kingdom: Plantae
Subkingdom: Tracheobionta
Superdivision: Spermatophyta
Division: Magnoliophyta
Subclass: Rosidae
Order: Myrtales
Family: Onagraceae

(Above classification is from U.S.D.A. Plants Database, 2001)

Genus: *Clarkia*
Species: *purpurea*
Subspecies: *quadrivulnera* (Dougl. *ex* Lindl.) *ex* H.F. & M.E. Lewis
Section Godetia (Lewis, 1955)

Clarkia purpurea (Curtis) Nels. & Macbr. ssp. *quadrivulnera* (Dougl.) H. Lewis & M. Lewis; Small-flowered Godetia

Synonyms:

Clarkia quadrivulnera (Dougl.) *ex* Lindl. (Douglas *et al*., 2001)

Clarkia quadrivulnera (Dougl. *ex* Lindl.) A. Nels. & J.F. Macbr.
Godetia quadrivulnera var. *vacensis* Jepson
Godetia purpurea (W. Curtis) G. Don var. *parviflora* (S. Wats.) C.L. Hitchc.
Godetia quadrivulnera (Dougl. *ex* Lindl.) Spach

(Above from ITIS data base, 2001; USDA Plants database, 2001)

Oenothera quadrivulnera Douglas (GRIN database, 2001)

Hitchcock and Jepson recognized two genera: *Clarkia* and *Godetia* based on petal shape The section Godetia consists of a diploid, tetraploid and hexaploid series, of which *C. purpurea* and *C. prostrata* is the latter (Lewis and Lewis, 1955). Lewis and Lewis (1955) felt that for *Clarkia purpurea* there were ephemeral local races due to hybridization. Some of these could be separated based on conspicuous morphological characters to the subspecies level. However, these subspecies were artificial and not distinct geographical nor ecological races.

The normal haploid chromosome number for *Clarkia purpurea* ssp. *quadrivulnera* is 26. (Lewis and Lewis, 1955), and the original ancestral *Clarkia* is assumed to have had a chromosome number of 7. An increase in chromosome number in *Clarkia* is correlated to habitat preference, usually towards more xeric habitats (Lewis, 1953a). Ancestral *Clarkias* were thought to have large lavender-pink, bowl-shaped flowers with petal markings. These were self-compatible, with some outcrossing. *Clarkia* speciation is thought to have occurred mainly in habitats from the north to south and from mesic to xeric sites (Sytsma and Smith, 1990).

Clarkia purpurea (hexaploid) is morphologically similar to *C. affinis* (allohexaploid) and it is thought that they have a common tetraploid parent. *Clarkia purpurea* also morphologically resembles *Clarkia tenella*, a South American tetraploid species. The tetraploid ancestor(s) of *C. purpurea* could have been close to *C. tenella.* Flowers in some *C. purpurea* ssp. *quadrivulnera* are very similiar to *C. davyi* that is an ecologically specialized coastal species of California (Lewis and Lewis, 1955).

The genus name honours Captain William Clark of the Lewis & Clark expedition of 1804-1806 (Clark 1976), while *purpurea* is likely in reference to the purple corolla.

Description:

Annual herb from a slender taproot; stems erect, 10-70 cm tall, usually simple or branched from the base, glabrous or hairy. Leaves linear to lanceolate, 1.5-5 cm long, entire, usually unstalked. Inflorescence an open spike, loosely-flowered, buds erect; hypanthium 2-10 mm long; corollas bowl-shaped, tending to close at night; petals lavender to purple and often with a darker spot above, fan-shaped to elliptic, 5-15 mm long; sepals staying fused in 2's or coming free, usually bent back; fertile stamens 8, all alike; stigmas elliptic-oblong, about 1.5 mm long, lavender to purple or dark wine-red; stigma not exceeding anthers. Fruits, capsules 1-3 cm long, round or 4-angled, ribbed, densely hairy, short-beaked. (Douglas *et al*., 2001).

Range and Known Distribution:

Rare in British Columbia, known only from Mt. Tzuhalem on Vancouver Island, and Saturna Island. South to Arizona and California and reported in Oregon and Washington (NatureServe web site, 2001).

Lewis and Lewis (1955) described the distribution from Washington, Oregon, California, Arizona (Gila and Pima counties) and Baja California.

Hickman (1993) for *C. purpurea* ssp. *quadrivulnera* he states that the range of the species is highly variable, whereas the Jepson Flora Project website says the range of the species is highly variable to Washington, Arizona and Baja California.

Hitchcock (1984) for *Clarkia quadrivulnera* states that this species occurs occasionally, but is rather rare on prairies from the Olympic Peninsula to Tacoma, and up the Columbia River Gorge to Klickitat County, Washington. From there, it occurs in the Hood River County and the Willamette Valley Oregon and further south where it becomes more abundant to the south, particularly in valleys and foothills into Baja California.

Habitat Description:

Lewis and Lewis (1955) state that *Clarkia purpurea* ssp. *quadrivulnera* occurs in open sites in grassland, woodland, chaparral and coastal sage. In California, this species is found in open, grassy or shrubby places at elevations of 500 m or less, west of the Sierra Nevada and in the southern mountains (Munz 1965). Peck (1961) describes *Godetia quadrivulnera* inhabiting dry, open grasslands west of the Cascade Mountains to Washington and California.

In British Columbia, this subspecies occurs in dry, open areas in the steppe zone. It has been collected from sunny, grassy slopes, often south or west-facing, and dry ridges and is frequently found growing in association with *Stipa lemmonii* and *Clarkia amoena* ssp. *lindleyi* (CDC HERB database, 2001). In assessing the horticultural potential of the subspecies, Hickman (1993) indicates that excellent drainage is required and that the plant does best in full sun. Elevations in British Columbia are 120 to 320 m.

Other species at risk were listed as occurring in same habitat for Mt. Tzuhalem are *Aster curtus*, *Balsamorhiza deltoidea*, *Sanicula bipinnatifida* and *Viola praemorsa* ssp. *praemorsa* (CDC HERB database, 2001). No information is available on habitat availability and net trends in habitat change. There are non-native grasses at the two sites (*Aira caryophyllea*, *Anthoxanthum odoratum. Bromus hordeaceus, B. sterilis* and *Cynosurus echinatus*).

This subspecies is common in California. In British Columbia, the Mt. Tzuhalem site is a protected area (Ecological Reserve), however, the Saturna Island site is on private land**.**

Status of Species:

Global rank: G5T5
Canada Heritage Rank: NE
British Columbia: S1; red-listed
California, Oregon, Washington: SR
Pennsylvania: SE

A related species, *Clarkia rhomboidea* (common clarkia) is blue-listed, but it occurs in southeastern British Columbia only (Douglas *et al.*, 2002).

This subspecies (CDC HERB database collections George W. Douglas #13337 and A. Ceska #31124) were originally identified as ssp. *vimena*, but they have been reindentified as ssp. *quadrivulnera* by George W. Douglas based on. The former species does not occur in British Columbia (Douglas, George, pers. com.).

No other uses e.g. pharmacological, ethnobotanical, horticultural, except that some species of *Clarkia* (*Godetia*) are garden cultivars (Bailey and Bailey, 1976).

The Ecological Reserve at Mt. Tzuhalem is 25.98 acres (10.5 ha) and is protected provincially.

Life History:

a) General – *Clarkia* is a genus of annuals endemic to western temperate North America. All the species occur in distinct colonies of varying sizes from several hundred to several thousand individuals. Colonies generally exist for many years (up to 20) with little changes at the same site (Lewis, 1953b). They are associated with well-drained soils in open sites in oak woodland. Other species may occur in adjacent, drier communities (Lewis and Lewis 1955).

b) Phenology – Blooms May to July (Hitchcock *et al*., 1961). *Clarkia* flowering is promoted by long periods of light and relatively high temperatures. However, these high temperatures can also prevent all or many of the seeds from germinating. Mature seeds are brown or gray and covered with tubercles or scales. (Lewis and Lewis, 1955).

c) Pollination Biology – All Clarkia are self-compatible, but outcrossing does occur due to the stamens being shorter than the stigmas. In *C. purpurea*, the style is short, and although the anthers are pressed next to the stigma before the flower opens, no pollen is shed until after the flower opens. The anthers then bend away from the stigma. When the flowers close at night, if cross-pollination has not occurred, it is possible that the stigma could receive pollen as the anthers are pressed in close contact with the receptive stigma (Lewis, 1953b). There are some species that have cleistogamous flowers and are therefore almost exclusively self-pollinated (Lewis and Lewis, 1955). Most species of *Clarkia* were found to be strongly protandrous as the stigma does not open until at least a day after the anthers start to shed pollen (Raven, 1979).

The anthers of *Clarkia* have sporogenous cells in each anther that are separated by vegetative cells and arranged into vertical packets. *Clarkia purpurea* ssp. *quadrivulnera* is a hexaploid and in *Clarkia* the pollen in some hexaploid species is usually 4-, 5-, or 6-cornered. In *Clarkia purpurea* ssp. *quadrivulnera*, the trichomes on the surface of the pollen grain are lax, with larger trichomes being the viscin threads that are common in Onagraceae (Small *et al*., 1971). Pollen is shed during two to three days, and if the flower is not fertilized, they remain fresh for at least a week (Lewis, 1953b).

The principal pollinators of the genus are various kinds of bees (Lewis and Lewis, 1955) and syrphid flies (Raven, 1979).

Lewis and Lewis (1955) did various cross-pollinations on *Clarkia* species but the majority did not produce seeds. In some cases, either the pollen did not germinate or did not penetrate the style. Fertilization normally occurs within 38 to 40 hours after effective pollination, and unpollinated flowers remained fresh for a week or two until they abscised simultaneously at the base and the tip of the ovary. The interspecific hybrids that were produced, showed a reduction in fertility when they were selfed, backcrossed to either parent, or open pollinated near one or both of the parents. These hybrids produced very few seeds, or none at all in the latter. Travers (1999) studied the effects of fire on *Clarkia unguiculata* pollen, and found that pollen tubes grew faster on burned-environment individuals. Smith-Huerta and Vasek (1984) found that pollen of *Clarkia unguiculata* lost viability at room temperature or on the plant, but pollen retained viability for 35 days when stored at 5^{o}C.

Jones (1996) investigated pollinator behaviour and post-pollination reproductive success in *Clarkia gracilis*. They found that plants with spots on the petals had a reproductive advantage. Reproductive success in plants depends on pollination followed by fertilization and seed maturation. Pigments in flowers may affect pollinator behaviour in approach to, and actual foraging on a plant, serving as long-distance advertisements or as nectar guides at shorter range (Waser 1983; Stucky 1984; Waser & Price 1985). Therefore pigmentation patterns may influence pollinator visitation by enhancing visibility or by decreasing handling time, which would increase the net reward for the foragers.

C. gracilis is pollinated by bees and no pollinator preference was observed for spotted plants. They noted that pollen from spotted plants was more successful, perhaps in fertilizing ovules or because embryos with spotted sires were less likely to be aborted. The presence of the dark spots may create a better environment for pollen, perhaps by increasing floral temperature that have been shown to affect pollen development in some species, or perhaps genes linked to the spot locus affect pollen performance (Bennett et al. 1972). Related *Clarkia purpurea* ssp. *quadrivulnera* often has a darker spot on the petals, so it may be that similar mechanisms apply to this plant as well.

d) Reproduction - The following information deals with the biology of the Onagraceae in general, or related species of *Clarkia*, and was felt to be possibly relevant.

The reproductive structures of Onagraceae are conspicuous in two respects. First, the pollen grains are united by viscin threads (Skvarla *et al*., 1975; 1976), which facilitates movement of large numbers of pollen grains at a time and increases efficiency of pollination. Secondly, the stigmas are quite large, which exposes a large surface to pollinators. The Onagraceae also have quite low pollen-ovule ratios. Cruden and Jensen (1979) developed the hypothesis that viscin threads, which hold large numbers of pollen grains together in large clumps, and stigmas that are relatively large to the area of pollen on the pollinator, contribute to quite efficient pollination, and low pollen/ovule ratios reflect this efficiency. Low pollen/ovule ratios are an evolutionary response to efficient pollination. The more efficient the delivery of pollen, the lower the pollen/ovule ratio.

The transfer of large numbers of pollen grains at a time would appear to be adaptive in species with large numbers of ovules such as *Clarkia.*

e) Survival - Although no research specifically dealing with survivability of *Clarkia purpurea* ssp. *quadrivulnera* has been obtained, some work has been done recently on the survivability of another rare annual *Clarkia* that occurs along the west coast of North America in California, *Clarkia springvillensis* (McCue & Holtsford 1998). McCue and Holtsford investigated the possibility that the seed bank of this rare annual could act as a buffer against small population size. Falk and Holsinger (1991) and Ellstrand and Elam 1993) suggest that seed banks could be particularly important for many rare plants because of the genetic challenges to long-term survival that they face. For example, small numbers of individuals increase the susceptibility of populations to genetic drift (Barrett and Kohn 1991) and will increase the chance of inbreeding (Ellstrand 1992). In

Clarkia springvillenis the populations have a narrow distribution and the number of individuals in most populations is small. Fluctuations appear to correlate with winter and spring rainfall levels. *C. springvillensis* varies from thousands to no adult plants each year.

Based on work of Lewis (1962), it has long been thought that *Clarkia* species do not usually produce persistent seed banks. Lewis noted local extinction of multiple populations of *Clarkia,* and concluded that *Clarkia* seeds do not persist over multiple seasons. He did, however, accept that it maybe that what appeared to be local extinctions might actually be cases of prolonged dormancy. Many species of *Clarkia* have now been shown to exhibit characteristics associated with species that possess seed banks e.g. annual growth habit, early successional taxa that occur in variable habitats (Thompson 1987; Thompson *et al*., 1993). McCue and Holtsford believed that the increase observed in populations (for example 0 to 150 plants) from one year to the next in *Clarkia springvillensis* must be due to viable seeds in the soil, because the species does not possess obvious mechanisms for long-distance seed dispersal. They state that: (a) *C. springvillensis* does not exhibit the extreme detrimental genetic effects that might be expected when small populations are further reduced in size by stochastic events (b) the levels of diversity are fairly consistent with levels found within ecologically similar species and with widespread and small-ranging congeners and (c) differentiation among populations is relatively low relative to species with similar ecological and life history attributes (Hamrick and Godt 1990; McCue *et al*., 1996). They found that the genetic diversity of the seed bank was significantly higher than in the adult population. They further proposed that the seed bank may be partially responsible for keeping diversity high and differentiation low among these populations. This was due to buffering of populations from the effects of chronically small populations or events such as drought, fire or floods.

McCue and Holtsford's results demonstrate empirically that seed banks can have important effects on the amount and distribution of genetic variation, especially in small populations. They conclude that examination of the evolutionary dynamics of rare plants and decisions for their conservation should include consideration of seed bank effects.

f) Physiology – Nothing known.

g) Dispersal – In *Clarkia*, seed capsules average approximately 50 seeds that are shed gradually over several weeks or months. There is no known dispersal mechanism, and the seeds fall close to the parent plant (Lewis 1953b).

h) Nutrition & Interspecific Interactions – Nothing known.

i) Behaviour/adaptability - There is a paucity of information dealing with the behaviour/adaptability of *Clarkia purpurea* ssp. *quadrivulnera.* Potentially applicable information obtained pertaining to other related members of the genus is presented below.

After many years of study, Harlan Lewis (1962) proposed that rapid speciation in *Clarkia* was due to "catastrophic selection" or extinction of marginal populations followed by colonization. Parnell (1968) stated that in *Clarkia*, barriers to gene exchange within the species is usually related to hybrid sterility.

In light of increasing atmospheric greenhouse gases and concern regarding potential impact on native vegetation, St. Omer and Horvath (1983) investigated the effects of long-term increased atmospheric CO_2 on the germination of three native plant species, including a species of *Clarkia, C. rubicunda.* Seeds were provided with optimal natural conditions for germination and development but had elevated levels of CO_2 (from 0.3-0.21%). They noted no significant effect on seed germination of any of the species under investigation.

Smith-Huerta and Vasek (1987) investigated the effects of environmental stress on components of reproduction in *Clarkia unguiculata.* Investigations of drought impacts showed fewer main stem flowers were produced, and sometimes seed weight and seed numbers were also affected in drought-stressed plants. Seed number was also lower in flowers with stigmas more than 7 days old and seed weight was lower in plants with drought-stressed ovules. One episode of drought treatment was enough to decrease plant growth resources and hasten onset of senescence.

In *Clarkia,* little or no response to drought stress over time may reflect evolutionary adjustments to environments characterized by late-season drought (Vasek 1977). Plants survive by reallocation and reduced production of resources. For example, seed set is influenced by age class. The youngest *Clarkia* plants had low seed set because the flowers compete for resources with developing leaves and shoots. Slightly older plants have high seed sets. They develop fruits when plants have large numbers of productive leaves and leafy bracts. The oldest flowers have lower seed sets as plants approach senescence and have fewer functioning leaves, and therefore lower resource production (Leopold & Kriedemann 1975 and others). Consequently seed weight is reduced late in the growth cycle on plants with heavy fruit loads. In *Clarkia unguiculata,* seed set was maximized in flowers with stigmas expanded halfway and decreased somewhat irregularly in older flowers with stigmas more fully expanded and increasingly reflexed.

How the species is at risk

There are only two known occurrences of this species in British Columbia, and only one is protected (Ecological Reserve).

Management Recommendations:

Ensure protection of the Saturna Island site for this species.

References/Literature Cited:.

Barrett, S.C.H. & J.R. Kohn. 1991. Genetic and evolutionary consequences of small population size in plants: implications for conservation. In D.S. Falk & K.E. Holsinger, eds. Genetics and Conservation of Rare Plants. Pp. 3-30. Oxford University Press, New York.

Bennett, M.D., J.B. Smith & R. Kemble. 1972. The effect of temperature on meiosis and pollen development in wheat and rye. Can. J. Genet. Cytol. 14: 615-624.

British Columbia Conservation Data Centre, HERB database. 2001. British Columbia Ministry of Sustainable Resource Management, Terrestrial Information Branch.

British Columbia Conservation Data Centre, Tracking List. 2002. British Columbia Ministry of Sustainable Resource Management, Terrestrial Information Branch. Web site: http://srmwww.gov.bc.ca/cdc/trackinglists/red_blue.htm.

Clark, L.J. 1976. Wildflowers of the Pacific Northwest. Gray's Publishing Ltd., Sidney, B.C.

Cruden, R.W. & K.G. Jensen. 1979. Viscin threads, pollination efficiency and low pollen-ovule ratios. American Journal of Botany 66 (8): 875-879.

Douglas, George W., Del Meidinger & Jim Pojar, eds. 1999. Illustrated Flora of British Columbia. Volume 3: Dicotyledons (Diapensiaceae through Onagraceae). BC Ministry of Environment, Lands & Parks and B.C. Ministry of Forests, Victoria.

Douglas, George W., Del Meidinger, and Jenifer L. Penny. 2002. Rare Vascular Plants of British Columbia. BC Ministry of Sustainable Resource Management and BC Ministry of Forests. (in press).

Ellstrand, N.C. 1992. Gene flow by pollen: implications for plant conservation genetics. Oikos 63: 77-86.

Ellstrand, N.C. & D.R. Elam. 1993. Population genetic consequences of small population size: implications for plant conservation. Annual Review of Ecology and Systematics 24: 217-242.

Falk, D.A. & K.E. Holsinger. 1991. Genetics and Conservation of Rare Plants. Oxford University Press, New York.

GRIN database. 2001. Germplasm Resources Information Network. National Genetic Resources Program. Web site: www.ars-grin.gov/.

Hamrick, J.L. & M.J.W. Godt. 1990. Allozyme diversity in plant species. In: A.H.D. Brown, M.T. Clegg, A.L. Kahler & B.S. Weir (eds.). Plant Population Genetics, Breeding and Genetic Resources pp. 43-63, Sinauer, Sunderland, MA.

Hickman, J.C. (ed.). 1993. The Jepson Manual: Higher Plants of California. Univ. Calif. Press, Berkeley, CA. 1400 pp.

Hitchcock, C.Leo, Arthur Cronquist, Marion Ownbey and J.W. Thompson. 1984. Vascular Plants of the Pacific Northwest. Part 3: Saxifragaceae to Ericaceae. University of Washington Press, Seattle and London. 614 pp.

International Taxonomic Information System (ITIS), 2001. Web site: http://www.itis.usda.gov/.

Jepson Flora Project website: http://ucjeps.herb.berkeley.edu/.

Jones, K.N. 1996. Pollinator behaviour and post pollination reproductive success in alternative floral phenotypes of *Clarkia gracilis* (Onagraceae). International Journal of Plant Sciences 157 (6): 733-738.

Leopold, A.C. & P.E. Kreidemann. 1975. Plant Growth and Development. 2nd ed. McGraw-Hill Book Co., N.Y.

Lewis, H. 1962. Catastrophic selection as a factor in speciation. Evolution 16: 257-271.

________. 1953a. Chromosome phylogeny and habitat preference of *Clarkia*. Evolution 7:102-109.

________. 1953b. The mechanism of evolution in the genus Clarkia. Evolution 8(1):1-20.

Lewis, Harlan and Margaret Ensign Lewis. 1955. The Genus Clarkia. University of California Publications in Botany 20:251-392.

McCue, K.A., E.S. Buckler & T.P. Holtsford. 1996. A hierarchical view of genetic structure in the rare annual plant *Clarkia springvillensis* (Onagraceae). Conservation Biology 10: 1425-1434.

McCue, K.A. & T.P. Holtsford. 1998. Seed bank influences on genetic diversity in the rare annual *Clarkia springvillensis* (Onagraceae).

Munz, P.A. 1965. Onagraceae. North American Flora, Series II. Part 5: 1-278.

NatureServe. 2001. An online encyclopedia of life. Version 1.5. Arlington, Virginia, USA: Association for Biodiversity Information. Web site: http://natureserve.org.

Parnell, Dennis R. 1968. Reproductive barriers in *Clarkia deflexa.* Brittonia 20:387-394.

Raven, Peter H. 1979. A survey of the reproductive biology in Onagraceae. New Zealand J. of Bot. 17:575-593.

St. Omer, L. & S.M. Horvath. 1983. Potential effects of elevated CO_2 levels on seed germination of three native plant species. Botanical Gazette 144 (4): 477-480.

Skvarla, J.J., P.H. Raven, & J. Praglowski. 1975. The evolution of pollen tetrads in Onagraceae. American Journal of Botany 62: 6-35.

Skvarla, J.J., P.H. Raven, & J. Praglowski. 1976. Ultrastructural survey of Onagraceae pollen. In I.K. Ferguson & J. Muller (eds.). The Evolutionary Significance of the Exine. Pp. 447-479. Linn. Soc. Sym. Ser. 1. Academic Press, London.

Small, E., I. J. Bassett, C.W. Crompton, and H. Lewis. 1971. Pollen phylogeny in Clarkia. Taxon 20(5/6):739-746.

Smith-Huerta, N.L. & F.C. Vasek. 1984. Pollen longevity and stigma pre-emption I Clarkia. Amer. J. Bot. 71(9):1183-1191.

Smith-Huerta, N.L. & F.C. Vasek. 1987. Effects of environmental stress on components of reproduction in *Clarkia unguiculata.* Amer. J. Bot. 74 (1):1-8.

Stucky, J.M. 1984. Forager attraction by sympatric *Ipomoea hederacea* and *I. purpurea* (Convolvulaceae) and corresponding forager behaviour and energetics. American Journal of Botany 71:1237-1244.

Sytsma, Kenneth J., James F. Smith and L.D. Gottlieb. 1990. Phylogenetics in *Clarkia* (Onagraceae): restriction site mapping of chloroplast DNA. Syst. Bot. 15(2):280-295.

Thompson, K. 1987. Seeds and seed banks. New Phytologist 106 (Supplement):23-34.

Thompson, K., S.R. Band & J.G. Hodgson. 1993. Seed size and shape predict persistence in soil. Functional Ecology:236-241.

United States Department of Agriculture, Plants Database. 2001. Natural Resources Conservation Service. Web site: http://plants.usda.gov/plants.

Vasek, F.C. 1977. Phenotypic variation and adaptation in *Clarkia*, section *Phaeostoma.* Systematic Botany 2: 252-279.

Waser, N.M. 1983. The adaptive nature of floral traits: ideas and evidence. Pp. 241-285, *In* L. Real, ed. Pollination Biology. Academic Press, Orlando, FL.

Waser, N.M. & M.V. Price. 1985. The effect of nectar guides on pollinator preference: experimental studies with a montane herb. Oecologia 67: 121-126.

Web pages searched:

Agricola (through UVIC library Gateway)

American Society of Plant Taxonomists: http://www.sysbot.org/members.htm

Annual Reviews of Ecology and Systematics (through e-journals) http://137.99.27.45/journals.html

Annual Reviews of Plant Physiology: http://plant.annualreviews.org/search.dtl

Botanical Electronic News: http://www.ou.edu/cas/botany-micro/ben/ben-srch.html

CalFlora: http://www.calflora.org

California Academy of Sciences: http://www.calacademy.org/

California Native Plant Society: http://ww.cnps.org/

California Natural Diversity Database: http://www.dfg.ca.gov/whdab/html/cnddb.html

Canadian Journal of Botany (through e-journals)

Center for Urban Horticulture: http://depts.washington.edu/urbhort/

Flowering Plant Gateway: http://www.csdl.tamu.edu/FLORA/newgate/cronang.htm

Flora of North America: http://hua.huh.harvard.edu/FNA/

Integrated Taxonomic Information System (IT IS): http://ww.itis.usda.gov/

International Journal of Plant Sciences (through e-journals)

International Organization for Plant Information: http://iopi.csu.edu.au/iopi/

Internet Directory for Botany: http://www.botany.net/IDB/

IUCN Species survival commission: http://iucn.org/themes/ssc/index.htm

Jepson Flora Project: http://ucjeps.herb.berkley.edu/jeps-list.html

Missouri Botanical Garden: http://www.mobot.org/welcome.html

National Agriculture Library: http://www.nal.usda.gov/

Native Plants Journal: http://nativeplants.for.uidaho.edu/

Nature Conservancy (NBII), National Biological Information Infrastructure: http://www.nbii.gov/search/sitemap.html

New York Botanical Garden Press (publications): http://www.nybg.org/bsci/spub/

Oregon Flora Project: http://www.oregonflora.org/index.html

Oregon Natural Heritage Program http://www.abi.org/nhp/us/or/index.htm

Oregon's Rare and Endangered plants: http://www.orst.edu/dept/botany/herbarium/info/re:html

Oregon State University Herbarium: http://www.orst.edu/dept/botany/herbarium

Search Index for American Literature (New York Botanical Garden): http://scisun.nybg.org:8890/searchdb/owa/www/ABL.searchform

Smithsonian Institute, Department of Systematic Botany: http://www.nmnh.si.edu/botany/

Smithsonian Institute, Department of Systematic Botany, publications: http://nmnhwww.si.edu/botany/pubs.htm

Synonymised Checklist of Vascular Flora of the United States, Canada and Greenland: http://shanana.berkeley.edu/bonap/checklist_intro.html

University of British Columbia, Herbarium: http://www.botany.ubc.ca/herbarium/

USDA Forest Service, Rare Plants: http://www.fs.fed.us/biology

USDA NRC Plant Materials http://plant-materials.nrcs.usda.gov/

US Fish and Wildlife Threatened and Endangered species systems (TESS): http://ecos.fws.gov/webpage/

US Fish and Wildlife Service, Endangered Species Program: http://endangered.fws.gov/

US Fish and Wildlife, journals on-line: http://www.fw.umn.edu/affiliate/journals.html

US Fish and Wildlife Service, Threatened and Endangered Plants and Animals: http://www.fws.gov

Washington Natural Heritage Program: http://www.wa.gov/dnr/htdocs/fr/nhp/wanhp.html

Washington Rare Plant Care and Conservation: http://depts.washington.edu/rarecare/

US Parks, Species in Parks: http://ice.ucdavis.edu/nps/

Authorities Consulted/Personal communications:

Clinebell, Richard. Missouri Botanical Garden, PO Box 299, St. Louis, MO. Phone: 314-577-0824. Email: Richard.clinebell@mobot.org (emailed, no response).

Hoch, Peter. Missouri Botanical Garden. PO Box 299, St. Louis, MO. Phone: 314-577-5175. Email: hoch@mobot.org (responded).

Janeway, Lawrence. Biol. Sciences Herbarium, California State University, 400 W 1st Street, Chico, CA. Phone: 530-898-5381 Email: LJaneway@csuchico.edu. (no response)

Jarrell, David. Dept. Biological Sciences/Jepson Science Centre, Mary Washington College, 1301 College Avenue, Fredericksburg, Virginia. Phone: 540-654-1196 Email: djarrell@mwc.edu (no response).

Levin, Rachel. Lab of Molecular Systematics, Smithsonian Museum Support Center, 4210 Silver Hill Road, Suitland, Maryland. Phone: 301-238-3444 Email: rlevin@onyx.si.edu (no response).