Liparis loeselii (L.) Rich. (yellow widelip orchid): A Technical Conservation Assessment

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Steven Rolfsmeier received his Master's degree in biology from the University of Nebraska–Lincoln in 1989 working on species richness gradients in the forest flora of the Missouri River valley. He received his Bachelor of Science degree from Doane College in Crete, Nebraska in 1987. He has worked periodically since 1985 as a curatorial assistant at the Bessey Herbarium of the University of Nebraska–Lincoln, and collections and database manager at the High Plains Herbarium at Chadron State College, Chadron, Nebraska. He has worked extensively on Nebraska floristics and community classification, and is a co-author of a forthcoming flora manual of the state. He is currently at the High Plains Herbarium, where he and his wife Susan carry out field work on floristics of the northern Great Plains, and systematic research on the genus *Lappula*, in addition to their duties creating a database of the herbarium's vascular plant specimens.

COVER PHOTO CREDIT

Liparis loeselii (yellow widelip orchid). Photo by Steven Rothenberger, used with permission.

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF *LIPARIS LOESELII*

Status

Liparis loeselii (yellow widelip orchid) is widespread in North America and Europe but is evidently rare through much of its geographic range. There are 24 known historical and extant occurrences in USDA Forest Service Region 2, with 14 of these having been discovered since 1980. The known occurrences in Region 2 are small, with most recorded as containing between one and eight individuals. Two of the known occurrences within Region 2 are on the McKelvie National Forest. Four other occurrences are found in or near the boundaries of the Niobrara National Scenic River, and three of these are preserved on The Nature Conservancy's Niobrara Valley Preserve. An additional occurrence is on land leased to the Nebraska Game and Parks Commission, and another is on the Waubay National Wildlife Refuge in South Dakota. All other known occurrences are on private property, and likely most of the historical ones as well.

Liparis loeselii is ranked as globally secure (G5) due to its broad distribution, but within Region 2, it is ranked as critically imperiled in Nebraska (S1S2) and South Dakota (S1), and it is considered extirpated from Kansas (SX). *Liparis loeselii* has no federal protection under the Endangered Species Act of 1973 and no state protection within Region 2, but it is designated a sensitive species by USDA Forest Service Region 2.

Primary Threats

The primary human-related threats to *Liparis loeselii* are habitat degradation and loss due to hydrologic alteration and conversion of suitable habitats for hay production. Other potential threats to these habitats include the likelihood of further hydrologic changes due to increasing demands for groundwater and declines in groundwater quality from excess nutrient accumulation. Due to the inconspicuous nature of the species and the remoteness of many existing occurrences, direct human impacts on existing habitats are probably slight. Within intact habitats, the greatest threat appears to be from ecological succession and competition from perennial wetland plants. Since many populations appear to be quite small, stochastic processes may also pose a threat. Alien species invasion may pose a threat to *L. loeselii*, but there is no evidence of this occurring at present. Herbivory has been cited as a threat to populations elsewhere (Wheeler et al. 1998), but it has not been documented in Region 2.

Primary Conservation Elements, Management Implications and Considerations

In spite of its broad geographic range, little is known about the overall distribution and abundance of this species in Region 2. Available data suggest that the plant maintains itself in small numbers in relatively undisturbed habitats. Key elements to consider in the conservation of the species include its reliance on occasional disturbance to create small openings for germination on wet, bare, nutrient-poor soils, and the effects of competition from other wetland plants in the absence of occasional disturbance. Although some known occurrences of *Liparis loeselii* have some protection on public lands (such as in the McKelvie National Forest), none of these sites is managed in such a way as to improve the viability of *L. loeselii* populations by maintaining beneficial disturbance and minimizing the effects of competition. Conservation tools applicable to Region 2 include conducting surveys to locate new and historic occurrences of the species, monitoring fluctuations in existing populations, characterizing features of the microhabitats in which it occurs, and determining how it responds to various types of disturbance. Since all known occurrences are very small, it is critical that surveys and monitoring efforts do not disturb existing plants. For the species as a whole, studies of the dynamics of seed production, dispersal, and seed bank longevity, population viability studies, and studies of gene flow would provide additional information to assist in creating conservation strategies.

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Introduction

This assessment is part of a series produced to support the Species Conservation Project for the Rocky Mountain Region (Region 2), USDA Forest Service (USFS). *Liparis loeselii* (yellow widelip orchid) is the focus of an assessment because it is designated a sensitive species in USFS Region 2 (USDA Forest Service 2003a, 2005a). Within the National Forest System, a sensitive species is a plant or animal whose population viability is identified as a concern by a regional forester because of a significant current or predicted downward trend in abundance or habitat capability that would reduce its distribution (USDA Forest Service 2005b). A sensitive species may require special management, so knowledge of its biology and ecology is critical.

This assessment addresses the biology, ecology, conservation status, and management of *Liparis loeselii* throughout its range in Region 2. The introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal

The goal of this document is to provide a comprehensive and synthetic review of the biology, ecology, and conservation status of *Liparis loeselii* within Region 2. The assessment goals limit the scope of this work to critical summaries of scientific knowledge, discussion of broad implications of that knowledge, and outlines of information needs. This assessment does not seek to develop specific management recommendations. Rather, it provides the ecological background upon which management must be based and focuses on the consequences of changes in the environment that result from management (i.e., management implications).

Scope

This assessment of *Liparis loeselii* examines the biology, ecology, conservation status, and management of this species with specific reference to the geographic and ecological characteristics of the USFS Rocky Mountain Region. Although the vast majority of the literature originates from field investigations outside Region 2 (and often outside the continent), this document places that literature in the ecological context of the Great Plains portion of this region. Similarly, this assessment is concerned with reproductive behavior, population dynamics, and other characteristics of *L. loeselii* in the context of the current environment rather than under historical conditions. The evolutionary environment of the species is considered in conducting this synthesis, but is placed in a current context.

In producing this assessment, refereed literature, non-refereed publications, and unpublished research reports were reviewed. Not all publications on *Liparis loeselii* are referenced in the assessment, nor were all published materials considered equally reliable. This assessment emphasizes refereed literature as much as possible, and non-refereed publications and reports were used when information was unavailable elsewhere. Unpublished data, such as Natural Heritage Program records and data from labels of herbarium specimens, were important for estimating the geographic distribution and ecological conditions of *L. loeselii* within Region 2. These sources require special attention in their interpretation because of the wide range of variation in detail and quality of the data collected.

Treatment of Uncertainty

Science represents a rigorous, systematic approach to obtaining knowledge. Competing ideas regarding how the world works are measured against observations. However, because our descriptions of the world are always incomplete and our observations are limited, science focuses on approaches for dealing with uncertainty. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference (Platt 1964). However, it is difficult to conduct critical experiments in the ecological sciences, and often observations, inference, good thinking, and models must be relied upon to guide the understanding of ecological relationships. (Chamberlain 1897, Hilborn and Mangel 1997).

In this assessment, the strength of evidence for particular ideas is noted, and alternative explanations are described when appropriate. While well-executed experiments represent a strong approach to developing knowledge, alternative approaches such as modeling, critical assessment of observations, and inference are accepted as sound approaches to understanding *Liparis loeselii*. Although a number of studies of *L. loeselii* exist, not all aspects of its autecology have been studied, and in some cases, it was necessary to make inferences based on studies of other *Liparis* or related orchid species. Since ecological literature for Region 2 is virtually nonexistent, it was necessary to consider studies and management protocols for areas outside the region, particularly with respect to threats and management implications.

Publication of Assessment on the World Wide Web

To facilitate use of species assessments in the Species Conservation Project, they are being published on the USFS Region 2 World Wide Web site (http://www.fs.fed.us/r2/projects/scp/assessments/index.shtml). Placing the documents on the Web makes them available to agency biologists and the public more rapidly than publishing them as reports. More importantly, it facilitates revision of the assessments, which will be accomplished based on guidelines established by Region 2.

Peer Review

Assessments developed for the Species Conservation Project have been peer reviewed prior to release on the Web. This report was reviewed through a process administered by the Center for Plant Conservation that chose two recognized experts to provide critical input on the manuscript. Peer review was designed to improve the quality of communication and to increase the rigor of the assessment.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

Within Region 2, two of the 24 known occurrences are on National Forest System lands of the McKelvie National Forest (**Table 1**) in Nebraska. Four other Nebraska occurrences are found in or near the boundaries of the Niobrara National Scenic River, and three of these are preserved on The Nature Conservancy Niobrara Valley Preserve. An additional occurrence is on land leased to the Nebraska Game and Parks Commission. One occurrence is on the Waubay National Wildlife Refuge in South Dakota. All other known occurrences are on private property, and likely most of the historical ones as well.

Liparis loeselii (L.) Richard is widespread in North America and Europe, but it is evidently rare throughout much of its geographic range. In Europe, this species appears on the International Union for Conservation of Nature and Natural Resources threatened list for every country in its range, and it is legally protected in Belgium, Finland, France, Germany, Liechtenstein, Switzerland, and the United Kingdom (UK) (Joint Nature Conservation Committee 2004). It is not listed as threatened or endangered in the United States in accordance with the Endangered Species Act of 1973 (U.S. Congress 1973), but it is included on the USFS sensitive species list for Region 2 (USDA Forest Service 2004). The species is also not listed by the Committee on the Status of Endangered Wildlife in Canada (2004). NatureServe (2004) has assigned *L. loeselii* a global heritage ranking of G5 (demonstrably secure), based on its wide geographic range, but it is considered vulnerable or imperiled in 20 of the 22 states in which it is ranked, and is believed extirpated in Kansas and the District of Columbia. It is also ranked as imperiled or vulnerable in six Canadian provinces (**Table 2**). *Liparis loeselii* is designated as endangered in Tennessee and Washington, threatened in Arkansas, Kentucky, New Hampshire, and North Dakota, and "exploitably vulnerable" in New York. (USDA Natural Resources Conservation Service 2004, USGS Northern Prairie Wildlife Research Center 2004, Kentucky State Nature Preserves Commission 2005), and it is listed as a red book species in British Columbia (Klinkenberg 2004).

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

At present, the most active conservation of *Liparis loeselii* is taking place in the United Kingdom, where it is listed as a protected species under Schedule 4 of the Conservation Regulations 1994 and Schedule 8 of the Wildlife and Countryside Act, 1981 (Halsbury's Statutes of England and Wales 1996), and a species recovery plan has been implemented (Wheeler et al. 1998). The species is currently known from only two sites in eastern England and from two coastal dune systems in South Wales, all of which are protected in national nature reserves (English Nature 2004). Management strategies have been developed for the East Anglian occurrences, and recovery work began on the Welsh occurrences in 1994 (English Nature 2004). The species action plan for *L. loeselii* proposes incentive programs for wetland conservation, restoration management to encourage regeneration from existing seedbanks, and introduction of propagated stock to areas in which such efforts are unsuccessful (English Nature 2004). A separate project to propagate British and European orchids was initiated in 1983, with the intention of re-establishing wild populations (Royal Botanic Gardens, Kew 2004). Continued research on the ecology and conservation of this species is also an important part of these plans. Restoration management by means of biomass removal from dune slacks in Southern Wales has been carried out with apparent success (Jones 1998).

Table 1. Summary of *Liparis loeselii* occurrences in USDA Forest Service Region 2.

State and ecoregion	County, location	Last observed	Ownership/ Management	Estimated abundance	Location of voucher specimen
Kansas					
CGP	Pottawotamie Co.	1899	Unknown	Unknown	KSC
Nebraska					
SH	Blaine Co., Milburn Dam Wildlife Management Area	1997	Public/Bureau of Reclamation (leased to Nebraska Game & Parks Commission)	3	Photo by Steve Rothenberger, University of Nebraska-Kearney
NB	Brown Co., Niobrara Valley Preserve, Barney Creek	1982	The Nature Conservancy	Ca. 30	NEB
NB	Brown Co., Fairfield Creek	1982	Private	"small population"	NEB
NB	Brown Co., Niobrara Valley Preserve, Kantak Coulee	1993	The Nature Conservancy	8	Unknown (NE Heritage element occurrence)
SH	Brown Co., Calamus Rivera	1999	Private	unknown	NEB
NB	Cherry Co., northeast of Valentine	1912	Unknown	unknown	NEB
SH	Cherry Co., Kennedy	1913	Unknown	unknown	NEB
SH	Cherry Co., south of Cody	1936	Private	unknown	NEB
NB	Cherry Co., south of Valentine	1966	Private	unknown	KANU
SH	Cherry Co., McKelvie National Forest, Buckhorn Springs	1995	Public/Nebraska National Forest	3-4	NEB
SH	Cherry Co., McKelvie National Forest, Drinkwalter Exclosure	1995	Public/Nebraska National Forest	3	NEB
SH	Cherry Co., Big Creek Fen	1996	Private	6	NEB
NB	Cherry Co., Niobrara Valley Preserve, south of county line bridge	1998	The Nature Conservancy	2	None (NE Heritage element occurrence)
SH	Garfield Co., Burwell	1910	Private	Unknown	NEB
SH	Holt Co., west of Atkinson	1941	Unknown	Unknown	MO, NEB
SH	Howard Co., Boelus	1902 or 1907	Private	Unknown	NEB
SH	Keith Co., Lonergan Creek	2002	Private	1	Fragment in possession of author
SH	Thomas Co., Halsey	1912	Unknown	Unknown	NEB
SH	Thomas Co., Thedford	1918	Unknown	Unknown	NEB
South Dakota					
PC	Day Co., Waubay National Wildlife Refuge	1996	Public/USFWS	Unknown	None (information provided by M. Leoschke)
PC	Roberts Co., Jurgens Fen	1996	Private	"infrequent"	SDC
PC	Roberts Co., Kriz Fens	2002	Private	1	SDC
PC	Roberts Co., east of One Road Lake	1996	Unknown	Unknown	None (information provided by M. Leoschke)

Ecoregions: CGP (Central Great Plains), NB (Niobrara Breaks), PC (Prairie Coteau), SH (Nebraska Sandhills).

Herbarium acronyms: KANU (R.L. McGregor Herbarium, University of Kansas), KSC (Kansas State University), MO (Missouri Botanical Garden), NEB (C.E. Bessey Herbarium, University of Nebraska–Lincoln), SDC (South Dakota State University).

Table 2. States and provinces in which NatureServe ranks *Liparis loeselii* (NatureServe 2004).

State/Province	Status Code	State/Province	Status Code
Alabama	S1?	Rhode Island	S1
Arkansas	S1	South Dakota	S1
District of Columbia	SX	Tennessee	S1
Illinois	S1	Vermont	S3
Indiana	S3	Virginia	S2
Iowa	S3	Washington	S1
Kansas	SX	West Virginia	S2
Kentucky	S2S3		
Maryland	S3	British Columbia	S1
Missouri	S2	Manitoba	S3?
Montana	S1	New Brunswick	S3
Nebraska	S1S2	Nova Scotia	S3S4
New Hampshire	S2	Ontario	S4S5
New Jersey	S4	Prince Edward Island	S2S3
North Carolina	S1	Quebec	S3
North Dakota	S2	Saskatchewan	S1S2

Status Codes: S1 = critically imperiled, S2 = imperiled, S3 = vulnerable, S4 = apparently secure, S5 = secure, SX = presumed extirpated.

Because *Liparis loeselii* is a sensitive species in Region 2, USFS personnel are required to "develop and implement management practices to ensure that species do not become threatened or endangered because of Forest service activities" (USDA Forest Service 2005b). These management practices may include developing an individual species conservation strategy. As of this writing, however, a conservation strategy has not been written for this species at a national or regional level by the USFS or any other federal agency.

Liparis loeselii is a facultative wetland indicator species in Nebraska where two occurrences are on National Forest System lands (USDA Natural Resources Conservation Service 2005). A facultative wetland species is one that usually occurs in wetlands (estimated probability 67 to 99 percent), but may occasionally be found in non-wetlands. In South Dakota, *L. loeselii* is considered an obligate wetland plant. An obligate wetland species is one that almost always (estimated probability 99 percent) occurs in wetlands under natural conditions. Wetlands that support occurrences of this species receive some protection under existing federal, state, and local statutes and policies. Executive order 11990, signed by Jimmy Carter, instructs federal agencies to "minimize the destruction, loss or degradation of wetlands." The Forest Service Manual chapter 2520 (USDA Forest Service 2005a) and the USDA Forest Service Technical Guide to Managing Ground Water (USDA Forest Service 2005c) provide agency-wide guidance on the definition, protection, and management of wetlands. Forest Service Handbook series 2509.25 (USDA Forest Service 2006) covers wetland management directives specific to Region 2. USFS memo 2070/2520-72620, signed by the Director of Renewable Resources, provides regional guidance on fens and emphasizes the protection, preservation, and enhancement of fens to all Region 2 forest supervisors (USDA Forest Service 2002, Proctor personal communication 2004). The U.S. Fish and Wildlife Service (USFWS) Regional Policy on the Protection of Fens (U.S. Fish and Wildlife Service 1998) made the protection of fens a priority in the USFWS Mountain-Prairie Region. This memo designates functioning fens as Resource Category 1 (considered "unique and irreplaceable on a national basis or in the ecoregion section"), with a mitigation goal of "no loss of existing habitat value." The USFWS Regional Policy on the Protection of Fens decreases the likelihood that the U.S. Army Corps of Engineers will permit peat mining under Section 404 of the Clean Water Act, but it does not prohibit the granting of permits. The primary federal law regulating wetland habitats is Section 404 of the Federal Water Pollution Control Act (Clean Water Act) of 1977 (33 U.S.C. ss/1251 et seq.). Activities in wetlands regulated under this Act are required to avoid wetland impacts where practicable, to minimize potential impacts to wetlands, and to compensate unavoidable impacts through restoration or mitigation. However, a recent Supreme Court decision has effectively removed federal regulation from certain wetlands. The 2001 Supreme Court decision in Solid

Waste Agency of Northern Cook County (SWANCC) vs. U.S. Army Corps of Engineers (USACE) determined that Section 404 does not extend regulatory coverage to wetlands that lack connections to surface water bodies, such as streams ("isolated wetlands"). Most fens are not connected to navigable waters via surface flow and therefore may be considered isolated under USACE jurisdiction through the Clean Water Act (Bedford and Godwin 2003).

Other Federal codes and regulations pertaining to federal actions or to those on National Forest System lands include the National Environmental Policy Act (NEPA) of 1969 (42 U.S.C. 4321-4347), the Organic Administration Act of 1897 (16 U.S.C. 475), the Multiple Use – Sustained Yield Act of 1960 (16 U.S.C. 528), the National Forest Management Act of 1976 (16 U.S.C. 1600-1602, 1604, 1606, 1608-1614), the Federal Land Policy and Management Act of 1976 (43 U.S.C. 1701-1782, FSM 2729), the Forest Service Manual, and individual Forest Management Plans. These codes and regulations all provide some degree of focus on the preservation of water resources, including wetlands. Finally, a policy of "no-net-loss" of wetlands has been a national goal since first announced as an administration policy under President George H.W. Bush in 1989.

Adequacy of current laws and regulations

The above-mentioned laws and regulations can be powerful tools for the conservation of *Liparis loeselii*, but they do not adequately protect the species in Region 2. Currently there are no statutes that provide legal protection to most *L. loeselii* occurrences in Region 2, and even the occurrences on National Forest System lands are not currently protected from certain threats such as off-road vehicle travel (Croxen personal communication 2004). At least one historical occurrence is believed to have been destroyed by construction associated with a federal highway (Freeman personal communication 2004), and no regulatory mechanism exists that would prevent loss of many of the remaining known occurrences via development, drainage, or conversion of land to agriculture. One available tool for protecting occurrences on private lands is conservation easement agreements between agencies and landowners, but no such agreements have been made on sites with known *L. loeselii* occurrences.

Regulations defined by the U.S. Department of Interior and the U.S. Department of Agriculture still consider peat a renewable resource (USDI Bureau of Mines 1994) and saleable mineral (USDA Forest Service Manual, 2822.1). For occurrences that might be found on privately owned lands, current laws and regulations are inadequate to prevent damage or destruction of the habitat. As of this writing, there were three active peat mining permits in Colorado (Colorado Division of Reclamation, Mining, and Safety 2006), but peat mining is not likely to be a threat in Nebraska or South Dakota. Future permitting of peat mining under Section 404 is unlikely due to the USFWS Regional Policy on the Protection of Fens, but the possibility has not been completely eliminated.

Adequacy of current enforcement of laws and regulations

Current knowledge of *Liparis loeselii* trends is insufficient to determine the adequacy of current enforcement of laws and regulations for most locations. There is one case in which an occurrence is believed to have been destroyed by construction of a federal highway. A number of *L. loeselii* locations in Region 2 have not been observed for many decades; it is impossible to determine if extirpations or impacts from human activities have taken place. It is also possible that the small size of some occurrences is the result of human activities. Given the small number of extant occurrences and the few plants at each location, any loss of individuals or occurrences may threaten the persistence of *L. loeselii* in Region 2.

Biology and Ecology

Classification and description

Systematics and synonymy

Liparis loeselii is a member of the orchid family (Orchidaceae Juss.), one of the largest families of flowering plants in the world and distributed from the equator to near the poles (Romero-González et al. 2002). The genus *Liparis* Richard is classified in the tribe Malaxidae Lindl. under the subfamily Epidendroideae Lindl., and it contains approximately 350 species that are distributed nearly worldwide (Mabberley 1997), but most are subtropical epiphytes (Ridley 1887). Only three *Liparis* species are native to North America, with *L. loeselii* the most widespread and the only one recorded from Region 2. *Liparis liliifolia* (L.) Richard *ex* Lindl. is a widespread endemic of eastern North America, and *L. nervosa* (Thunb. *ex* Murr.) Lindl. is a pantropical orchid that occurs in subtropical Florida (Magrath 2002). The only other North American representatives of the Malaxidae are in the genus *Malaxis*, and a single species, *M. brachypoda* (A. Gray) Fernald, is recorded from Region 2, where it is known from two localities in the Colorado Front Range (USDA Forest Service 2003b).

Taxonomic history and knowledge of the species

Linnaeus described *Ophrys loeselii* in 1753, in honor of German botanist Johann Loesel (Magrath 2002). Louis C.M. Richard transferred the species to his newly described genus *Liparis* (meaning "greasy", after the appearance of the glossy leaves of many species) in 1817, designating it the type species of the genus. Two years earlier, the American botanist William P.C. Barton published descriptions of this species under the names *Malaxis correana* and *M. longifolia* (both names are often mistakenly attributed to William Bartram in the literature). In 1828, the German botanist Curt Sprengel transferred *M. correana* to *Liparis*, but he did not detect its equivalence with *L. loeselii*. It appears that none of Barton's names or their synonyms were widely used by the late nineteenth century. In 1893, Conway MacMillan transferred *L. loeselii* to the genus *Leptorchis*, following an 1891 work by Carl Kuntze in which most of the species of *Liparis* (but oddly not *L. loeselii*) were transferred to the genus *Leptorchis* Thouars, a name that predates publication of *Liparis* by eight years (International Plants Names Index 2004, Missouri Botanical Garden 2004). The name *Liparis* has been conserved against *Leptorchis* (Greuter et al. 2000). The oldest published observation of the orchid's presence in Region 2 (Pool 1914) is under the name *L. loeselii*, but all subsequent botanical works that include Region 2 use *Liparis loeselii*. Small plants with broad blunt-tipped leaves described from dune habitats in south Wales are often recognized as *L. loeselii* var. *ovata* Ridds. *ex* Godfrey, but it is unclear that this name was ever validly published and it does not appear in standard nomenclatural databases (International Plant Names Index 2004, Missouri Botanical Garden 2004).

The first and only monographic work in which *Liparis loeselii* is included appeared 70 years after the combination was published (Ridley 1887). It was one of the first orchids to have its developmental history described (Fuchs and Ziegenspeck 1927), and several studies of the pollination mechanism of this species followed (Kirchner 1922, Hagerup 1941, Catling 1980). Apart from these studies, most of the information on the natural history of *L. loeselii* is compiled in various regional orchid manuals (e.g. Summerhayes 1951, Luer 1975, Correll 1978). The first published studies of the population biology of the species did not appear until fairly recently (Jones 1998, Wheeler et al. 1998, McMaster 2001), but two earlier unpublished works (McLain 1968, Bornstein 1998) included some of these topics.

Description of the species

Like most orchids, *Liparis loeselii* is an herbaceous perennial, but it is unique in that it has a partially exposed, thickened stem base called a pseudobulb, which consists of a swollen terminal internode of the rhizome surrounded by fleshy leaf bases, and serves as a water storage organ (Rasmussen 1995). Pseudobulbs are common in epidendroid orchids, particularly epiphytes, but within Region 2, these are found only in the two representatives of the Malaxidae. Two other orchids in Region 2 have subterranean cormose storage organs at the base of the stem (*Aplectrum hyemale* (Muhl. *ex* Willd.) Nutt. and *Calypso bulbosa* (L.) Oakes), but these are found to the east and west, respectively, of the regional range of *L. loeselii*. Both are also associated with forests; in late summer or autumn, they produce leaves that persist through winter (Sheviak and Catling 2002).

The pseudobulb of the current year is often attached to the remains of the mother pseudobulb from the previous season, which is usually enveloped by scales and remnants of last year's leaf bases. In spring, two leaves are produced at the base of the plant that sheath the pseudobulb and often the lower portion of the flowering stem. The dark green, glossy leaves are ovate to elliptic in shape, somewhat erect, and slightly folded lengthwise and keeled at the base. A leafless flowering stem 4 to 30 cm tall arises from the pseudobulb and contains a terminal raceme of two to 18 inconspicuous yellowish green flowers. The flowers, which are smaller (<1 mm) than those of most orchids in Region 2, have three narrow sepals, two tubular petals, and a broader lip petal or labellum. As in all orchids, the stamens and pistil are united into a structure called a column, which contains a hinged anther cap at the tip and stigmatic surfaces on the underside. One anther is present, and the pollen in each anther sac is fused into two spherical masses called pollinia. The flowers are evidently ephemeral (Luer 1975), and most herbarium specimens seen from Region 2 were of plants collected in fruit. The tendency toward more fruiting plants in regional herbaria may be due to the fact that the fruiting capsules are larger than the flowers (9 to 13 mm long), are regularly set, and persist throughout the season and apparently into the next (**Figure 1**). Additionally, many known sites are fairly remote and visited infrequently by botanists, especially early in the season, so that flowering plants are likely not to be seen. *Liparis*

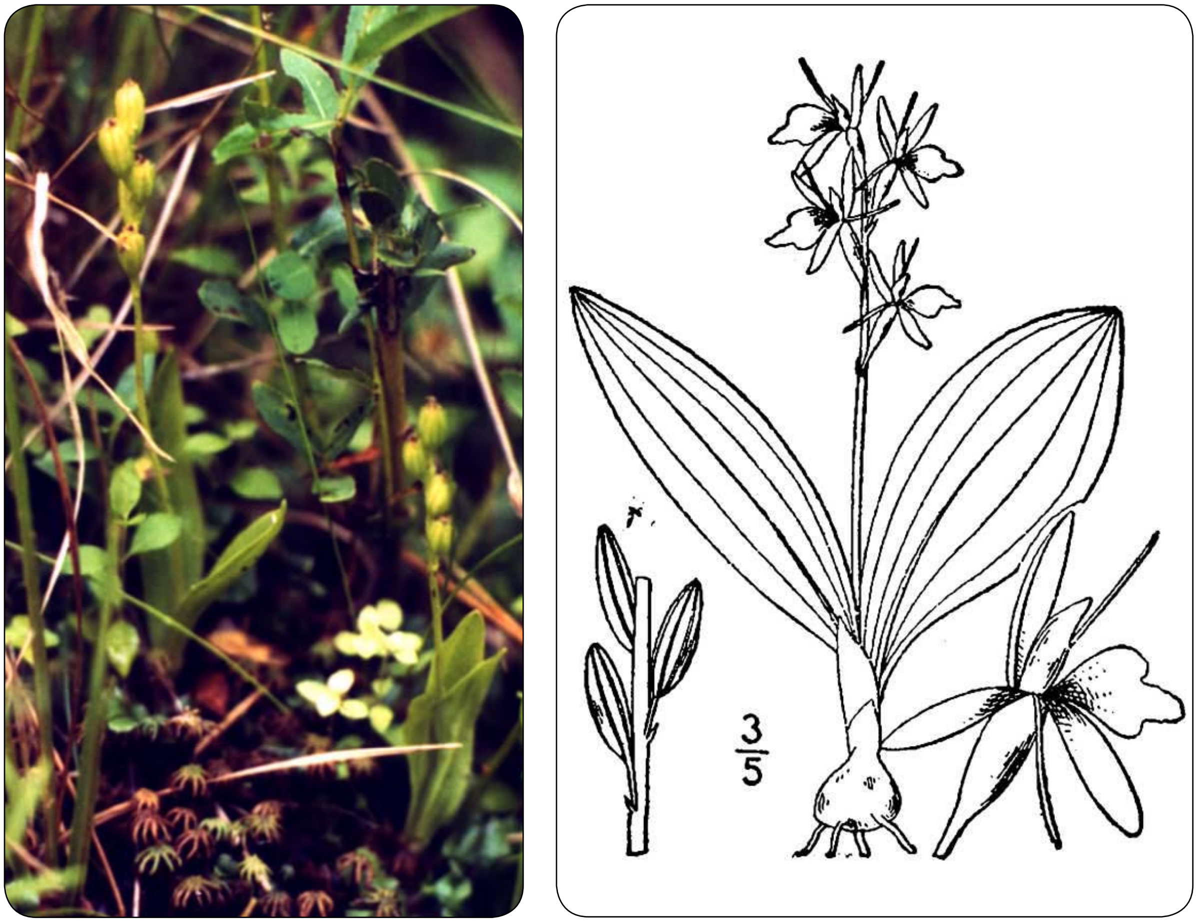

Figure 1. (Left) *Liparis loeselii* at the Milburn Dam site in Nebraska. Photo by Steve Rothenberger, used with permission. (Right) Illustration of *L. loeselii* showing reproductive features (USDA Natural Resources Conservation Service 2004b).

loeselii is unlikely to be confused with other plants in the area, with the exception of a few other orchids that produce a pair of basal leaves in the early spring such as *Galearis spectabilis* (L.) Raf. or depauperate specimens of *Cypripedium candidum* Muhl. *ex* Willd., both of which are found in drier sites and lack pseudobulbs. The only orchid that commonly occurs in sites containing *L. loeselii* in Region 2 is *Platanthera aquilonis* Sheviak, a very dissimilar plant that produces pale green leaves on erect leafy stems. A complete technical description of *L. loeselii* can be found in Magrath (2002). An illustration of the plant is provided in **Figure 1**, and more complete illustrations appear in Correll (1978).

Distribution and abundance

Global distribution and abundance

Liparis loeselii has a relatively large geographic range, having been documented in 19 nations on three continents (McMaster 2001). In Eurasia, it is found in southern England and the southern Scandinavian Peninsula, through mainland Europe from France northeastward to Estonia and adjacent Russia, and south to northern Italy, the north part of the Balkan Peninsula, and the Ukraine (Luer 1975). It tends to be absent from areas of marked summer drought and extremes of temperature within its Eurasian range, being found primarily in lowlands (mostly <600 m [1,969 ft.]) in cool rainy regions (Summerhayes 1951). While the typical form is found nearly throughout the distribution of the species, variety *ovata* is restricted to coastal dunes in South Wales and northern France (Jones 1998, Gremillet 1993). Although *L. loeselii* was likely never common in Eurasia, it has become increasingly rare in Great Britain and in parts of the European mainland (Wheeler et al. 1998).

In North America, *Liparis loeselii* has been documented from 31 states and the District of Columbia, and from 10 Canadian Provinces (NatureServe 2004). Its main range in North America stretches from New England and the Canadian maritime provinces westward through the Great Lakes region, northwestward through Minnesota and Manitoba to Saskatchewan, and southward to northeastern Iowa, northern Illinois, Indiana, Ohio, and irregularly in the Appalachians to North Carolina and Tennessee (Hoyama 1993). Unlike Eurasian occurrences of *L. loeselii*, many North American occurrences are in regions that experience a broad range of temperatures and periodic drought, and the overall range of elevation is broader (100 to 1,100 m [328 to 3,609 ft.]) (Magrath 2002). Many of the occurrences found outside of the cool, rainy regions of the continent are disjunct from the main range of the species, occurring southward in Alabama, Tennessee, Arkansas, and southern Missouri; westward in Kansas, Nebraska, Montana, Washington, and British Columbia; and northward in northwestern Saskatchewan and the Northwest Territories (Hoyama 1993, McMaster 2001). Although its historic abundance in North America is not well documented, *L. loeselii* is considered rare through much of its range, even in places where numerous occurrences have been recorded. For instance, this species has been recorded from 58 of 67 counties in New England, but it is officially ranked as vulnerable or imperiled in three states there (McMaster 2001).

Regional distribution and abundance

Twenty-four occurrences of *Liparis loeselii* have been documented from Region 2 (**Table 1**, **Figure 2**), with the oldest collection made in Pottawotamie County, Kansas, in 1899 (Magrath 1974). The first published report of its presence in Kansas did not appear until much later (Gates 1940). It is believed that the collection was made in the Flint Hills ecoregion (ecoregion names after Chapman et al. 2001) north of the Kansas River in the vicinity of St. George, near several historic seeps and springs at the contact of Pleistocene eolian sands and Permian limestones and shales. Efforts to relocate the occurrence have been unsuccessful; it is believed that much of this site was destroyed by construction associated with U.S. Highway 24 (Freeman personal communication 2004).

The species appears to have been first collected in Nebraska in either 1902 or 1907 in the Central Great Plains ecoregion near Boelus in Howard County by Rev. J.M. Bates. Between 1910 and 1918, Bates made five collections in the Nebraska Sandhills ecoregion near Burwell (1910), Halsey (1912), Kennedy (1913), and Thedford (1918), and an additional collection from the Niobrara River Breaks area of the Northwestern Great Plains ecoregion near Valentine (1912). The first published report of *Liparis loeselii* in the state is in a list of secondary species of Sandhills wet meadows (Pool 1914), but no specimen documenting this report is known. The plant is included in subsequent flora manuals as occurring "in wet soil" at only the Halsey and Valentine locales (Petersen 1923), and Winter (1932) reported a specimen taken at Halsey by Dr. Pool that has never been located. An additional Sandhills occurrence was documented in the Niobrara River Valley south of Cody by William Tolstead in 1936, who later collected it from along the southern periphery of the Northwestern Glaciated Plains ecoregion west of Atkinson in Holt County in 1941. No further collections are known for the next 25 years, until Steve Stephens collected it along the Niobrara River south of Valentine in 1966. In 1982, Craig Freeman discovered two more sites in the Niobrara River Breaks near the present Niobrara Valley Preserve, and between 1993 and 2002, eight more occurrences were documented in and along the periphery of the Nebraska Sandhills. None of the recent records appears to be a recollection from an historic occurrence.

In 1996, Mark Leoschke discovered four occurrences of *Liparis loeselii* in Roberts and Day counties in the Prairie Coteau region of the Northern Glaciated Plains ecoregion in northeastern South Dakota. Other occurrences are nearby in this ecoregion in Minnesota and North Dakota (Ownbey and Morley 1991, Larson 1993).

McMaster (2001) suggested that the recent discoveries of the species in South Dakota, Montana (Shelly and Mantas 1993), and Kentucky (Thompson and MacGregor 1986) might be regarded as evidence of the species expanding its range. There is some evidence that suggests that *L. loeselii* is undergoing range expansion in Indiana (Hoyama 1993), possibly due to an increase of available habitat; this also appears to be the case for the related *L. liliifolia* (Mattrick personal communication 2006). The increase in new occurrences in Region 2 is probably less likely due to range extension than to the recent upsurge in interest in the flora of peatlands in Nebraska and South Dakota. Peatlands there received little attention until relatively recently (Steinauer et al. 1996, Ode personal communication 2004).

Occurrences on the glaciated plains in South Dakota are very close to the periphery of the main range of *Liparis loeselii* as defined by Luer (1975) and Hoyama (1993), but the occurrences from unglaciated regions in Nebraska and Kansas are distinctly disjunct from the

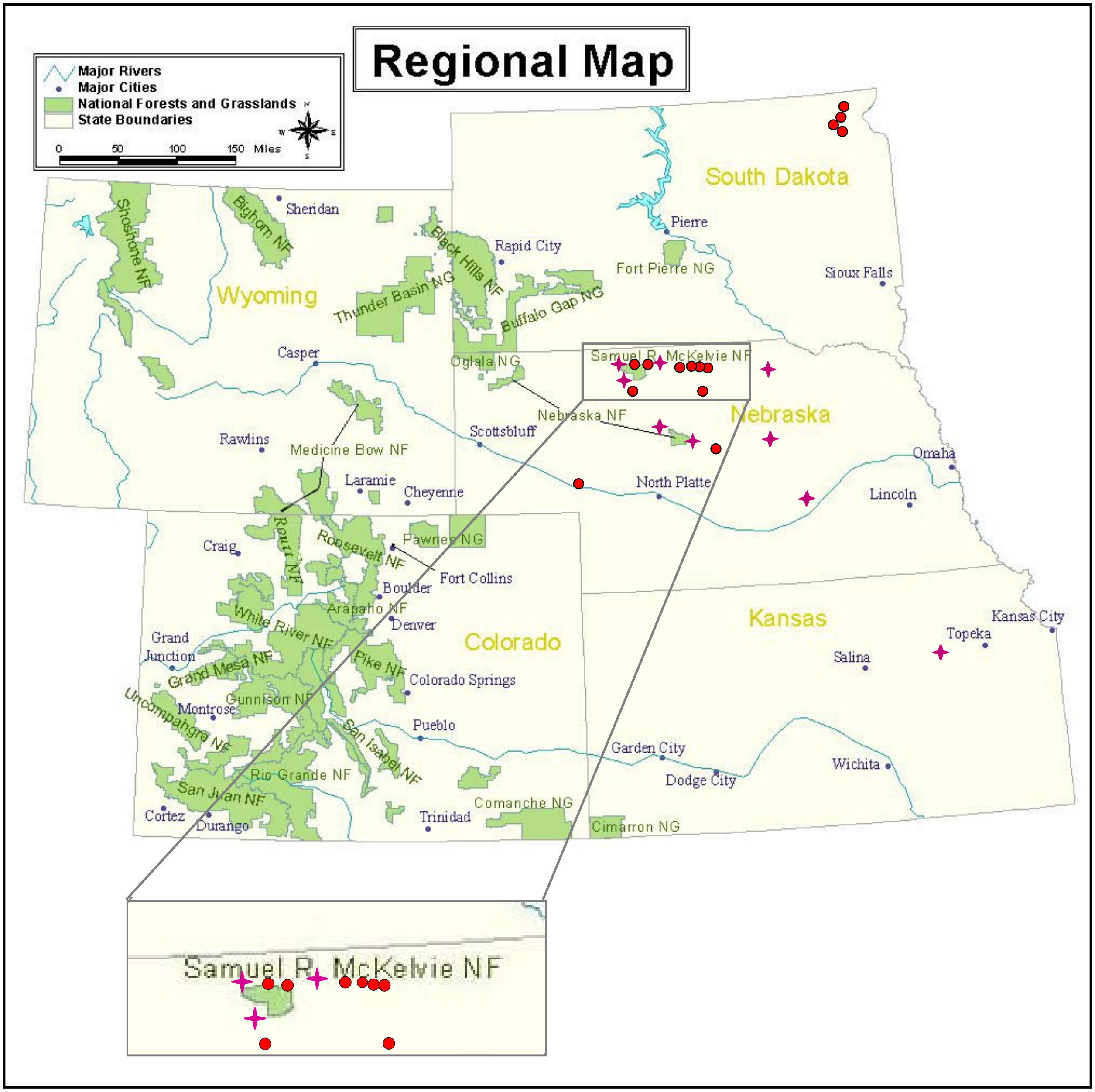

Figure 2. Distribution of *Liparis loeselii* in USDA Forest Service Region 2. Occurrences last observed before 1980 are indicated by crosses.

main range of the species, with the northeasternmost Nebraska locality (Atkinson) found some 330 km (205 mi.) southwest of the nearest peripheral locality in northwest Iowa. In Nebraska, the species is considered an indicator of fens (Steinauer et al. 1996), and it occurs in fens and peaty seeps with a suite of species similarly disjunct from their main ranges to the north and east. Many of these Sandhills fen species are considered relicts of the late Pleistocene (Steinauer et al. 1996), as are many species in the Niobrara River Breaks region (Kaul et al. 1988). Although the nature of its presence in Kansas is open to speculation, Steyermark (1963) considered disjunct occurrences in southern Missouri as representing Pleistocene relicts as well.

Population trend

Trend for the species

The decline of populations of *Liparis loeselii* in Great Britain is well documented (Wheeler et al. 1998), but the overall trend in North America is not. On the basis of heritage rankings, McMaster (2001) stated that the species is in decline in over half the states in its historic range in the United States, but little evidence has been published documenting its disappearance from known sites. It has been suggested that the recent discovery of new disjunct and peripheral occurrences indicates that the species appears secure on the edges of its range (McMaster 2001), but this supposition does not take into account the intensity of historical collecting (or lack thereof) in these areas. Evidence suggesting the decline of this species in North America includes changes in land-use patterns and effects of succession on sites capable of supporting *L. loeselii*.

Similarly, the population trend in Region 2 is difficult to judge due to a lack of information regarding its historical abundance. Since locality data for specimens collected prior to 1966 are often imprecise, no efforts have been made to revisit locations of historic occurrences (outside of Kansas). There is evidence, however, to suggest that Steinauer et al. (1996) surveyed one of Bates' sites, and another may be what is now the location of the Valentine fish hatchery. Estimates of the population trend in Region 2 must therefore also rely on speculation regarding changes to habitats capable of supporting *Liparis loeselii*. Steinauer et al. (1996) surveyed six large fens in Cherry County, Nebraska in 1996 and found *L. loeselii* in only one site, which happened to be the only site that had not been extensively modified by drainage for hay production. Although the precise reason for its presumed absence from these sites is unknown, drainage has been implicated as a factor in the decline of the species in Great Britain (Wheeler et al. 1998), and a number of sites apparently capable of supporting *L. loeselii* in South Dakota have been modified by drainage or even destroyed (Ode personal communication 2004).

Trend for individual populations

Another factor complicating the detection of long-term population trends in *Liparis loeselii* is its well-documented tendency for short-term fluctuations in individual populations. For instance, in a study in South Wales, a segment of a population of var. *ovata* increased from 50 to 75 individuals between 1987 and 1989 then fell to fewer than 25 individuals by 1995 (Jones 1998), and in eastern England, a population of typical *L. loeselii* underwent a large population spike, followed by a crash and subsequent decline in a seven year period (Wheeler et al. 1998). The trend in Region 2 is virtually unknown. Abundance has been recorded at only one of the South Dakota occurrences, and while the number of plants at six Nebraska sites has been recorded, occurrences at only two sites have been censused over more than a single growing season. Both these populations, like most in Region 2, are very small (fewer than 10 individuals), and at one site (Buckhorn Springs), very little change was noted, with three plants recorded in 1992 and four in 1995 (Nebraska Natural Heritage Program 2004). At the second site (Lonergan Creek), a single plant was observed in 2002, and attempts to relocate it in 2004 were unsuccessful. This site has been visited frequently by botany classes at the nearby Cedar Point Biological Station since 1975, but the orchid was not observed there prior to 2002 (Kaul personal communication 2004). Given the frequency of small occurrences in Region 2, it is possible that occurrences persist with few plants in the absence of favorable conditions, but more data are needed to establish this.

Habitat

The broad geographic distribution of *Liparis loeselii* is evidence of its adaptability. Although it primarily occurs in or near saturated wetland habitats such as bogs, fens, wet meadows, forested wetlands and seeps, it can occasionally be found in drier upland habitats as well (McMaster 2001). The range of habitats capable of supporting the species varies throughout its geographic range. In much of Europe, occurrences are restricted to base-rich, wet, oligotrophic herbaceous fens, with East Anglian occurrences found in reflooded turbaries (abandoned peat excavations) (Wheeler et al. 1998). Occurrences referred to var. *ovata* are restricted to coastal dune slacks (moist interdunal depressions), but evidently both varieties are present in these habitats in northern France (Jones 1998), where the species is evidently restricted to coastal dune slacks and submaritime calcareous fens (Géhu and Wattez 1971).

Although no mention of *Liparis loeselii*'s presence in coastal habitats in North America could be found in the literature, its overall range of habitats is much broader than that reported in Europe. In North America, the species is predominantly found in wetlands (herbaceous and wooded), and is most frequently reported from fens, wet meadows, marshes, forested seep springs, marly lake borders, mats of floating peat, and moist calcareous sands in interdunal swales. The substrate tends to be peat or sand, usually with high levels of organic matter. Although it is sometimes presumed to occur only on calcareous or alkaline soils (Luer 1975), this species can also be found in slightly to moderately acidic substrates as well (Correll 1978, Hoyama 1993). It can also be found in areas of little or no soil development, such as in wet sand in the bottoms of abandoned sand pits (Catling 1980, Case 1987). The species has even been found in uplands in some parts of its American range, and has been recorded growing in dry brushy old fields and young regrowth forests in southern Indiana (Hoyama 1993), secondary successional upland woods in southwest Ohio (McLain 1968), in a dry remnant oak savanna in Wisconsin (Hapeman 2004), and along the upper edge of a dry, weedy old road in Kentucky (Thompson and MacGregor 1986). In fact, it appears that *L. loeselii* has recently expanded its range into such habitats in southern Indiana, and it is theorized that these plants may represent a genotype with greater habitat amplitude (Hoyama 1993), but this has not been investigated.

Along the western periphery of its range, however, the variety of habitats in which *Liparis loeselii* is found is not quite as variable, and it tends to be restricted to saturated wetlands and surrounding ecotones. In British Columbia, it is known from two sites in moist thickets and fens (Klinkenberg 2004); in Washington, it is known from two sites in sphagnum bogs (Washington Natural Heritage 2004); and in Montana, it is known from six sites in semi-shaded carrs and fen-forest ecotones (Shelly and Mattas 1993). The Region 2 occurrences are primarily from permanently wet sites including fens, spring seeps, and marshes with peaty soil, but a single collection (Atkinson) was made along the margin of a pond in an old sand pit. The South Dakota sites are all calcareous fens and wet meadows (Leoschke personal communication 2004) while in Nebraska the species is known from peaty sites in fens, springs, and marshes (**Figure 3**).

Microhabitat and environmental characteristics

Even though it is found in a fairly broad range of habitats, *Liparis loeselii* is often localized within these sites and appears to show preferences for specific microhabitats based on disturbance, substrate, and water regime. Throughout its range, the species thrives in moist, sterile ground with little competition from other plants, and gradually disappears as sod develops (Case 1987, Mattrick personal communication 2006). An association between the presence of *L. loeselii* and disturbance such as peat excavation or bomb craters has been long reported in Europe, and at present all current (and probably most former) East Anglian occurrences are found in abandoned turbaries (Wheeler et al. 1998). In these sites, it is highly localized on the upland margin of semi-floating mats of vegetation growing across shallow, reflooded peat workings (Wheeler et al. 1998). It has been reported from sparsely-vegetated disturbed sites in North America (e.g., abandoned sand pits, ditch banks), but it is frequently associated with openings in more densely-vegetated habitats, such as in pathways or deer trails or along the margins of open water such as streamlets in fens and seeps (**Figure 3**; Case 1987, Swink and Wilhelm 1994). Nonetheless, it often grows among dense vegetation, but usually in low abundance. Very little detail concerning disturbance and its effect on microhabitat preference is known for habitats in Region 2. Most of the sites from which it is currently known show relatively little obvious effect of human disturbance, but plants from one site (Milburn Dam) were observed on the banks of a manmade drainage channel.

Despite the epiphytic tendencies of most members of the genus *Liparis*, *L. loeselii* tends to grow rooted on the substrate surface. In a few cases, though, it may root in moss mats, dying sedge tussocks, or even on the surface of fallen logs and dock pilings above the fen surface (Case 1987, Wheeler et al. 1998). Soil pH is sometimes mentioned in association with *L. loeselii* habitats, but it appears that soil fertility may be a more important controlling factor in determining the presence of this species. In eastern England, *L. loeselii* tends to occur in microhabitats with lower than average substrate fertility as determined by phytometric assay, and it is often found in stands of vegetation that are less vigorous than usual (Wheeler et al. 1992). Subsoil may also exhibit an effect on the presence of the species; it has been observed in these same occurrences that the orchid tends to grow on floating peat mats underlain by deep peat, and is never found on sites with an underlayer of brackish estuarine clay (Wheeler et al. 1998). Unfortunately, few studies of substrate parameters exist for North American occurrences. Groundwater conductivity, pH, and calcium and magnesium levels have been published for one site (Big Creek fen) containing *L. loeselii* in Region 2 (Steinauer et al. 1996).

Water table fluctuation may also have an impact on occurrences of *Liparis loeselii*. Most occurrences are in saturated habitats in which the water table is approximately at ground level. It is unknown whether the plant can survive prolonged periods of inundation, but it appears to tolerate regular short-term flooding. At least one British occurrence thrives in a site that is regularly inundated through the winter, and occasionally during the growing season, as submerged flowering plants have been observed (Wheeler et al. 1998). Likewise, a population of 500 individuals occurring below a dam in New Hampshire is inundated for 20 to 30 minutes at a time several times daily and has survived submerged for longer periods while in bloom (Mattrick personal communication 2006). In some sites, such as in dune slacks, the water table may fall to 0.5 m below the

(A)

(B)

Figure 3. *Liparis loeselii habitat* **(A)** Buckhorn Springs in the McKelvie National Forest in Nebraska. **(B)** Opening in habitat along small seepage stream, Buckhorn Springs. Photos by Gerry Steinauer, used with permission.

ground surface in late summer, and it is likely that the pseudobulb buffers the plant from the effects of periodic drought (Jones 1998, McMaster 2001). The fact that a few North American occurrences are recorded from upland sites indicates that some plants may be quite drought resistant.

In addition to the environmental stresses of disturbance, extremes in substrate chemistry, and periodic drought, plants of *Liparis loeselii* can also thrive in shaded sites, and atypically large specimens have been observed growing in swampy woods in Michigan (Voss 1972) and in heavily shaded swamps in Vermont (Mattrick personal communication 2006). Coastal occurrences of var. *ovata* in South Wales are apparently resistant to the effects of salt spray, with one population of 300 flowering plants observed in which only three flower spikes were not shriveled by salt-laden wind, but which appeared to be flourishing nonetheless (Lang 1980).

Vegetation associations

Because of the wide geographic range and habitat amplitude of *Liparis loeselii*, it is impractical to describe in detail the full range of known vegetation associations in which it occurs. As with most aspects of the plant's biology, the vegetation associations in which *L. loeselii* occur have been more closely studied in the United Kingdom than in North America. East Anglian occurrences are in the distinctive *Peucedano-Phragmitetum caricetosum* community (after Wheeler 1980), which is usually dominated by *Carex diandra* and *C. lasiocarpa*, and either *Phragmites australis* or *Cladium mariscus*. This community appears to be a transient successional phase in the natural revegetation of abandoned peat excavations (Wheeler et al. 1998). The largest Welsh populations have been recorded from several variants of the *Salix repens* - *Campylium stellatum* community, and plants are reportedly rare in the related later seral *Salix repens* - *Calliergon cuspidatum* community (Jones 1998).

In North America, where the range of habitats in which *Liparis loeselii* occurs is much broader, vegetation associations are much more difficult to summarize, and detailed community descriptions are virtually lacking. Variously detailed lists of species associated with *L. loeselii* have been published for northern Illinois (Swink and Wilhelm 1994), Indiana (Hoyama 1993), Kentucky (Thompson and MacGregor 1986), Massachusetts (McMaster 2001), Missouri (Bornstein 1998), Montana (Shelly and Mantas 1993), and Washington (Washington Natural Heritage Program 2004). Western occurrences of *L. loeselii*, which are found in a narrower range of habitats than occurrences in its main range, likely occur in a narrower range of plant communities as well. Far western occurrences from Washington and Montana tend to be associated with coniferous forest, while Great Plains occurrences tend to be restricted to herbaceous saturated wetlands.

In Region 2, vegetation associations for South Dakota and Kansas occurrences have not been recorded. Based on lists of associated species (Loeschke personal communication 2004), it appears that a calcareous fen site in Roberts County, South Dakota (Sisseton) may best fit the *Carex* spp. - *Triglochin maritima* - *Eleocharis quinqueflora* Marl Fen (NatureServe 2004). Although several associated species are listed for a rich fen site at Owens Creek (South Dakota Natural Heritage Program 2004), information is not sufficient to determine vegetation alliance; it may bear some similarity to Sandhills fen sites in Nebraska (Ode personal communication 2004). Species associated with *Liparis loeselii* in the Prairie Coteau of South Dakota are listed in **Table 3**.

In Nebraska, *Liparis loeselii* has been documented from two vegetation associations. It occurs in the *Carex interior* - *Eleocharis elliptica* - *Thelypteris palustris* Herbaceous Vegetation Alliance at two sites in the northern Sandhills (Steinauer and Rolfsmeier 2003). At both sites, specimens of *L. loeselii* were collected on sedge tussocks, probably in the "sedge zone" of Steinauer and Rolfsmeier (2003) or the "peat mound zone" of Steinauer (1995). Pool (1914) included the species in his "Rush-Sedge Association," which appears to include sedge-dominated portions of this fen community, and wetter phases of the *Calamagrostis canadensis* - *Juncus* spp. - *Carex* spp. Sandhills Herbaceous Vegetation Alliance.

Two sites are known along the south periphery of the Nebraska Sandhills from small seepage marshes above streams or rivers. These are part of the broadly-defined *Typha latifolia* - *Equisetum hyemale* - *Carex* (*hystericina, pellita*) Seep Herbaceous Vegetation Association (NatureServe 2004). The particular sites in which the orchid was found represent a phase with peat or muck soils and higher than typical species diversity, which has been segregated by Steinauer and Rolfsmeier (2003) as the "Marsh Seep" community. At the Milburn Dam site, plants were observed on the bank of a drainage channel at the margin of this community. Associated species recorded from this and the Calamus River site are recorded in **Table 3**.

The remaining known extant sites are in the drainage of the Niobrara River and tend to be associated with spring-fed streams and their drainages in the floodplain of the river. The two sites from the Sandhills ecoregion in the McKelvie National Forest are associated with springs that emerge from the base of steep bluffs on the south side of the river. Both sites are wetland complexes consisting of small spring streams and areas of shrubs and herbaceous marsh vegetation associated with peaty soils. The portions in which *Liparis loeselii* are found are similar to the aforementioned "Marsh Seep" phase of the *Typha latifolia* - *Equisetum hyemale* - *Carex* (*hystericina, pellita*) Seep Herbaceous Vegetation Association. Complete species lists for these sites were compiled by Steinauer and Rolfsmeier (1995), and species associated with the orchid are recorded in **Table 3**.

Table 3. Vascular plant species reported in association with *Liparis loeselii* in USDA Forest Service Region 2.

Species	PC	SH	MF	CL	Species	PC	SH	MF	CL
Amorpha fruticosa		x		x	*Juncus arcticus* var. *balticus*				x
Andropogon gerardii				x	*Juncus dudleyi*				x
Apocynum cannabinum				x	*Lobelia kalmii*	x			
Asclepias incarnata				x	*Lycopus americanus*				x
Boehmeria cylindrica				x	*Lycopus asper*				x
Caltha palustris	x				*Lycopus uniflorus*		x		x
Campanula aparinoides		x	x	x	*Lysimachia ciliata*				x
Carex aquatilis	x				*Lysimachia thyrsiflora*	x		x	
Carex aurea			x	x	*Mentha arvensis*				x
Carex comosa			x		*Menyanthes trifoliata*		x		
Carex diandra			x		*Muhlenbergia glomerata*	x			
Carex emoryi				x	*Ophioglossum pusillum*			x	
Carex granularis				x	*Platanthera aquilonis*		x	x	
Carex hystericina				x	*Polygonum sagittatum*		x		
Carex interior			x	x	*Pycnanthemum virginianum*				x
Carex lacustris				x	*Rosa arkansana*				x
Carex pellita				x	*Rudbeckia hirta*				x
Carex praegracilis				x	*Rumex brittanica*			x	
Carex utriculata	x				*Salix eriocephala* var. *famelica*				x
Cerastium fontanum			x		*Schoenoplectus acutus*		x		
Cornus sericea			x		*Schoenoplectus pungens*				x
Dulichium arundinaceum		x			*Spartina pectinata*				x
Eleocharis compressa				x	*Stellaria longifolia*			x	
Eleocharis quinqueflora	x				*Symphyotrichum boreale*	x			
Epilobium leptophyllum		x			*Symphyotrichum ericoides* var. *stricticaule*			x	
Eupatorium perfoliatum				x	*Symphyotrichum lanceolatum*			x	
Eutrochium maculatum	x				*Symphyotrichum praealtum* var. *nebraskense*			x	
Fraxinus pennsylvanica				x	*Thalictrum dasycarpum*			x	
Galium tinctorium			x		*Toxicodendron rydbergii*			x	
Gentiana andrewsii			x		*Triglochin palustris*	x			
Hypoxis hirsuta				x	*Vernonia fasciculata*			x	
Impatiens capensis			x		*Vitis riparia*			x	

PC = Prairie Coteau, SH = Sandhills (Milburn Dam and Calamus River sites), MF = McKelvie National Forest (Buckhorn Springs and Drinkwalter sites), CL = County Line Bridge site

In the Niobrara River Breaks area, *Liparis loeselii* is often associated with marshes along the margins of springfed streams and wetlands near the mouth of these streams in the floodplain. There is little detail recorded in regards to the floristic composition of most sites. In three sites, the plants occur in or along the margins of shrub thickets. In the fourth site, it appears to occur under woodland canopy in a springbranch canyon. Quantitative cover data were collected at one site (County Line Bridge) containing the orchid, which is fairly unlike most other sites in the region. At this site, *L. loeselii* occurs in a wet depression in wet-mesic tall-grass prairie in the Niobrara River floodplain. It is not permanently saturated, and the substrate consists of about 30 cm layer of sandy loam overlaying alluvial sand. The vegetation is most similar to the *Spartina pectinata - Calamagrostis stricta - Carex* spp. Herbaceous Vegetation Alliance (the “northern cordgrass wet prairie" of Steinauer and Rolfsmeier [2003]), though some species typical of peaty seeps are associated with the site. All species recorded from this site are recorded in **Table 3**.

Extent and quality of potential habitat in Region 2

The fact that half of the 24 sites documented from Region 2 were discovered since 1993 is indicative of the historical lack of botanical attention to the peatland habitats that support this species. Although the presence of fen plants has long been reported (Saunders 1899, Bates 1914, Pool 1914, Tolstead 1942), the presence of fens in Region 2 was not documented until 1980 (Ode 1981). The first intensive survey of fen sites in Nebraska was not carried out until 1992 (Steinauer 1995), and as recently as 1996, it was believed that most Sandhills fens were concentrated in Cherry County in the north-central Sandhills. Recent field work has uncovered numerous fens and fenlike sites supporting presumed Pleistocene relict species throughout the Nebraska Sandhills west to Garden County, south to Logan County, east to Wheeler County and to the east and south of the Sandhills along rivers originating from the Sandhills (Steinauer and Rolfsmeier 2003). Similarly, intensive studies of the vegetation of the Niobrara River Breaks area were not carried out until the early 1980's, despite the area's long history of botanical and ecological attention (Churchill et al. 1988).

Despite the recent increase in botanical attention of peatlands, relatively few sites have been found that contain *Liparis loeselii* populations, and only one has been documented to contain more than 10 individuals. This suggests that the known habitat in Region 2 is marginal, and there are currently no exemplary sites known within the region against which they can be compared. This may be due to the elimination of certain types of disturbance from these habitats; populations thriving elsewhere, including two that have been extensively studied (Wheeler et al. 1998, McMaster 2001), are in sites that were recently subject to disturbances such as substrate removal, fires, trampling, mowing, and hydrologic alteration.

Reproductive biology and autecology

Habit and reproductive strategy

Liparis loeselii is a short-lived perennial that shows characteristics of a ruderal species according to the CSR model (Grime 2001). Its ability to thrive in unproductive habitats such as nutrient-deficient soils is typical of a stress-tolerant species. Many epiphytic organisms (the common condition in the genus *Liparis*), such as bryophytes and lichens with wind-dispersed "dust" seeds or spores, show characteristics of the "stress-tolerant" strategy. Its tendency to produce large numbers of propagules is characteristic of an "r" adapted species (McArthur and Wilson 1967).

As is typical for a ruderal species, disturbance appears to be a factor in establishment of new populations of *Liparis loeselii*. Natural disturbances such as winter fires probably create openings, as do anthropogenic disturbances such as peat removal or mining and biomass removal through mowing or grazing. Studies in the United Kingdom indicate that *L. loeselii* is a seral species of early successional communities (Jones 1998, Wheeler et al. 1998).

Vegetative reproduction

Liparis loeselii is a perennial that can reproduce vegetatively by rhizomes produced by axillary buds below the swollen terminal internode inside the pseudobulb. The bud elongates into a rhizome in the autumn and is terminated by a pseudobulb primordium that will mature into a daughter pseudobulb during the winter and following spring. Roots are developed in the spring (Rasmussen 1995). Under exceptional conditions, an additional bud may elongate, resulting in two daughter pseudobulbs that may be produced at a distance of 1 to 3 cm from the mother pseudobulb. This suggests that some limited clonal growth may be possible, but the new pseudobulbs may detach from the parent plant. Because of this, Jones (1998) chose to recognize dense clumps of *L. loeselii* as single genets in his demographic study.

Phenology and pollination

Flowers are produced in the spring, with herbarium material from Region 2 showing a range of flowering from 30 May (Kansas) to 2 July (southwest Nebraska), with most collected in June. Outside the region, plants may flower as late as August in cold bogs to the north (Case 1987). The flowers are ephemeral and lack a detectable floral fragrance, and no record of nectar production has been documented (Summerhayes 1951). Fruiting specimens have been collected from Region 2 as early as 28 June, and apparently, the fruiting stalk may persist through the winter (Rasmussen 1995).

Unlike most orchids, which are strictly outcrossers that rely on specific species of insects for pollination (Case 1987, Hoyama 1993), *Liparis loeselii* is self-pollinating as first shown by Kirchner (1922), who demonstrated that plants from which pollinators were excluded set fruit. After a flower opens, the anther cap tissue begins to disintegrate within four days, causing it to lift upward and release the two pollinia, which fall downward and adhere to a ridge above the stigmatic surface. Although in some cases the pollinia land directly onto the stigmatic surface, they usually remain attached to the ridge until a rain droplet hits the anther cap, causing the pollinia to slide or rotate onto the stigma. In the presence of rain, the likelihood of pollination is increased by a factor of four (Catling 1980). Catling also demonstrated that agamic apomixis does not occur in this species, since self-pollination is necessary for fruits to form.

Seeds, dispersal, and germination

Like most orchids, *Liparis loeselii* produces large numbers of dustlike seeds. Seeds of *L. loeselii* are 0.4 mm long by 0.1 mm wide, and in one small population, a mean of 4,270 seeds were produced per capsule (McMaster 2001). Viability of seeds is unstudied for the species as a whole, but it was estimated at 80 percent in one natural population in Great Britain (McMaster 2001), whereas only 25 percent germination has been reported in culture (Henrich et al. 1981).

Seeds tend to be wind-dispersed and are commonly perceived to have the potential for long-distance dispersal; modeling experiments, however, indicate that most orchid seed should fall close to the maternal plant (Chung et al. 2004). The small stature of *Liparis loeselii* and its tendency to grow among taller plants probably limits the likelihood of long-distance dispersal. Orchid seeds are buoyant and waterproof, and water dispersal has been observed in some bog species but not in any holarctic species such as *L. loeselii* (Rasmussen 1995). Capsules of this species tend to stay closed until autumn or through the winter, opening in response to increased atmospheric moisture or being weighted down by snow cover (Huber 1921, Ziegenspeck 1936). In general, the large number of seeds produced offsets losses from insect predation and dispersal to unsuitable habitats (Rasmussen 1995).

Orchid seeds lack the differentiation into embryo, endosperm, and seed coat typical of most flowering plants. The orchid seed consists of an outer testa with netlike thickenings surrounding a mass of undifferentiated cells. Nutrient reserves are small and tend to be stored in the embryo cells as lipid and protein bodies to the near exclusion of other organelles (Rasmussen 1995). As in most angiosperm seeds, suitable temperature, aeration, and water are necessary for germination. Many orchids require darkness for germination, but like a number of bog species (Rasmussen 1995), *Liparis loeselii* can germinate in the presence of light (Zoltán 2003). As newly germinated orchid seeds have very little stored resources, a symbiotic relationship with a fungus is necessary for survival. In nature, *L. loeselii* requires the presence of the fungus in order for germination to occur, a condition typical of tropical epiphytic orchids (Knudsen 1925), but not true for all orchid species in our region (Rasmussen 1995). The fungal symbiont digests the seed coat and outer embryo cells, providing nutrition to the undifferentiated inner cells, which begin to differentiate into an embryonic structure called a protocorm.

Life history and mycorrhizal relationships

Seeds of *Liparis loeselii*, like those of most orchids, germinate in the spring, and protocorms have been observed in nature in May (Mrvicka 1990). In the protocorm stage, seedlings are relatively undifferentiated, with a basal end that forms mycotrophic tissue and a functioning meristem in the opposite end. Protocorms of *L. loeselii* are pale, uniformly hirsute with embryonic roots called rhizoids, and only 0.8 to 1.2 mm long (Mrvicka 1990). Zoltán (2003) observed green, photosynthetic protocorms grown in culture, a condition that is typical of the protocorms of tropical epiphytes, but occurs in some terrestrial orchids as well (Case 1987). The protocorms derive much of their nutrition from endophytic fungi, and they can evidently survive underground for a period of weeks, months, or even years (Rasmussen and Whigham 1993). Several species of fungus may occur symbiotically in a given species, and several species of imperfect fungi grouped in the artificial genus *Rhizoctinia* have been identified occurring in tissues of *L. loeselii* (Zoltán 2003). The fungus remains in association with the developing plants, particularly in the rhizome and leaf bases surrounding the pseudobulb. The process and rates of fungal infection are unstudied for *L. loeselii*, but fungal infection through epidermal cells has been observed in seedlings of the related *L. liliifolia* grown *in vitro* (Rasmussen 1995).

The next stage of growth, known as the mycorrhizome stage, begins when the apical meristem elongates and roots begin to form. Juvenile pseudobulbs and the first foliage leaf may appear by autumn, and mature roots appear the spring following germination (Mrvicka 1990). By some estimates, however, the first foliage leaf does not appear until the fourth year (Lang 1980). The fully developed pseudobulb consists of the swollen terminal internode of the rhizome surrounded by sheathing scale leaves. The internode is separated from the older portion of the rhizome by a layer of hardened cortical tissue through which the endophyte cannot pass. In order to inoculate the new growth, an internal root grows from the new rhizome segment into the old rhizome segment and produces hairs through which the endophyte can pass.

Once the first foliage leaf has appeared, plants of *Liparis loeselii* reach the two-leaf stage the following year, and they may persist at this stage several years before flowering. It appears that plants in the two-leaf stage do not revert to the single-leaf stage and that only two-leaved plants produce flowers (Wheeler et al. 1998). Flowering has been noted in the fourth year following emergence of the first foliage leaf, and plants that flower in a given year are likely to flower again in subsequent years (Wheeler et al. 1998). The life span of *L. loeselii* is unknown, but some plants have been recorded to have survived at least eight years (Jones 1998).

Cryptic phases

Since, in at least some cases, it may take as long as four years before the first foliage leaf is produced following germination, the protocorm and mycorrhizome stages may occur underground, completely dependent on fungal symbionts for survival. It is unclear whether pseudobulb dormancy occurs in *Liparis loeselii*, as appears to be the case in a number of orchid genera in which the aboveground parts are not produced some years, but subsequently reemerge as full-sized photosynthetic plants (Rasmussen 1995). Jones (1998) and Wheeler et al. (1988) noticed that marked plants of *L. loeselii* in a population disappeared and then reappeared in subsequent seasons, but they indicated that these situations were fairly uncommon and probably represented situations where a plant was overlooked or died and was replaced by new recruits. McMaster (2001) attempted to locate dormant pseudobulbs in an excavated portion of a small population of marked plants that did not flower in a given year, but found none. Jones (1998) questioned whether dormancy was possible since the pseudobulb is photosynthetic and often partly exposed.

Seed dormancy and seed bank longevity of orchids are poorly studied. In dry storage, most orchid seeds apparently are viable for less than one year, but they may survive longer if imbibed with water (Rasmussen 1995). Mrvicka (1990) germinated seeds of *Liparis loeselii* that overwintered in the inflorescence six months after seed maturation, and *L. liliifolia* seeds can apparently survive in dry storage for four years with no detectable loss of viability (Mattrick 2004).

Phenotypic plasticity

For such a broad ranging species, there is remarkably little morphologic variation throughout its range, and hybrids are unknown. Only the European coastal material described as var. *ovata* shows unique, consistent morphologic features that appear to correlate with geography. Size dimorphism is occasionally reported, often correlated to ecological factors. Voss (1972) reported plants at the upper limits of the species' size range occurring in shaded sites. McMaster (2001) interprets this tendency toward increased size in the shade to a reduction in competition.

Demography

Genetic characteristics

Since *Liparis loeselii* is an obligate, self-pollinating species with relatively little morphologic variation, studies of gene flow (which occurs primarily through seeds) have not been carried out to date, and no information on inbreeding depression is available. Naturally, hybridization is very unlikely.

Life history characteristics

Several demographic studies of populations of *Liparis loeselii* have been published in recent years, and vital rates are available for the visible phases of the life cycle based on populations studied in Massachusetts (McMaster 2001), eastern England (Wheeler et al. 1998), and southern Wales (Jones 1998). All of these studies have shown high mortality rates in *L. loeselii* populations, with the individuals marked in the initial year of one study declining by 97 percent over five years (McMaster 2001), and 82 percent and 90 percent over a period of eight years in the United Kingdom studies. The annual mortality rate was 55 percent in the Massachusetts population and 34 percent in the East Anglian population, in which the rate jumped from 20 to 35 percent the first 4 years to over 60 percent for the following 2 consecutive years (Wheeler et al. 1998). In this population, individuals in earlier life cycle stages showed higher yearly mortality with single-leaf plants declining an average of 54 percent per year, followed by two leaf (29 percent) and flowering (22 percent) plants.

Although recruitment was not recorded on a yearly basis from the Massachusetts population, the overall population size showed a decline of 52 percent, whereas the subpopulation initially studied declined 97 percent (McMaster 2001). Both United Kingdom studies showed a decrease in the rate of recruitment over time, with recruitment dwindling to zero in the south Wales population after the fourth year (Jones 1998). Effect on population size due to vegetative reproduction of multiple daughter pseudobulbs was not taken into account in these studies.

There are few data on the percentage of flowering individuals in a population in a given year. Wheeler et al. (1998) estimated that 10 to 20 percent of plants produce flowering stems in a given year, with a 22 percent likelihood of any plant flowering again the next season. McMaster (2001) reported a remarkable 85 percent likelihood of a given individual flowering the following season, but it is unclear whether he included single-leaved plants in his study, and this may have biased his figures toward more mature plants. Time for maturation varies from one to five years, with nearly equal percentages of plants seen flowering one, two, three, and four years after their first appearance in the East Anglian populations (Wheeler et al. 1998).

A life cycle diagram with known transition rates (from Wheeler et al. 1998) for the visible life cycle stages is shown in **Figure 4**. Hypothesized stages are shown by broken lines, and no attempt to represent vegetative reproduction has been made. Due to the missing data for the cryptic stages, it is not possible to generate a population matrix model for this species, and no instances of population viability models for *Liparis loeselii* have been located in the literature. Elasticity values from a population viability model of the terrestrial mesophytic orchid *Platanthera praeclara* indicated that seed set, germination rates, and seed viability most strongly contribute to increasing population growth rates (Sieg et al. 2002). Given the seral nature of *L. loeselii* populations, it is appears that further study of seed bank dynamics and early embryonic stages might be key to setting up future population viability models.

Spatial characteristics

Given the apparent disjunct nature of most *Liparis loeselii* occurrences in Region 2, it appears that metapopulation theory does not apply, in that most habitat patches are probably too isolated to allow for recolonization (Freckleton and Watkinson 2002). Although its seeds are wind dispersed, the small stature of the plant and its tendency to grow among tall vegetation probably limits the likelihood of colonization of suitable habitats on anything other than a local basis. It is commonly perceived that orchid

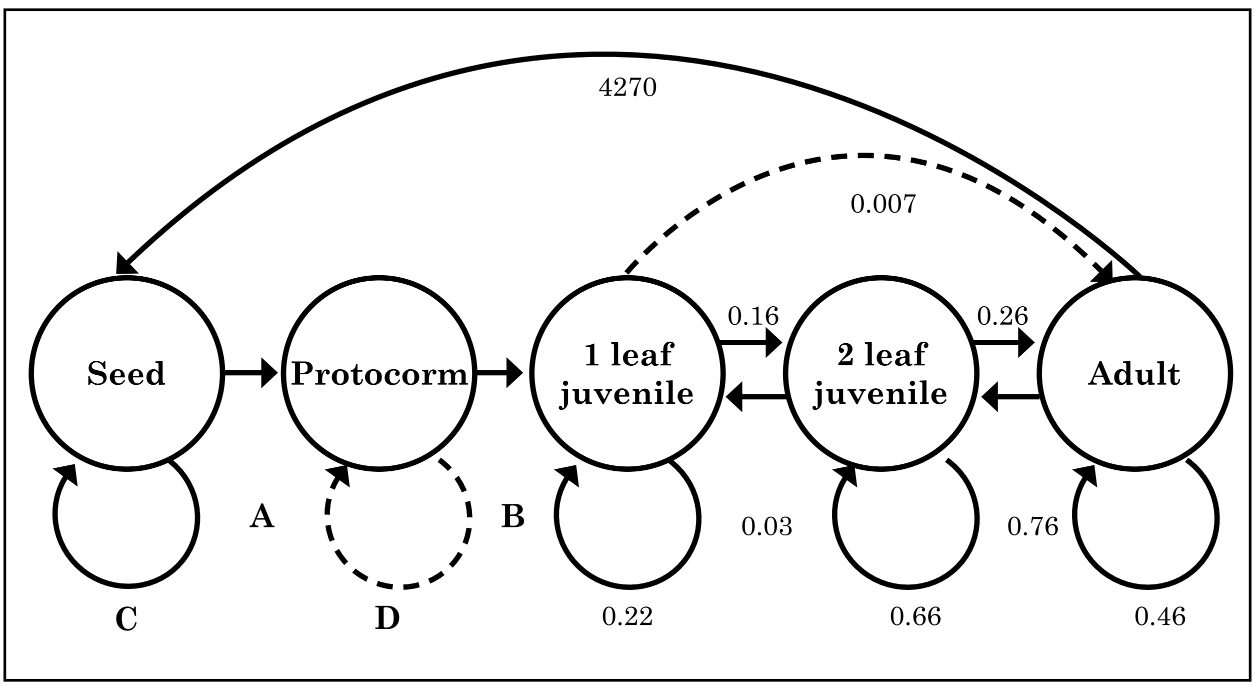

Figure 4. Life cycle diagram for *Liparis loeselii* (L.) Rich (after Caswell 2001). Vital rates from Wheeler et al. (1998), average seed set value from McMaster (2001). Wheeler et al. (1998) give a transition value for single-leaved plants flowering the next year, but state in the text that only two-leaved plants flower. Rates for stages A-D are not known. Broken lines indicate transitions that are unconfirmed.

seeds have the potential for long-distance dispersal, but a study of a terrestrial Korean orchid indicated that most seed dispersal occurs over distances of less than 10 m (Chung et al. 2004). *Liparis loeselii* in the Nebraska Sandhills appears to be an example of a "remnant population," persisting despite negative population growth because of possible recruitment from a seed bank. Freckleton and Watkinson (2002) consider the *L. loeselii* populations of eastern England to be an example of an "island population" (or a nonequilibrium metapopulation) in which colonization and migration are nearly nonexistent. The remaining isolated populations on the Great Plains probably also fit this definition, with the possible exception of those in the Prairie Coteau and Niobrara River Breaks.

Since the South Dakota occurrences are peripheral to the main range of the species and are mostly limited to a relatively small area (Roberts County), they could theoretically become extinct and subsequently recolonize. Although there is no evidence of new colonizations in the Prairie Coteau currently, it is possible that the known populations represent remnants of a former metapopulation. In the Niobrara River Breaks area, there may also be a number of occurrences in relatively close proximity that may function as a metapopulation. Churchill et al. (l988) reported *Liparis loeselii* occurring as "scattered populations" along the river from the mouth of Fairfield Creek eastward to the mouth of Barney Creek, a distance of only 8 km (5 miles); however, populations were documented at only those two sites. Farther upstream, a single individual of *L. loeselii* was found in a non-saturated wet meadow habitat unlike those typical for the species elsewhere in Region 2, after the site was burned in the two years preceding (Behrens personal communication 1998). The presence of *L. loeselii* in an unusual habitat from which biomass had recently been removed by fire suggests that populations in this area may demonstrate a source-sink metapopulation structure, with persistent populations maintained along the numerous spring-fed streams emerging from the bluffs in the area. The occurrence at the sandpit in Atkinson is also evidence of colonization of a recently disturbed area, but whether such occurrences persist or are likely to be recolonized following extirpation is open to speculation. Fens in the Sandhills from which peat was harvested or that were leveled for hay production have so far yielded no occurrences of *L. loeselii*. However, this may be due to competition from seeded alien grasses and current management practices, rather than isolation from persistent populations.

Limiting factors

It appears that hydrology is a very important factor limiting reproduction and growth of *Liparis loeselii*. Wheeler et al. (1998) noted a large decline in recruitment and an increase in mortality associated with an unusually dry season. It is reasonable to assume that a low level of moisture in spring would negatively affect seed germination and seedling survival, and that infrequent summer rains could impact the amount of fruit set by reducing pollination success. Wheeler et al. (1998) also suggested that a lack of inundation at the time of leaf emergence might increase grazing damage from mollusks.

Herbivory has an adverse effect on population dynamics, but McMaster (2001) observed that it might not be as devastating as implied by Wheeler et al. Individuals in the Massachusetts population experienced slightly reduced survivorship and were slightly less likely to produce flowers or fruit the following year, and those that did had smaller inflorescences. In the year following herbivory, damaged plants that bloomed produced fewer flowers, but the same number of fruits as undamaged plants. McMaster did not, however, record effects of herbivory on single-leaf plants, which Wheeler et al. imply may be more vulnerable to herbivores.

Another important factor limiting germination success is the presence of safe sites for germination. In addition to moisture, the presence of an appropriate fungal symbiont is necessary. Safe sites with adequate levels of moisture and presence of the fungus may be limited by competition as a result of succession. Jones (1998) suggested that succession in dune slacks that resulted in a lower percentage of bare soil and a higher percentage of litter (in this case a dense moss layer) reduces the extent of sites suitable for establishment of new plants. Competition from marsh plants near suitable sites may also act as a barrier to dispersal, as many of the seeds are likely to land on persistent vegetation (Rasmussen 1995).

Community ecology

Effects of herbivory

Populations of *Liparis loeselii* are negatively impacted by herbivores to varying degrees. Mollusks evidently may graze off young shoots (Wheeler et al. 1998). McMaster (2001) reported damage such as small holes in leaves, stems, flowers, and fruits caused by insects and other invertebrates, and complete removal of shoots and stems, likely by vertebrates such as deer or rabbits. Case (1987) indicated that the overwintering pseudobulbs (which he describes as vanilla-scented) are attractive to mice. No reports of herbivory in Region 2 are available, and the plant's small stature and tendency to grow among taller vegetation may reduce its likelihood of being selectively grazed. There are no data on the palatability of *L. loeselii* to grazing ungulates, but deer are known to favor plants of *L. liliifolia* (Mattrick 2004). *Liparis loeselii* plants observed at Buckhorn Springs in 1995 were apparently untouched while individuals of the more visible orchid Platanthera aquilonis were selectively browsed, likely by deer (Rolfsmeier, unpublished data).

Liparis loeselii grows in at least one site known to be grazed by cattle (Lonergan Creek), and several of the other sites on private land are probably grazed periodically, with at least one site on the Niobrara Valley Preserve (Barney Creek) accessible to grazing bison. Some orchids thrive in pastured sites, and a few, such as *Spiranthes lucida*, are apparently most abundant in heavily pastured sites (Case 1987). Light trampling may create sufficient disturbance to open up sites for orchid germination. For instance, Salzman (1992) found that grazing appears to slow plant succession and increase plant species diversity in some Massachusetts fens, but the increased nutrients and soil compaction from grazing can result in loss of some fen plant species and increase the likelihood of invasion by aggressive wetland plants. *Liparis loeselii* is associated with tussocks formed by cattle grazing in Nebraska Sandhills fens.

Effects of competition

The spread of aggressive, perennial wetland plants can limit the establishment of *Liparis loeselii*, but in Region 2, competition from native plants because of succession appears to affect the orchid more than competition from alien species. No alien species have been recorded occurring with *L. loeselii* in Region 2 (**Table 3**), but competition from aliens may contribute to the elimination of occurrences. *Liparis loeselii* has not been recorded from hayed fens seeded to rhizomatous Eurasian grasses such as redtop (*Agrostis gigantea*), despite the fact that many of these sites have been subject to disturbances like peat removal and leveling. This could in part be the result of haying practices, which favor these species to the detriment of native species (Steinauer et al. 1996). Aggressive native species such as *Phragmites australis* tend to occur in habitats that are not as wet as those that typically support *L. loeselii*, but in Great Britain, it has been observed that the percentage of flowering stalks decreases in response to increased growth of dominant vegetation following mowing (Lang 1980).

Interactions with cryptic organisms

The most important cryptic organisms that interact with *Liparis loeselii* are, naturally, the symbiotic fungi occurring in the soil. No record of fungal pathogen infection or disease is recorded for this species in the wild, but in cultivation it apparently may be susceptible to fungal pathogens (Correll 1978). As *L. loeselii* depends on abiotic factors for dispersal and pollination, no other symbiotic or mutually beneficial relationships appear likely.

Effects of abiotic factors

Abiotic factors that affect *Liparis loeselii* and the organisms that interact with them include hydrology, soil fertility, and rain. Stochastic factors such as fire, flood, and drought are also important, with drought generally decreasing germination success and increasing the vulnerability of the plants to herbivore damage (Wheeler et al. 1998). Fire may have a beneficial effect on *L. loeselii* by decreasing biomass of competing vegetation and providing less cover for herbivores. The effects of flood are unknown. Boorstein (1998) reported a population in Missouri that likely was destroyed by flooding due to construction of a beaver dam, but Case (1987) states that floods may create new niches favorable for the establishment of orchids. Hypothetical interactions of biotic and abiotic factors affecting *L. loeselii* are illustrated in **Figure 5**.

CONSERVATION

Threats from Habitat Destruction and Conversion

Although there is no evidence that any occurrence of *Liparis loeselii* has been extirpated in Region 2 (other than perhaps the Kansas occurrence), it appears likely that some populations have been severely impacted if not eliminated through habitat modification. Some historic fens in South Dakota have been destroyed (Ode personal communication 2005), and many others in the Nebraska Sandhills have been degraded by conversion to agricultural fields (Steinauer 1995). White and Chapman (1988) grouped disturbances to fens into three categories: those that disrupt fen hydrology, those that degrade the quality of groundwater supplying fens, and those that disrupt the fen soils and vegetation. Of these,

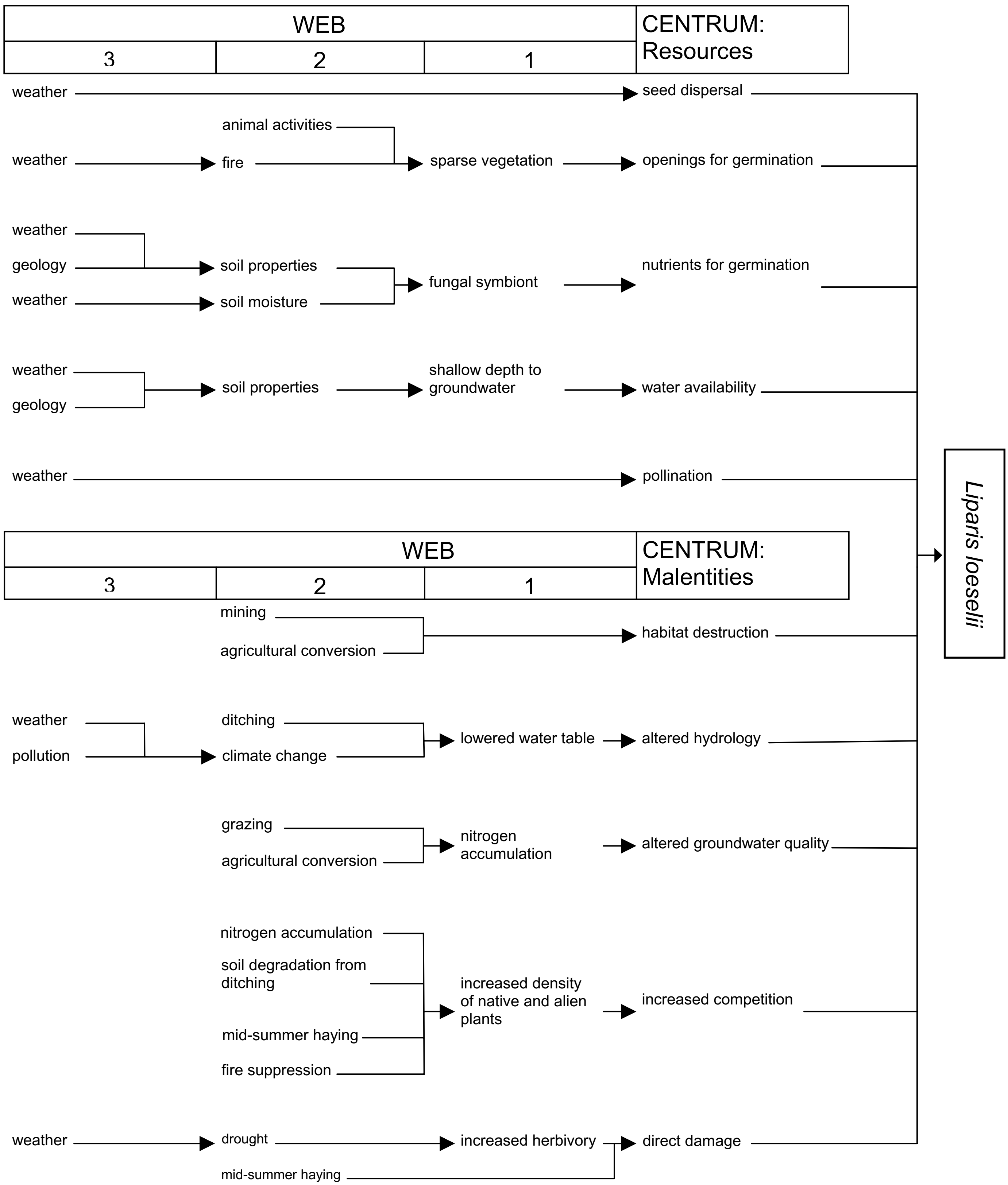

Figure 5. Envirogram outlining potential resources and malentities for *Liparis loeselii* (after Andrewartha and Birch 1984).

alteration of hydrology has likely been the greatest historical threat to *L. loeselii* in Region 2, and may continue to be among the major long-term threats to the integrity of its habitat this century.

Disruption of hydrology

Nebraska Sandhills fens have been extensively ditched and drained for hay production. A survey of 39 fens in Cherry County indicated that 34 had at least some ditching (Steinauer 1995). Ditching alters peatlands by lowering the water table and causing decomposition and compaction of organic soils through oxidation, and lowered water table levels can significantly affect the composition and structure of the vegetation. Soil compaction and decomposition in Nebraska Sandhills fens is most pronounced in the vicinity of drainage ditches, and these areas are often dominated by near monocultural stands of *Phalaris arundinacea* (reed canarygrass) (Steinauer 1995). In Iowa, fens have been tapped for watering livestock, and this can alter groundwater flow and cause detrimental changes (Thompson 1990). In South Dakota, some potential *Liparis loeselii* habitat may be threatened by construction of dugouts in or near fens to collect water for cattle (Leoschke personal communication 2005).

On a broader scale, one of the greatest long-term threats to *Liparis loeselii* in Region 2 will likely be mining of water from the Nebraska Sandhills. Sixty-two percent of the available groundwater in the Ogallala aquifer is found in Nebraska (Kromm and White 1992), and the deepest part of the aquifer is found beneath the Nebraska Sandhills (U.S. Water News Online 1996). With increasing pressures from irrigation and continued population growth and urban development in the West, demands on groundwater are increasing, despite a national decline in water consumption (Jehl 2002). These demands could increase further if global warming results in prolonged drought. Although threats from urban development are minimal in the sparsely populated Sandhills, rapid population growth in Colorado and eastern Nebraska could very soon result in large-scale transfer of groundwater from the Sandhills. Already a Colorado company has looked into the possibility of pumping water from the western Sandhills and transporting it by rail (Messersmith 2003). Mining the Sandhills for water could affect fen and other wetland species that depend on a high water table, as well as species associated with springbranch canyon streams in the Niobrara River Valley, which are fed by water from the Sandhills.

Degradation of water quality

Peat soils have a great capacity to absorb nutrients, and excess nutrients, such as nitrogen, can lead to shifts in species composition and lower species diversity. In Iowa, groundwater nitrate concentrations at eight of 20 sampled fens were higher than the drinking water standard, and pesticides were found in the groundwater at 10 of the fens (Thompson 1990). In the Prairie Coteau, cropland surrounded many fen sites. At one site near Big Stone Lake in South Dakota, a fen was observed that had been invaded by *Phragmites australis*. It was on a side slope below a crop field that was located on top of the recharge zone of the fen aquifer, and the invasion by this aggressive wetland grass could have been the result of excess nutrient accumulation (Ode personal communication 2005). Presently, center-pivot irrigation development and row crop agriculture pose only slight threats in the Nebraska Sandhills, but the highly porous sands make aquifers extremely susceptible to nitrate and pesticide contamination (Steinauer 1995).

Disruption of soils and vegetation

Although peat has been harvested from Nebraska Sandhills fens for heating on a small scale by homesteaders (Hardy 1992), the threat of commercial peat mining in these fens appears low, probably due to the interspersed layers of sand and muck in the peat and the remoteness of the area from major population centers (Steinauer 1995). Many fens have been leveled for hay production, and while disturbances to the peat appear to be beneficial to certain populations (e.g., Wheeler et al. 1998), management activity associated with hay production is probably detrimental to the species. Gravel mining is evidently a serious threat to some fens in Minnesota, and it is possible that some fens in the Prairie Coteau may have been destroyed or are at risk, but no instances of mining fens for gravel in South Dakota are known (Ode personal communication 2005).

Threats from management activities or natural disturbance on habitats and populations

Occurrences of *Liparis loeselii* in Region 2 contain so few plants that the consequences of management activities, recreation or other human use, or natural disturbances could seriously affect their viability. In contrast to threats from disturbance, *L. loeselii* is also vulnerable to suppression of disturbance. Some amount of disturbance appears to be necessary for establishment and survival of the species. Suppression of disturbance may be detrimental to habitat quality and long-term persistence of individual occurrences. However, reintroducing simulated natural disturbance, if not carried out with care as regards to timing and intensity, could severely damage or limit the reproductive success of the occurrences in the region because of their small size.

Whereas restoration of hydrology is often a foremost concern in restoration and management of wetlands, the sites with known occurrences of *Liparis loeselii* have been minimally impacted by drainage. As a seral species, *L. loeselii* depends on moderate natural disturbance including fire, windthrow, insect damage, grazing, and beaver activity in order to reduce competition and to open microsites for germination (McMaster 2001). Grazing, mowing, and burning are the relevant management practices for creating disturbance, and most known sites are not hayed, grazed minimally, if at all, and not subject to fire. Succession and litter accumulation due to this lack of intervention are potentially the most serious management impacts in the region and represent the primary threats to existing occurrences.

Although grazing and trampling are listed as threats to fen habitats (Steinauer 1995, Faber-Langendoen 2001), a small amount of grazing timed appropriately may be beneficial. Currently, only a few known occurrences of *Liparis loeselii* are subject to grazing. Because of the wet, spongy nature of peaty soils in these habitats, cattle are often restricted to the drier outer margins of fens and the areas adjacent to ditches (Steinauer 1995). Excessive grazing may hinder the spread of the species due to soil compaction and increased nutrient accumulation that could stimulate competition from nitrogen-tolerant species. Some ranchers prefer to winter-graze when the soils are frozen and access to the fen by cattle is improved, and this practice appears to minimize some of these impacts (Steinauer 1995). Sites in the McKelvie National Forest are fenced off to exclude grazing, but some short-term cattle grazing has occurred accidentally in the Drinkwalter site (Steinauer and Rolfsmeier 1995).

Although removal of biomass by mowing or haying is sometimes recommended for improving the viability of *Liparis loeselii* occurrences (Jones 1998), fens that are managed primarily for hay production in the Nebraska Sandhills are not known to have occurrences of *L. loeselii*. Annual mid-summer haying, as normally carried out in these sites, promotes the growth and spread of cool-season alien grasses and native sedges, and most regularly-hayed sites have a dense cover of graminoids in which *L. loeselii* may not be able to thrive. Mid-summer haying may also affect the plants directly by removing inflorescences before seeds mature, further impacting the chances of recruitment.

Prescribed burning has been recommended as a management option for fen sites; however, spring burns timed to set back alien cool-season plants could negatively affect the aboveground parts of *Liparis loeselii*, which also initiates growth in the spring (Steinauer 1995). Peat fires are considered a threat in some sites, but in the saturated soils in which this species is frequently found, the threat is probably minimal.

Interactions with alien species

At present, no alien species are recorded occurring in the immediate vicinity of occurrences of *Liparis loeselii*. *Lythrum salicaria (*purple loosestrife*), Phalari*s *arundinacea,* and the native *Phragmites australis* ssp. *americanus* pose potential threats, particularly if sites become drier or if siltation or nutrient accumulation becomes a problem. *Lythrum salicaria* has not yet been found in Prairie Coteau wetlands (Ode personal communication 2005), but it is abundant in the Niobrara River Breaks region. The alien species redtop (*Agrostis gigantea*), Kentucky bluegrass (*Poa pratensis*), and clovers (*Trifolium* spp.) are frequently found in mowed fens and could be present at some sites. However, these non-native species are generally not regarded as being nearly as aggressive as common reed, purple loosestrife, and reed canarygrass.

Overutilization and other human impacts

Due to the remote nature of many occurrences of *Liparis loeselii*, overutilization of these sites is not an apparent threat. Roads have been built through a few sites that have the potential to support *L. loeselii* occurrences, and it is thought that road building may have contributed to the elimination of the Kansas occurrence. Unless a site is destroyed or its hydrology is severely affected by road construction, such activity may have a short-term positive effect in creating disturbance for recruitment of new individuals (Case 1987). Inappropriate recreational activity may also pose a threat by causing direct damage to plants, but at present, this risk appears slight. Although off-road vehicle use is permitted at McKelvie National Forest, the remoteness of the occurrences, and the fact that they are fenced off, may minimize such potential impact, and the travel management plan in production will further serve to protect these locations (Croxen personal communication 2004).

No commercial or folk uses for *Liparis loeselii* are known in the literature, and due to its inconspicuous nature, it is very unlikely to be harvested for ornamental use. Other species of *Liparis* have apparently been subject to historical overcollection elsewhere (Mattrick 2004). However, due to the paucity of botanists in the portions of Region 2 in which it occurs, *L. loeselii* has not, nor is it likely to be, threatened by botanical collecting for scientific study.

Conservation Status of Liparis loeselii in Region 2

Since its historical abundance is unknown and trends in existing Region 2 occurrences have not been studied, it is unclear whether *Liparis loeselii* is in decline. It is probably safe to say that the Kansas occurrence has disappeared, but there is no direct evidence of any other known occurrence having been extirpated from the region. It is very likely that some of the historic occurrences and other sites that once supported or were capable of supporting the species have been destroyed or degraded to the point where occurrences have disappeared.

Kaul (2005) suggests that the species has apparently not declined much in abundance in the Nebraska Sandhills because its habitats are relatively undisturbed. However, many areas of apparently suitable habitat exist in which the species has not been found. Nearly all known occurrences are from minimally-disturbed fens or saturated wetlands with peaty soils, and it appears that these habitats are capable of supporting occurrences over time, even at low densities. The full range of potential habitat in the region is unknown, and it appears that other habitats can support the species in the presence of a disturbance such as fire. Whether these atypical habitats can support the species in the absence of the disturbance is unknown. The appearance of *Liparis loeselii* in a wetland depression in sandy loam soils in the Niobrara River floodplain may represent a recent colonization following fire, but it is possible that the species was present before this event. The paucity of records from habitats other than fens and seeps suggests that other sites are less capable of supporting occurrences over a long period of time.

Liparis loeselii is an opportunist that thrives in early successional habitats of moderate disturbance, and the populations consistently decline as succession occurs (Jones 1998). In the case of occurrences in Region 2, it appears that even in certain mature, scarcely disturbed habitats, the orchid maintains itself, albeit in low numbers, for what appears to be a long period of time. Many sites in which the orchid is found have not received management intervention and have likely remained in a fairly consistent state for many years. However, given their small size, inherent population fluctuations, and a lack of management for favorable germination microsites, most existing occurrences appear particularly vulnerable to environmental extremes, particularly the very small occurrences such as those at Lonergan Creek or the Kriz fens.

Management of Liparis loeselii in Region 2

Implications and potential conservation elements

Liparis loeselii is apparently very rare in Region 2. Fewer than 60 plants have been documented, but there are no abundance figures from 15 of the 24 reported occurrences. At least nine occurrences have not been revisited since they were originally documented and may be considered historic. Three occurrences and approximately half the total number of known plants are located on reserves managed by The Nature Conservancy. The abundance and conservation status of occurrences on most private lands are unknown. Only two occurrences are known from National Forest System lands in Region 2, both on the McKelvie National Forest in Nebraska, but apparently suitable habitat exists in the remainder of the region. National Forest System lands and The Nature Conservancy preserves play a critical role in providing necessary protection and serving as a resource for observing and monitoring effects of natural and managed disturbances on the species in Region 2. Collaboration with private landowners and managers of other public lands can also further these goals. Such collaborative interactions may make it possible to collect sufficient data for determining future management needs and appropriate actions for Region 2 occurrences.

In general, conditions and events that maintain or increase the condition and extent of microhabitat suitable for germination of *Liparis loeselii* seeds allow the species to thrive in a given area. Among the most important features of these microhabitats are consistent soil moisture, bare and nutrient-poor soils, and the presence of mycorrhizae. The largest historical impact on these sites since the arrival of European settlers has been changes to hydrology, which have nearly always negatively affected the species. Conversion of these sites for agricultural use has usually resulted in alterations of hydrology through drainage, resulting in degradation of soil and invasion by alien species, often intentionally cultivated in these sites. Ongoing hay production increases the cover and dominance of cool-season grasses, resulting in habitat homogeneity and decreased species diversity, leading to fewer potential regeneration niches and eventually to the elimination of the species from these habitats.

Liparis loeselii is still present in sites that have not been converted for hay production, but these sites may be subject to the impacts of intensive agriculture to groundwater levels and quality. In "undisturbed" sites, natural events such as fire, flooding, and occasional grazing may assist in opening niches for germination, and suppression of any of these factors (or overuse thereof) may negatively impact the species, particularly in "marginal" habitats such as seasonally moist swales.

Many sites with occurrences of *Liparis loeselii* receive little or no management attention, and for those that are subject to occasional grazing or prescribed burns, no assessment of the implications of management has been conducted. Most management activities in place in the region do not appear to have enhanced or increased potential regeneration niches. At best, they have allowed the species to maintain itself in small numbers in certain habitats. Due to the lack of monitoring of known sites, the impacts of management actions on these plants in the region cannot be stated definitively.

In general, most occurrences appear to exist as isolated "islands" that are unlikely to be recolonized following a local extinction event, and given the small size of most occurrences, such events appear likely. Preserving habitat connectivity increases the possibility of recolonizing these sites, and preserving areas with large complexes of wetland habitat could be considered a potential conservation element. Maintaining and improving quality of existing habitat with regard to creating regeneration niches is another. In general, this includes maintaining current hydrology or restoring it, and maintaining or simulating natural disturbance as much as possible. These actions will likewise reduce the risk of soil degradation and alien species invasion. Protecting existing sites from conversion to hay production, prolonged heavy grazing, drainage, or increased human traffic is also a necessary element in maintaining existing occurrences.

Tools and practices

Species inventory

No known surveys specifically aimed at locating *Liparis loeselii* occurrences have been carried out in Region 2, but some occurrences were found during surveys for multiple species of potential conservation concern. Due to the inconspicuous nature of the plants, it is likely that some may be present in appropriate habitats that have already been surveyed for other species. Due to the difficulty in locating flowering plants, surveys for *L. loeselii* are probably best conducted during the summer or fall after the fruiting capsules have formed. It might be possible to search in very early spring for the previous season's fruiting stalks, but in areas with much winter wind and snowfall, these stalks tend not to survive (Mattrick personal communication 2006).

Occurrences of *Liparis loeselii* are probably best sought in open areas within appropriate habitats, such as animal paths and along streams flowing through seepage areas. Once an occurrence is located, the number of individuals (including sterile basal rosettes) could be tallied and the locality recorded with a geographic positioning system with little additional effort. This will help to create a baseline for future studies of the spatial characteristics and effects of management approaches (or lack thereof) on the populations over time.

Habitat surveys

Areas with the greatest potential for suitable habitat include the Niobrara River Breaks, Prairie Coteau, Nebraska Sandhills, and the Niobrara, Elkhorn, and Loup River systems east of the Sandhills, including areas along the Dismal River at the Bessey District of the Nebraska National Forest (Steinauer personal communication 2005). The historical presence of this orchid in northeastern Kansas indicates that peaty seeps and fens in southeastern Nebraska and northeastern Kansas might also contain the species; however, these areas appear less likely to contain it and are best considered as a lower priority for surveys. *Liparis loeselii* has been recorded in the Rocky Mountains in northwestern Montana, and while it is conceivably present in fens in mountainous areas, known occurrences appear to be associated with Pacific Northwest biota outside of Region 2. McMaster (2001) reported that this species appears to be found in the same niches as *Ophioglossum pusillum* (northern adder's-tongue), and the two have been observed growing together at Buckhorn Springs in the McKelvie National Forest

(Steinauer and Rolfsmeier 1995). A few known sites with *O. pusillum* exist in the Nebraska Sandhills and Niobrara River Valley from which *L. loeselii* is not known, and these sites would be good starting points in the search for new occurrences.

Surveys to locate areas of potential habitat within the Nebraska Sandhills have been conducted by examining soils maps for inclusions of peat soils (Steinauer 1995), and such methods would be useful in areas with known occurrences. Aerial photography might also be employed to eliminate sites with appropriate soils that have been altered by drainage, agricultural conversion, or that are in close proximity to production agriculture. Areas mapped as springs and seeps within these regions are likely candidates for *Liparis loeselii* occurrences, as are areas of high quality fen and seep communities recorded by Natural Heritage programs, and these would also qualify as priority sites for future surveys. Additional habitats in which the orchid might be present are in the Niobrara River Valley. Surveys of sparsely vegetated headwaters of springbranch streams or sandy moist lowlands in the Niobrara River floodplain, at such places as the Niobrara Valley Preserve, might also be considered, if time and resources permit.

Population and habitat monitoring

Since there are virtually no data on population trends among occurrences of *Liparis loeselii* in Region 2, revisiting known occurrences may yield valuable information on the persistence of the species in the area. Ideally, a census of known occurrences should be carried out annually, at the very least. Given the small number of occurrences and small size of populations, yearly surveys of a few sites should be possible with a minimum of resources, but even a bi- or tri-annual census is preferable to none at all. Jones (1998) suggested inventorying shoot numbers in late summer or early fall, as this is the time of the year at which stem production is highest. McMaster (2001) and Wheeler et al. (1998) surveyed several times during the season, beginning in early June and July, in order to collect data on basal rosettes and to record the effects of herbivore damage.

In order to collect demographic data, McMaster (2001) marked individual plants with tags, but he reported that the tags frequently disappeared. Wheeler et al. (1998) applied a more rigorous and time consuming procedure, in which positions of plants were mapped in a permanent 10 meter-square grid that was returned to year after year. Given the small size of populations in Region 2, either procedure might be utilized if data regarding the fate of individuals is desired. A less time-consuming approach might be to mark occurrences with a global positioning system (GPS) or with a permanent site marker and census the population annually, employing these and other sampling techniques in the unlikely event that these populations become too large to casually count. Considering the low numbers of plants recorded at most occurrences, care should be taken to avoid damaging existing plants during the monitoring process, as the loss of even a single plant could impact population trends. Use of GPS data and population census data on areas such as McKelvie National Forest and the Niobrara Valley Preserve could provide the groundwork for future studies of metapopulation dynamics of the species in this region.

Once occurrences have been located, surveys could include a census of sterile and fertile individuals, and these could be conducted early in the season when non-flowering individuals are most readily visible. Presence/absence surveys should be avoided. Due to the small size of populations, monitoring numbers of individual plants is not much more time-consuming than locating occurrences in the first place.

Habitats that show potential for *Liparis loeselii* could be searched periodically for occurrences in the late summer or fall, particularly following any changes in management that might create regeneration niches.

Management approaches

While beneficial management actions have not been described in detail, Wheeler et al. (1998) suggested that since *Liparis loeselii* plants are short-lived, conservation management needs to provide conditions for establishment of new individuals, as well as suitable conditions for maintaining existing plants. More work is needed to establish what constitutes "suitable conditions," for this species, particularly in Region 2. Reducing competition by mowing may help to maintain existing plants, but mowing may be accompanied by some form of disturbance to open microsites for germination. Jones (1998) noted the appearance of unrecorded individuals of *L. loeselii* following a season of close mowing, but could not determine whether these represented new recruits, or previously-recorded plants that were not visible under the dense vegetation canopy. Wheeler et al. (1998) noted a peak in numbers of individuals in the year following a prescribed burn, and suggested that winter burning or light trampling damage may be helpful in creating appropriate disturbance. Jones (1998) suggested a more detailed management protocol for dune slack occurrences including close mowing and turf stripping to create bare soil microsites, but the implications of these actions outside of these typically dynamic dune systems has not been evaluated. McMaster (2001) suggested excluding competition (including herbivores) and providing moderate disturbance including controlled burning and woody plant cutting (in the northeast United States). Highly interventionist management policies are suggested by Wheeler et al. (1998) as necessary to preserve the species in Great Britain, and future management efforts should assess the effects of such management on this and other species in sites containing *L. loeselii*, including the possibility of reintroduction of the plant to appropriate sites at historic localities. Seedlings were introduced into one extant and three former sites in East Anglia in 2000 (Royal Botanical Gardens, Kew 2000), but at present, no seed storage or propagation programs are known for this species in North America.

Information Needs

Distribution and habitat

Despite over a century of collections in Region 2, the distributional data for *Liparis loeselii* are still incomplete, as indicated by the large percentage of occurrences discovered since the initiation of state heritage programs within the last 25 years. Knowledge of the total extent of fen/seep habitats in the Nebraska Sandhills, Prairie Coteau, and Niobrara River Valley has been greatly expanded by surveys conducted in recent years (e.g., Churchill 1988), and based on the prevalence of suitable habitat there, careful surveys of these areas are likely to turn up new occurrences. Attempts to relocate historic occurrences in Nebraska could be considered a priority for understanding the longevity and persistence of existing populations. Locating occurrences in North Dakota could also prove helpful, and coordination of effort with Region 1 might lead to a more complete picture of the status of the species in the Prairie Coteau region. However, finding a number of new occurrences is unlikely to affect the conservation status of the species if they are all rather small occurrences such as those currently known. A number of large occurrences would have to be found in order for the species to be regarded as secure in Region 2, and unless this happens, it is best to maintain its sensitive species status.

Life cycle, habitat, and population trend

The cryptic stages of the life cycle of *Liparis loeselii* are poorly understood, as they are for most orchids, and more work is needed to determine whether seeds remain viable for a sufficient amount of time in natural habitats to form a seed bank. The contribution of the seed and seedling stages of the life cycle could be crucial for understanding the population dynamics of this species.

The full range of habitats in the region is poorly understood, and surveys of wet, sandy bare areas in the general proximity of *Liparis loeselii* habitats, such as wet meadows, could be searched as time permits.

If possible, an annual census of one (or several) accessible occurrences of *Liparis loeselii* could be conducted to establish duration of persistence and the nature of population fluctuations in these sites, which are currently unknown in Region 2.

Responses to change

Other than a general assumption that some disturbance is necessary for establishing new individuals, the effects of habitat changes have not been evaluated with the exception of the survey by Jones (1998), in which population flux was evaluated with regard to succession. Changes in recruitment following an observed disturbance were noted by Wheeler et al. (1998), and Wheeler et al. (1998), Jones (1998), and McMaster (2001) all noticed a reduction of population in response to lack of management. Effects of changes in habitat due to different management strategies are also poorly known, and experiments will be necessary to address these effects. Interactions of populations of *Liparis loeselii* with alien species have yet to be addressed.

Metapopulation dynamics

No studies of metapopulation dynamics have been conducted, and it appears that most stands currently operate as island populations. Whereas studies have documented short-term declines in populations in the absence of management regimen (Jones 1998, Wheeler et al. 1998, McMaster 2001), no studies have documented the long-term persistence of populations in the absence of management. Methods for monitoring population trend exist in the literature and are summarized in the Population and habitat monitoring section of this assessment.

Demography

Demographic studies have been carried out at the local level in several cases (e.g. McMaster 2001), and relationship of population flux to the persistence of populations have not been evaluated in North America. In particular, seed dispersal and seed bank dynamics are poorly understood and are likely crucial to the long-term persistence of the species. No such data are available for Region 2. Detailed methods for carrying out demographic surveys are given in Wheeler et al. (1998).

Restoration methods

Studies of restoration methods have not been carried out, in part due to the expense of restoring hydrology of degraded wetland systems. The species has been reintroduced at sites from which it has disappeared in the United Kingdom, but the restoration protocol and results are unknown.

Research priorities for Region 2

- monitor the status of existing populations
- conduct surveys for additional occurrences in the Nebraska Sandhills and along rivers that drain the Sandhills, along with additional surveys of fens in the Prairie Coteau region; in particular, surveys of National Forest System lands along the Dismal River at the Bessey Division of the Nebraska National Forest should be conducted
- characterize more rigorously the array of habitats supporting the species and the microsites in which the species occurs
- conduct additional research on autecology and demography of the species, particularly in terms of its response to various kinds of disturbance
- study the effects of seed production, dispersal, and seed bank longevity, and its relationship to persistence of populations.

Additional research

As the conservation of *Liparis loeselii* continues to be a much more urgent issue in Europe than in North America, it appears that for the time being, Region 2 botanists and land managers will have to continue to rely on European studies for new insights into its biology, ecology, and genetics. However, a degree of caution should be taken in applying these results directly to regional populations due to inherent differences in habitats and potential genetic variation between European and Region 2 plants. A recent study of the conservation genetics of *L. loeselii* in the United Kingdom and mainland Europe (Royal Botanical Gardens, Kew 2000) could not be incorporated into this assessment, and other studies of the spatial characteristics of European populations have been seen, but they have little direct bearing on Region 2.

DEFINITIONS

Agamic apomixis – producing seeds without genetic recombination.

Alien – non-indigenous.

Anther cap – the structure at the tip of the column which contains the pollinia in orchid flowers.

Anthropogenic – pertaining to human activity.

Axillary – pertaining to the angle between the stem axis and the base of a leaf.

Bog – a permanent, peat-filled wetland with strongly acid, mineral-poor soil, and supplied with water from rainfall rather than groundwater (Steinauer 1995).

Calcareous – containing calcium.

Carr – a fen with woody vegetation.

Column – in orchids, the organ formed from the union of the stamens and pistil.

Cortical – referring to tissue occurring between the epidermis and vascular tissue.

Competitive/Stress-tolerant/Ruderal (CSR) model – a model that characterizes the life history strategies of plants based on resource allocation; competitive species primarily allocate resources to growth, stress-tolerant species primarily allocate resources to maintenance, and ruderal species primarily allocate resources to reproduction; some species, such as *Liparis loeselii*, may show characteristics of more than one strategy.

Demography – the study of population dynamics, in particular age and stage structure and transitions.

Dune slacks – interdunal depressions.

Endangered – defined by the Endangered Species Act as any species at risk of extinction in all or a large part of its range.

Endemic – native to a particular region, generally referring to a distribution contained entirely within that area.

Endophyte – an organism that lives inside a plant.

Endosperm – food storage tissue in a seed.

Epiphyte – an organism that lives attached to another organism but does not parasitize it.

Fen – permanent, groundwater-fed wetlands with organic soils generally >30 cm (12 in.) (Steinauer 1995).

Genet – a group of plants occurring close together that may resemble distinct individuals, but are genetically identical and may be attached underground.

Habitat amplitude – the range of habitats inhabited by an organism.

Herbaceous – non-woody.

Hirsute – with coarse, somewhat stiff hairs.

Imperfect fungi – an artificial group of fungi grouped together on the basis of not having a known sexual stage.

Inbreeding depression – reduction of fitness in the offspring produced by inbreeding.

Indicator species – a species regularly associated with a particular community such that its presence is evidence of the presence of the community.

Keeled – having a longitudinal ridge.

Labellum – the modified uppermost petal of an orchid flower (appearing to be the lowermost, since orchid flowers rotate 180° as they develop).

Meristem – a region of undifferentiated cells from which new cells arise.

Metapopulation – a set of populations of the same species among which there may be gene flow and local extinction and recolonization events.

Mycorrhizome stage – the portion of the life cycle of an orchid that immediately follows the protocorm stage and that is initiated when the stem tip elongates and the first roots form (Rasmussen 1995).

Mycotrophic – deriving nutrition from fungi.

Oligotrophic – a body of water with low dissolved nutrient and usually high dissolved oxygen levels.

Perennial – a plant that continues to live and reproduce one or more years after producing reproductive structures.

Pleistocene relict – an organism that has theoretically experienced range contraction following the glacial advances of the Pleistocene, with the exception of some remaining occurrences in isolated areas with suitable (often cool and wet) environmental conditions.

Pollinia – coherent pollen masses.

Primordium – an organ in its earliest stages of development.

Propagules – a portion of a plant (usually a fruit or seed) that can give rise to a new individual.

Protocorm – the earliest stage of the developing embryo of an orchid seedling that can be defined as the period from germination to the formation of a shoot tip with primordial leaves (Rasmussen 1995).

Pseudobulb – the thickened base of an orchid stem formed by swollen leaf bases and which may function as a water storage organ.

"r"-adapted – an organism that has characteristics in which reproduction and rapid population growth are more important than competitive ability.

Raceme – an unbranched inflorescence of stalked flowers.

Rhizoid – a root-like structure that anchors an organism but contains no vascular tissue.

Rhizome – an underground stem or stemlike organ.

Ruderal – an organism that primarily allocates resources to reproduction.

Secondary succession – succession occurring on a site that was previously occupied by organisms, but which has undergone severe disturbance.

Seed bank – dormant seeds buried in soil.

Seral – a species or assemblage of species that occupy a site only temporarily as part of a series of successional stages.

Springbranch – usually a narrow canyon containing a small spring-fed tributary stream.

Stochastic – an indeterminate or random process not part of a predictable cycle, such as fire or flood.

Symbiont – an organism that participates in a mutually beneficial relationship with a different organism.

Testa – seed coat.

Threatened – defined in the Endangered Species Act as any species likely to become endangered in the foreseeable future in all or a large part of its range.

Turbary – an abandoned peat mine.

Vital rates – rates of recruitment and death in a plant population.

Wet meadow – a sub-irrigated (high water table) grassland occurring on mineral soils and dominated by hydrophytic grasses and sedges (Steinauer 1995).

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