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Status of Four Orchid Species at Silver Lake Fen Complex[1]

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The native orchids *Liparis loeselii* and *Spiranthes romanzoffiana* inhabit hydric-mesic sapric histosol soils supporting three distinct fen vegetation zones at Silver Lake Fen State Preserve. *Platanthera hyperborea* and *Cypripedium candidum* primarily inhabit adjacent mesic-hydric aquoll mollisols supporting wetland and marsh vegetation. The fen orchids possessed shallow subterranean storage organs and perennating buds bathed in shallow water, while the non-fen orchids exhibited deep storage organs and perennating buds above a deep water table. Ramet census demonstrated all orchids possessed reproductive efforts greater than 90%, except *C. candidum* which exhibited 52% effort, probably due to low pollination. Genet analyses suggest *L. loeselii* and *S. romanzoffiana* total 267 and 22 individuals respectively, while *C. candidum* and *P. hyperborea* respectively total 666 and 2797. The fen orchid populations are smaller, but the larger non-fen species populations may be declining due to encroachment and competition from *Fraxinus*, *Typha* and *Phragmites*.
INDEX DESCRIPTORS: Dickinson County, Iowa, Fen orchids, Orchidaceae, Silver Lake Fen, Species Biology.

The fens of Emmet and Dickinson counties have received botanical attention from studies which detail algae (Gashwiler and Dodd 1961), diatoms (Shobe et al. 1963), and vascular plants (Shimek 1915, Wolden 1926, Conard 1952, Anderson 1943, Holte and Thorne 1962, Holte 1966). More recently van der Valk (1975, 1976) has provided a quantitative analysis of the vascular plants comprising the three major vegetation communities or zones of two Dickinson County fen complexes and further presented analyses of competitive factors and productivity which contribute to their distinctive zonation. Physiochemical factors of the fens and especially their waters are reported by Carter (1939), Hempstead and Jahn (1939), Gashwiler and Dodd (1961), Holte and Thorne (1962), Eickstaedt (1964), Holte (1966), and van der Valk (1975, 1976).

Two works are devoted to the Orchidaceae of Iowa. Fitzpatrick and Fitzpatrick (1900) provide the first treatment for the 22 taxa of the group in their publication. Niemann (1975) later provided a meticulous account of the specimens, literature, distribution, habitat and status of the 25 species and 2 natural hybrids then inhabiting the state. Other studies only refer to Iowa orchids as brief citations in regional or county floras, taxa cited in vegetation descriptions or as associates of other reported taxa.

Several species of orchids are often cited as inhabitants of northwest Iowa fens. The species include *Cypripedium candidum* Muhl. ex Willd. (Shimek 1915, Anderson 1943, Conard 1952, Niemann 1975), *Platanthera hyperborea* (L.) Lindl. (Wolden 1926, Holte and Thorne 1962, Niemann 1975), *Liparis loeselii* (L.) L. C. Rich. (Fitzpatrick and Fitzpatrick 1900, Wolden 1926, Anderson 1943, Hayden 1943, Holte and Thorne 1962, Holte 1966, Niemann 1975), *Spiranthes romanzoffiana* Cham. (Wolden 1926, Holte and Thorne 1962, Niemann 1975) and *Spiranthes cernua* (L.) L. C. Rich. (Anderson 1943, Conard 1952). Both Grant (1953) and Niemann (1975) refute the occurrence of *S. cernua* in Dickinson County fens because the reports are seemingly based upon a *S. romanzoffiana* specimen. The 4 species all occur in the Silver Lake Fen Preserve and have in part been reported from tallgrass prairie, marsh and *Sphagnum* bog habitat types in Iowa as well.

Orchids have continued to decline in abundance in Iowa because of habitat depradation (Fitzpatrick and Fitzpatrick 1900, Niemann 1975). Since 3 of the 4 species are listed along with 10 other orchid species by Roosa and Eilers (1978) as either "endangered" or "threatened" in the state, comparative species knowledge of distribution-habitat relations, growth, reproduction, and population states on protected land are essential to assist preservation and management efforts. Elaboration on these topics for the orchids occurring in the Silver Lake fen complex is the objective of the paper.

METHODS

Study site

Investigations were conducted from 18 June - 9 July, 1981 at the Silver Lake fen complex located in the northwestern corner of section 32, Silver Lake Township, along the southwest shore of Silver Lake in Dickinson County. A major portion of the complex occurs within the Silver Lake Fen State Preserve, a 4 hectare tract of land protected by the Iowa State Preserve System. The remainder of the complex occurs on a contiguous ⅓ hectare parcel south and east of the Preserve and is a segment of a Conservation Wildlife Management Area surrounding the lake.

Silver Lake and the fen complex are situated in a large pothole of the Bemis Moraine which comprises the outermost margin of the Des Moines Lobe (Prior 1976). Deep deposits of glacial drift underlie the fen complex and allow large quantities of cool, calcareous spring water to surface at particular sites. The mineral laden discharge waters gradually precipitate layers of tufa or marl which with peat deposition produce conical knolls which protrude above the undulating terrain. Quaking mats of fen vegetation on the knolls and adjacent gentle slopes are provisioned by the water, as well as the numerous, small pools interspersed in the sedge mat vegetation below the discharge cones. Because Silver Lake is lower in elevation than the several discharge cones, the intervening lowlands are also influenced by lake level fluctuations. Wetland and marsh vegetation develop on the moist to hydric lowlands and intergrade with the higher-elevation fen vegetation.

The three distinct fen zones reported by van der Valk (1975, 1976) provide the framework of the distributional comparisons for the orchids (Fig. 1). A central discharge zone (DZ), an elevated knoll where the alkaline water surfaces, is commonly dominated by *Carex* ssp., *Phragmites communis*, and *Helianthus grossesseratus* at Silver Lake fen. The tall-statured species of the zone are distinct from the adjacent short-statured vegetation of the sedge mat (SZ) or middle zone which is downslope from the discharge zone. The dominant species of the gently sloping sedge mat zone are *Rhynchospora capillacea*, *Triglochin maritima*, *Lobelia kalmii* and *Muhlenbergia racemosa*. This distinct zone of sedge mat sod and the numerous, interspersed small pools which may support aquatic plants like *Chara hypnoides* and *Utricularia* spp. characteristically differentiates the northwest Iowa fen from other

related communities. A third zone, border zone (BZ), characteristically circumscribes the middle zone and has intermediate height vegetation. Dominant species of the zone include *Parnassia glauca, Scirpus americanus, Scirpus acutus, Triglochin maritima* and *Carex aquatilis*. The vegetation of the border zone is variable and commonly possesses species which may dominate adjacent wetland and marsh vegetation.

Two additional zones adjacent to the Silver Lake fen complex which contribute to orchid distribution are wetland and marsh zones. The wetland zone (WZ), sloping gently downslope from the border zone, may possess various fen species. The dominant species are herbaceous, broadleaf forbs. Common forbs which form a canopy include *Silphium perfoliatum, Helianthus grossesseratus, Solidago* spp., *Eupatorium* spp., while *Pedicularis lanceolatus, Pycnanthemum virginianum* and *Rosa suffulta* in part form an understory vegetation. The zone exhibits great compositional and spatial variation. A marsh zone (MZ), topographically lower in position than the wetland zone, is commonly submerged by shallow water during longer periods of the year. The zone at the Silver Lake fen site is restricted to the lake margin and its backwater areas as well as to the margins of two man-made ponds south of the preserve. The dominant marsh species around the margin of both the lake and the ponds is *Typha angustifolia*, whereas, the intervening marsh areas under greater fen-water influence are dominated by *Typha latifolia*. Specific areas of the marsh zone are dominated by large stands of *Phragmites communis*.

Species studies

The vegetation zones provided the spatial construct within which each species was censused and studied. For each zone a total species count was conducted or where impractical several subsample plots of 25 m^2 (5 × 5m) were enumerated and their values used to estimate population size. For each species all ramets (above ground stems) were counted and scored for the following characteristics: ramet vegetative or reproductive; inflorescence with flowers and/or fruits; inflorescence damaged; and, aborted flowers and/or fruits. For a random selection of ramets of each species the number of flowers and fruits were counted.

Since each species potentially formed a genet (individual or clump derived from a seed) with multiple ramets, several isolated genets of each species were excavated to determine: ramet interconnectedness, number, and distance; depth of pseudobulbs, rhizomes, and roots; and, relationship of underground structures to substrate characteristics. The developmental patterns and characteristics of vegetative growth and reproductive structures were also determined.

Several substrate cores were obtained from each zone to a depth of 70 cm with a soil probe to determine profile constituents and their respective depth relations. The depth of water within the profile was also recorded.

RESULTS
Distribution and habitat characteristics

Orchid distributions at the Silver Lake fen complex are correlated with the vegetation and substrate characteristics. Both *Liparis loeselii* and *Spiranthes romanzoffiana* were confined to the three fen vegetation zones while *Platanthera hyperborea* and *Cypripedium candidum* were more prevalent in the wetland and marsh vegetation zones (Table 1). No orchid species was distributed throughout a particular vegetation zone (Fig. 1).

The fen associated species, *L. loeselii*, inhabited each of the three vegetation zones, whereas *S. romanzoffiana* occupied only a marginal position of the sedge mat zone adjacent to a discharge cone. *Liparis loeselii* was most abundant in the sedge mat and border vegetation zones. At both the east and south fens, greatest abundance was along the transition of these two zones. The discharge zone occurrences of *L. loeselii* were confined to small interspersed areas of short-statured sedge mat-like vegetation within the tall-statured vegetation at the west and south fens. The areas resembled the typical sedge mat vegetation zone.

The non-fen associated species, *P. hyperborea* and *C. candidum*, were most abundant in the wetland vegetation zone. Their most expansive distribution and greatest density were in the wetland zone to the east of the large west fen. Here *P. hyperborea* and *C. candidum* respectively averaged 20 and 25 ramets per 25 m^2 subplot. No other large area equaled this density. Both species were more abundant in the less frequently inundated marsh vegetation where *Typha* was less dense. This region of the zone was in close proximity to the transition with the herb dominated wetland zone. The east and south fens possessed the greatest number of marsh inhabitants. Along the east flank of the west fen both species could have been interpreted to occupy border zone vegetation positions, but their occurrences were in close proximity to the wetland-border vegetation transition so they were scored as wetland zone inhabitants. Of lesser density importance but greater distribution significance were the discharge zone inhabitants which occupied restricted areas of dense, tall herbaceous cover on or near the margin of the discharge cone. These particular individuals made indistinct the fen to non-fen habitat associations of the four orchid species.

Comparative substrate profiles for the vegetation zones and their major variations are diagrammatically depicted in Figure 2. The subdivision profiles of the west fen cone characterize the discharge zone (DZ) where an elevated quaking sedge mat subdivision (Sm) is flanked by marginal subdivisions of *Phragmites communis* (Pc) and herbaceous forbs (Hf) characteristic of the wetland zone. The sedge mat which varied in thickness was supported by a layer of leached peat with interspersed granular marl floating on an aqueous slurry of sandy-clay. Where the mat adjoined the *Phragmites* margin, the

Table 1. Orchid ramet census by vegetation zone at Silver Lake fen complex.

Zone	Fen	*Liparis*	*Spiranthes*	*Platanthera*	*Cypripedium*
Discharge	W	6	—	4	6
	E	—	—	3	—
	S	3	—	3	21
Sedge mat-Border	W	9	—	—	—
	E	185	11	—	—
	S	64	—	—	—
Wetland-Marsh	W	—	—	3040[a]	2460[a]
	E	—	—	40	207
	S	—	—	43	216
	TOTAL	267	11	3133	2910

[a] Includes subsample-to-area occupied estimates.

substrate was a firm composite of *Phragmites* rhizomes and layers of leached peat with interspersed consolidated marl. The southeast portion of the cone supported wetland vegetation on a profile of shallow mineral soil, thick layer of leached peat and interspersed granular marl, and an aqueous slurry of sandy-clay to a depth of at least 70 cm. The water level of the zone ranged from 15 to 33 cm below the sedge mat surface.

The sedge mat (SZ) and border (BZ) zone profiles both exhibited very shallow water levels which fluctuated within a pronounced layer of porous, consolidated marl ranging from 1-4 cm in thickness. The marl supported the vegetation mat and was most evident in the *Scirpus acutus* subdivision (Sac) of the border zone. The sedge mat profile was predominantly a thick layer of leached peat with granular marl supported by an aqueous sandy-clay slurry. The border zone subdivi-
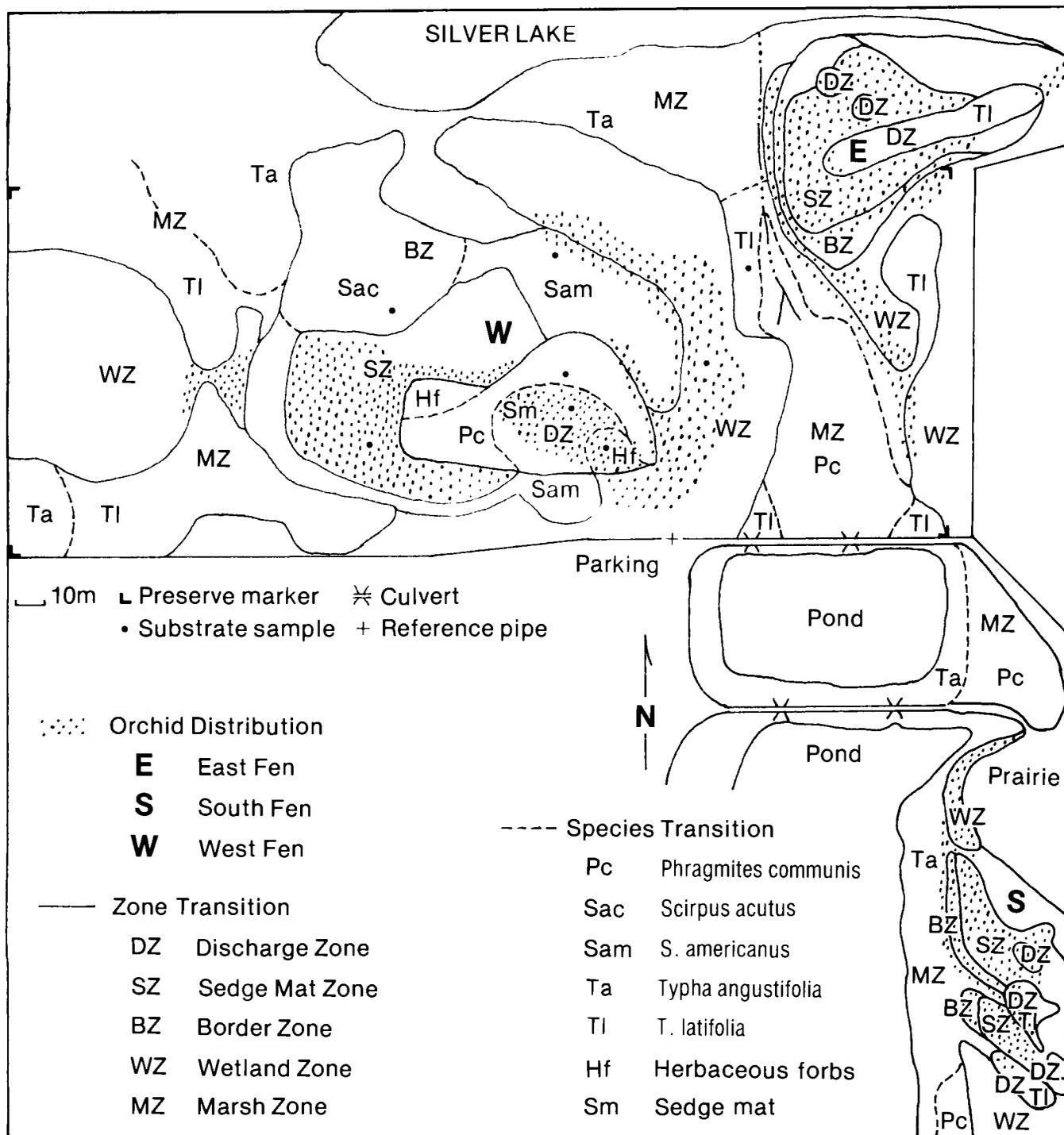

Fig. 1. Map of fen, vegetative zones, and orchid distributions at Silver Lake fen complex.
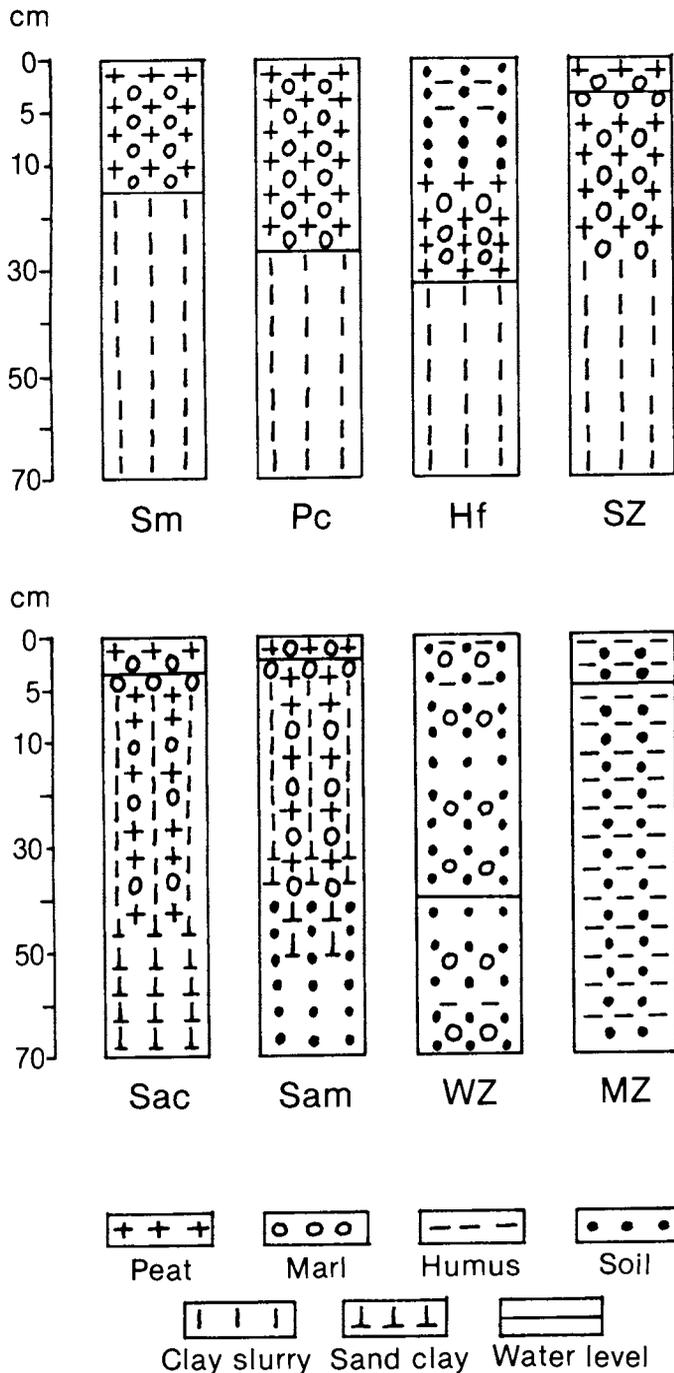
Fig. 2. Substrate profiles for vegetation zones at Silver Lake fen complex.

sions possessed complex compositions of dense slurry with interspersed peat and marl. At the base of each profile the slurry was quite solid and in the *S. americanus* subdivision (Sam) the major component of the basal profile was mineral soil.

The wetland (WZ) and marsh (MZ) zone profiles were distinguished by their mineral soil content and interspersed layers of humus and granular marl throughout. The marsh zone had the greater humus content and the higher water table. Even though it varied consider-

ably, the wetland zone consistently exhibited a water table below 25 cm in depth.

The orchid species clearly demonstrated substrate specificity. Both *L. loeselii* and *S. romanzoffiana* inhabited only peat substrate with shallow water tables, while *P. hyperborea* and *C. candidum* predominately occupied mineral soils with deep water tables. Although the latter two species had greater substrate amplitude, the four species exhibited strong affinities for particular substrates.

Subterranean organ relations

The substrate depth relations of subterranean organs such as roots, rhizomes, storage organs and perennating buds are diagrammatically depicted in Figure 3. Although there is considerable individual variation, each diagram depicts average positions of the organs within the substrate profile.

The two species which inhabited the fen zones clearly exhibited the shallower organ depth positions. In particular, only the basal portion of the partially exposed pseudobulb of *L. loeselii* was imbedded in the peat substrate. Its roots were primarily confined to the black peat and humic matter above the shallow water and marl layer. The elongated fasiculate storage roots of *S. romanzoffiana* extended into the gray leached peat layer below the water table. The root-stem tuberoids of *P. hyperborea* superficially resembled those of *S. romanzoffiana* although they were 2-3 cm longer in length and therefore occupied deeper depths in the mineral soil substrate. The rhizome and adventitious root system of *C. candidum* was the deepest of the four species. The rhizome system ranged from 6-10 cm in depth and the fibrous roots extended an additional 4-6 cm. All underground organs of the latter two species were above any apparent water table.

Vegetative growth characteristics

Excavation of the orchids in late June disclosed distinct morphological patterns of vegetative growth which assisted quantitative interpretation of the species. Although the morphological descriptions are not detailed, comparative initial ramet growth patterns (Fig. 3) were established.

An old fleshy pseudobulb of *L. loeselii* which had apparently flowered the previous year was observed to give rise to a current fruiting ramet from a meristematic region near its base. The old bulb still possessed a portion of the inflorescence stalk as well as remnants of the enveloping leaf scales of an older pseudobulb from which it may have arisen. Dissection of the current ramet provided no immediate evidence of a new ramet initial from its small developing pseudobulb to perpetuate the growth pattern. The cenus of 82 plants yielded no individual with multiple ramets.

The ramet initial on a mature flowering *S. romanzoffiana* was observed on the upper portion of the largest tuberous root of the fascicle. Although several tuberous roots were present, the meristematic one was clearly the largest and lightest in color. The remaining tuberous roots were darker brown in color and more slender. The superficial layer of the meristematic root was split to expose the ramet initial which consisted of an upward stem-like protuberance and a root-like or tuberloid-like element pointing downward. The current flowering ramet appeared to arise from a shriveled tuberous root. Only 1 of 11 censused individuals exhibited multiple (2) ramets.

The origin of new ramets for *P. hyperborea* were similar to *S. romanzoffiana* with the major differences being the larger size of the meristematic fusiform tuberoids of *P. hyperborea* and its possession of an additional tuberoid-like structure comprising the initial. For the 170 putative genets censused, 14 exhibited double ramets and 3 possessed triple ramets. The model genet possessed an average of 1.12 ramets.

The rhizome system of *C. candidum* provided a distinctly different pattern of ramet initiation. The initials appeared to annually arise

from the terminous of the rhizome as a part of the longitudinal growth process. The resultant pattern placed each succeeding ramet 6-8 mm distant. Although few genets were excavated, no new ramets were observed at old nodes although a branched rhizome was observed. For the 161 putative genets censused, ramet numbers ranged from 1-28 with a mean of 4.37. A total of 54, 28, 16, 16 and 14 genets respectively occurred in the first 5 ramet classes while 15 were in the 6-10 ramet class, 15 in the 11-20 ramet class and only 3 in the >20 ramet class.

Reproductive characteristics

All orchids species exhibited one or more sexual reproductive phases during the study. Figure 4 contrasts observed flowering phenology with the extreme flowering dates reported by Niemann (1975) and establishes some fruiting phenology relationships. The late June flowering of *S. romanzoffiana* appears to be an early record while the late July flowering of *P. hyperborea* appears to be a late record. Although *C. candidum* flowering was not observed, three species demonstrated flower overlap and all species exhibited fruit overlap.
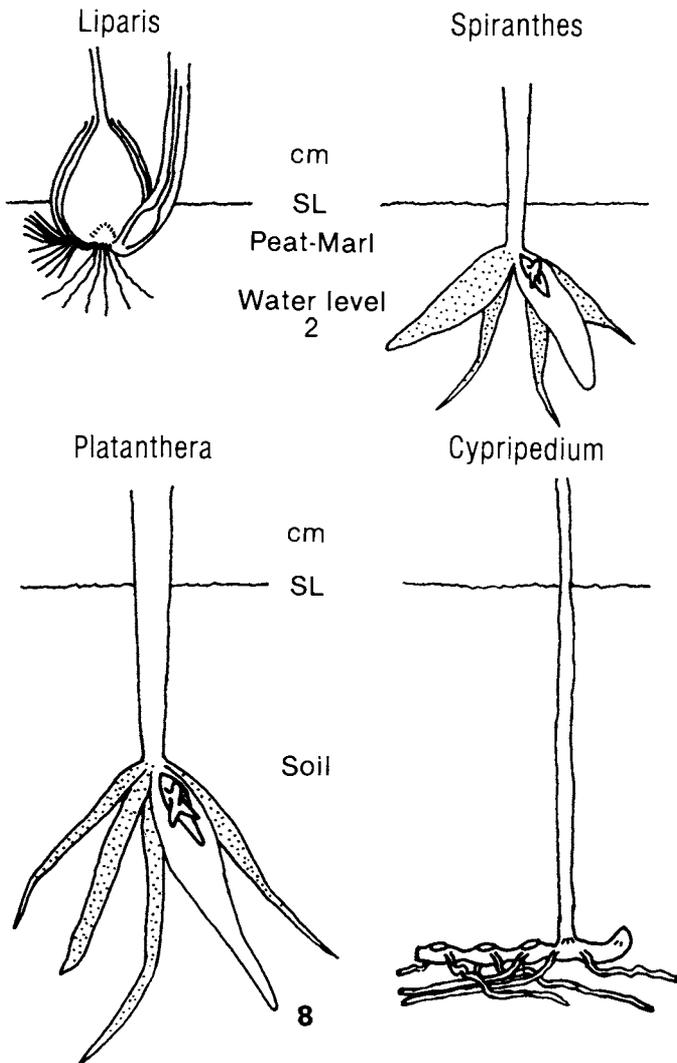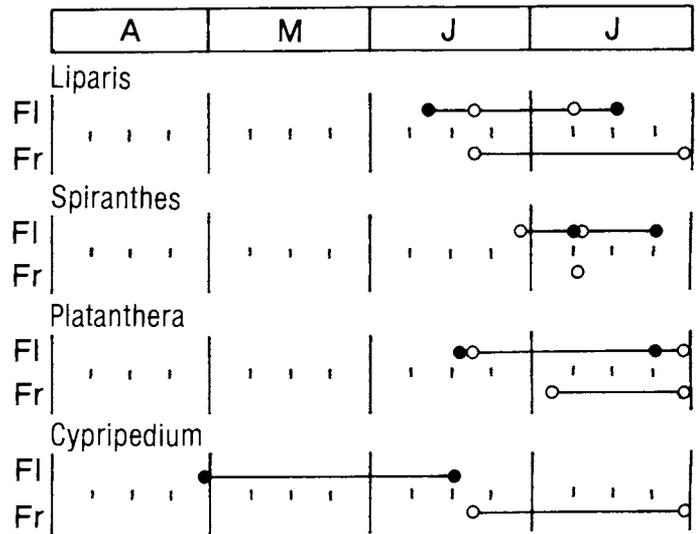

Fig. 4. Relationship of Silver Lake fen orchid phenology to state herbarium records (Niemann 1975). Closed circles represent records and open circles observations.

The census and classification of 1208 ramets provided comparative reproductive patterns for each species (Table 2). All species exhibited less than 10% vegetative ramets except *C. candidum* which had 52% vegetative ramets. An estimated 30-40% of the *C. candidum* ramets inhabited the dense *Typha* vegetation of the marsh zone. Inflorescence damage was low in each species although a 29 July site visit revealed all *S. romanzoffiana* ramets grazed to ground level. Although abortive flowers and fruits were not scored on multiple-flowered species, 17% of the single-flowered *C. candidum* ramets possessed pedicel scars in the axil of the bract suggesting non-pollination or abortion.

The census of ramets for flowers and fruits provided a range of reproductive structures (Fig. 5). Only two ramets of *C. candidum* possessed 2 maturing fruits suggesting that multiple structures are uncommon. The multiple-flowered orchids exhibited great variation with both *P. hyperborea* and *S. romanzoffiana* providing the best examples. The number of flowers and fruits on *L. loeselii* ramets were quite similar, although the flower bearing ramets possessed the lower values.

Reproductive effort, found by multiplying the maximum number of ramets (Table 1) by the reproductive ramet percentage (Table 2) and the mean number of reproductive structures per ramet (Fig. 5), were 909, 150, 116520, and 844 for *L. loeselii, S. romanzoffiana, P. hyperborea* and *C. candidum* respectively. The large reproductive effort of *P. hyperborea* clearly exceeds the other three species. Because seed number per fruit and viability are unknown, further reproductive analysis is unwarranted.

Fig. 3. Schemmatic diagram of orchid subterranean organs depicting substrate and perennation bud relations.

Table 2. Orchid ramet census by class at Silver Lake fen complex.

Species	I[a]	II	III	IV	Ramets
Liparis	25	24	—	218	267
Spiranthes	1	—	—	10	11
Platanthera	10	7	—	226	243
Cypripedium	358	19	114	196	687

[a]I Vegetative class   III Fruit aborted class
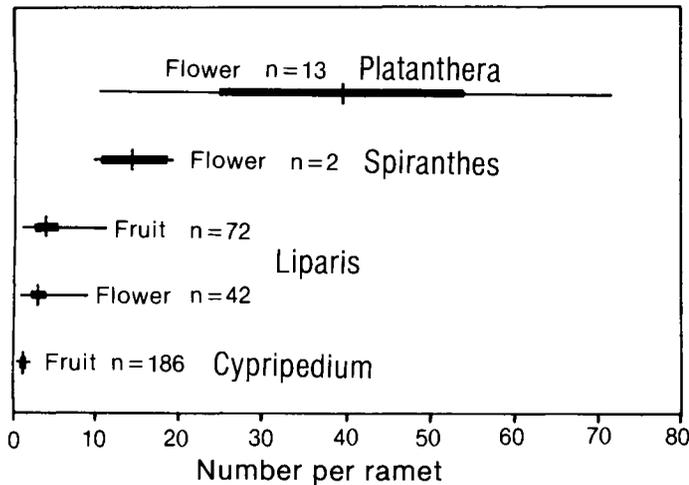II Inflorescence damaged class   IV Flower and/or fruit class

Fig. 5. Orchid reproductive efforts at Silver Lake fen complex.
Horizontal line, range of values for reported ramets (n);
vertical line, mean; and, broad line, 95% confident
interval of standard error.

Population status

A definitive population status analysis derived from short-duration
studies is tenuous. Extrapolation of individuals or genets from ramet
totals (Table 1), utilizing the mean number of ramets per genet for *L.
loeselii, S. romanzoffiana, P. hyperborea,* and *C. candidum,* respectively
yielded 267, 10, 2797, and 666 genets in the fen complex. The
significance of the crude numbers is unknown, however, *S. romanzof-
fiana* is clearly the lowest and could be on the verge of extirpation at
the fen.

Both fen inhabiting *S. romanzoffiana* and *L. loeselii* possessed the
smaller population sizes suggesting that the exposed nature of their
habitats may render them more vulnerable to predation and extirpa-
tion. Clearly they are more visible to collection, but whether the total
destruction of reproductive structures on *S. romanzoffiana* is typical of
annual predation is uncertain. Frequent incidences of such consump-
tion can reduce the species' seed bank.

The two species which occupied the heavily vegetated wetland and
marsh zones, *P. hyperborea* and *C. candidum,* possessed the larger
population sizes, perhaps indicative of a habitat with less vulnerability
to predation and extirpation. The wetland zone provided little cover
during the spring flowering of *C. candidum,* but tall, dense cover
followed the mid-summer flowering of *P. hyperborea.* The number of
damaged inflorescences for both species suggest minimal predation
pressure. Reduced reproductive ramets for both species in the dense
marsh zone also suggest some habitat cover influence.

The influence of the several hundred *Fraxinus pennsylvanica* saplings
along the east margin of the west fen to the wetland orchid inhabitants
is unknown. The saplings, based upon counts of both bud scale scars
and annual growth increments, ranged form 6-11 years of age.
Current orchid densities in the cohabitation zone are great, but only
limited numbers of both orchid species occurred under the dozen
mature *Fraxinus* trees inhabiting the fen complex. Because sapling
survivorship success and longevity are unknown, their current and
future impact upon the orchids are uncertain. Numerous *Acer sac-
charinum* seeds germinate annually in the sedge mat zone, but the
germlings seldom exceed a crimson, six-leaved stage.

DISCUSSION

Sympatry at the Silver Lake fen complex of the four orchids could
not be anticipated based solely upon their respective distribution
patterns. Both *Liparis loeselii* and *Platanthera hyperborea* approach the
southwestern limit of their Great Plains distribution near the Silver
Lake region, while *Spiranthes romanzoffiana* presence represents a Great
Plains outlier (Luer 1975). While the three have extensive northern
continental distributions as well as Old World or Far East extensions,
Cypripedium candidum is restricted to the central Great Plains and
southern Great Lakes region (Luer 1975, Correll 1950).

The orchid habitat types as reported by both general (Luer 1975,
Correll 1950) and specific treatments (Case 1964, Sheviak 1974,
Niemann 1975) clearly indicate common occurrence by 2 or 3 species,
but seemingly never by all four. Except for *C. candidum,* the types
most commonly cited for each were bogs, muskegs, meadows,
swamps, marshes, thickets, low or mesic prairies and open woods or
forests. For *C. candidum* the most cited habitats were meadows,
swamps, thickets, and low prairies, apparently excluding bog and
arborescent habitat types. The habitat substrates range from near-
hydric to xeric moisture conditions with organic to mineral soils of
acid to alkaline pH regimes.

The west fen substrate stratigraphy exhibits the superficial charac-
teristics of the nearby Excelsior fens detailed by Holte (1966). Had a
greater portion of the fen stratigraphy been analyzed, greater variabili-
ty might have been found. Soils of the fen and wetland-marsh
complex compare favorably to those detailed by Sheviak (1974) for
equivalent Illinois orchid habitats. The organic fen soils which
support *L. loeselii* and *S. romanzoffiana* are similarly composed of
leached shallow fibric to less-shallow black sapric Histosols (Steila
1976). The mineral soils of the wetland-marsh complex inhabitated
by *C. candidum* and *P. hyperborea* are Aquoll Mollisols with large
quantities of intermixed decomposed organic matter. These dark-
brown to black loamy-clay glacial soils are of moist-prairie vegetation
origin.

The anomalous occurrence of *C. candidum* and *P. hyperborea* on the
discharge zone of the west fen is correlated with mineral soil
distribution. The soil layer is apparently an erosional lens extending
from a once present hill to the south of the fen or the layer was
transported onto the southeast section of the discharge zone during
hill removal to construct the current parking lot (Niemann 1975). In
either case, the layer overlies peat and slurry. Aeolian transported soil
may account for the small pockets of mineral soil at other discharge
zones which support these two orchids.

Other factors reported to influence orchid distributions include
pH, mineral status and competition. Wherry (1918, ne U.S.),
Stuckey (1967, RI), Sheviak (1974, IL), and Niemann (1975, IA)
report all four orchid habitats in their study regions to range between
pH 7.1 and 7.9 except for *P. hyperborea* and *L. loeselii* which may range
to 5.7 and 4.2 respectively. Niemann's nutrients studies of Iowa
habitats suggest *C. candidum* and *P. hyperborea* sites to generally exceed
3500 ppm Ca, 225 ppm Mg, and 20 me/100 g cation exchange
capacity, whereas, *L. loeselii* and *S. romanzoffiana* sites were respective-
ly less. He reported no major site difference for N, P, K, Mn, Fe, Cu,
and Zn. Van der Valk (1976) reported, as suggested by Holte (1966),
that sedge mat zone associates of *L. loeselii* and *S. romanzoffiana*
apparently experience more severe competitive and mineral stress than
their counterparts in the discharge and/or border zones. He reported
individuals of the latter zones to range 1.6 to 2.7 times taller and
exhibit 1.8 to 5.4 times more biomass than their sedge mat zone
counterparts. The mineral and competitive stress results support the
observed soil distribution patterns of the Silver Lake fen orchids.

The subterranean organs of the orchids as detailed by Dressler
(1981) and Withner et al. (1974) indicate the storage structures to be
modified root in *S. romanzoffiana,* modified stem in *L. loeselii* and *C.
candidum,* and modified root-stem in *P. hyperborea.* The associated
perennating buds were respectively 1-3 cm, 0.5-1 cm, 6-10 cm, and
2-5 cm deep in their particular substrate. Such depths qualify the
latter two to be classified as cryptophyte while *L. loeselii* and *S.*

romanzoffiana are hemicryptophyte (Raunkier 1934). Clearly the hemicryptophyte is afforded less substrate protection and encounters greater shallow-root competition.

The observed variation in storage organ morphology in both *S. romanzoffiana* and *P. hyperborea* and the endogenous emergence of the perennating bud from a particular organ is further detailed for *S. romanzoffiana* by Godfrey (1933) and Summerhayes (1951). Because the special organs have similar morphology and bud positions, Ogura (1953) grouped such orchids into one of five growth-pattern classes. In both orchids the bud produces a new stem the succeeding year and a new complement of storage organs. One of the organs, rarely more, develops a bud, thus limiting the number of ramets per genet to approximately one.

A description of the *L. loeselii* pseudobulb and its growth is provided by Raunkier (1934, Fig. 31). The multi-budded pseudobulb, a modified stem, can produce several leaves, an inflorescence, and one or more perennating pseudobulbs (Summerhayes 1951). This potentiality accounts for the varied number of reported pseudobulbs per genet and following the degradation of the parental bulb, supports the description of "groups of flowering plants" confined to small areas (Summerhayes 1951). Although groups of ramets were not observed at Silver Lake fen, a less disturbed site might yield such growth aggregations.

Curtis (1943) provides extensive development and growth detail for several *Cypripedium* species including *C. candidum*. Although the study details seedlings, the growth pattern of 6 to 10 year old plants supported our observations. He reports *C. candidum* to produce numerous small plants from adventitious buds at the tips of their 2 to 3 year old rhizomes. These buds, rhizome branching, and gradual death of older rhizome (Summerhayes 1951) could produce in close proximity a multi-rameted genet.

The interrelations of storage organ and perennating bud characteristics significantly effect the probability of continued perennation and longevity under both natural and unnatural conditions. The rather large, shallow storage organs of *L. loeselii* and *S. romanzoffiana* with their few, shallow buds are quite vulnerable to herbivory and limited digging or burrowing activity by the local fauna. The relatively deeper storage organs of *P. hyperborea* and *C. candidum* with their respectively few to numerous deep buds afford greater protection. Complete excavation, natural or unnatural, diminishes the population by one genet or individual for all species except possibly *C. candidum*. A portion of perennating rhizome could maintain the diminished genet.

The phenological events of reproduction for native orchids are inadequately documented to allow detailed comparisons. The observed flowering periods for the fen orchids closely coincide with the reported dates of Sheviak (1974) for Illinois conspecifics. Both *L. loeselii* and *P. hyperborea* are coincident with the northern Illinois dates, whereas, *C. candidum* closely coincides with southern dates. Clinal flowering variation is not reported for Iowa orchids.

The reproduction patterns, efforts, and successes of native orchids are most commonly reported as incidental observations, although Curtis (1954), Salisbury (1942), Tamm (1948, 1972) and Wells (1967, 1981) detail elements of their reproduction for individuals, subpopulations, and populations for extended time-periods within their habitats. The 18 year study of Curtis on 12,138 crowns (ramets) of *C. candidum* in 8 populations of Wisconsin and Upper Michigan yielded average crown/plant and flower/crown ratios of 9.12 and 0.60. Equivalent ratios of 4.37 and 0.48 for Silver Lake fen inhabitants are indicative of reduced effort. Flower/crown ratios for the several ramet-sized classes were variable as reported by Curtis, although only the 6-10 and 11-20 ramet-sized genet classes possessed ratios greater than 0.50 (0.69 and 0.68 respectively).

For a 4 year study on fewer *C. candidum* populations, Curtis reported average fruit/crown and fruit/flower ratios of 0.12 and 0.22.

Comparable ratios at Silver Lake fen were 0.30 and 0.62, indicative of greater fruit production success following an apparent poor flower production effort. The large number of fruit abortions, as evidenced by pedicel scars, may support the reported importance of Andrenine bees as pollen vectors in both *C. candidum* and *S. romanzoffiana* (Pijl and Dodson 1966, Stoutamire, 1967, Catling 1982). The added effect of rain-assisted (Catling 1980), bud (Hagerup 1952), and flower autogamy (Gray 1862, Kichner 1922) may have augmented the apparently high flower-fruit/crown ratios of our *L. loeselii* (0.91) and *P. hyperborea* (0.96). A single flower/crown ratio of 0.63 for the latter species as reported by Curtis is lower than our 0.96 value. Clearly, the small fen populations vary from the large populations studied by Curtis; however, most values fall within the range of Wisconsin population variation. These results may lend support to Curtis' concept of regional reproductive success stability even though great environmental variation exists across the region and factor variation causes annual fluctuations of effort and success.

Numerical status records for native orchid populations are few. The consecutive population records of Curtis (1954) and Curtis and Greene (1953) detail great annual fluctuations and significant declines in population number and size in Wisconsin from the 1930's through the 1950's. The *C. candidum* and *P. hyperborea* populations of the Silver Lake fen complex are similar in number to Wisconsin populations, however, the ramet/genet ratio of the former is considerably reduced. Both fen populations are reported by Niemann (1975) to have been artificially reduced by the parking lot construction of the mid-1970's. A significant annual fluctuation was documented on a late-July, 1982, visit to the fen. In addition to the earlier censused east fen inhabitants, 12 *S. romanzoffiana* individuals were observed in flower along the discharge-sedge mat zone transition of the west fen. Although the population status of *S. romanzoffiana* and *L. loeselii* are smaller and uncompared, observed fluctuations are reported for other orchids (Case 1964, Tamm 1972, Wells 1967).

The observed decline of orchid population number and size in the midwest by Curtis (1954), Sheviak (1974), and Niemann (1975), is primarily attributed to vegetation or habitat change and predation. Although habitat destruction is the major cause of extirpation, modification by drainage is significant. Predation, if intense at reduced population size, can severely limit recruitment and induce gradual decline. Conversely, the cessation of grazing, mowing or fire can induce habitat change which cause orchid decline.

The influence of vegetation change on prairie and meadow orchid populations is well documented in middle Sweden and Wisconsin by Tamm (1972) and Curtis (1946) respectivley. Tamm carefully documented 3 meadow orchids to decline during 30 years in both number and flowering events as the vegetation in permanent plots increased following the cessation of haying and/or grazing. Curtis documented during a five year period a marked increase in the number of *C. candidum* ramets in experimental plots mowed to control native shrub invasion. The unmowed control plots exhibited declines in both vegetative and flowering ramets. Similarly, a fall burn on the margin of a fen in sw Michigan stimulated *C. candidum* the subsequent June to triple flowering ramets and increase vegetative ramets by 10 to 25% (Kohring 1981). Drawing upon Curtis' report, Stuckey (1967) observed similar decline patterns for the bog and meadow orchids, *Arethusa bulbosa* and *Habenaria blephariglottis*, following grazing cessation in Rhode Island.

Clearly, the vegetation change studies suggest that if *Fraxinus*, *Typha* and *Phragmites* continue to increase or expand in the fen complex, management will be warranted to favor the *C. candidum* and *P. hyperborea* populations. The mode of management, if any, is not clear for *L. loeselii* and *S. romanzoffiana*; however, Case (1964) reports both species grow abundantly on bare, wet, raw sands in Michigan.

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