

Conservation biology of an endangered grassland plant species, *Pseudorchis albida*, with some references to the closely related alpine *P. straminea* (Orchidaceae)

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Pseudorchis albida s.s. is today a rather rare grassland orchid with a declining distribution in Scandinavia, as well as in other parts of Europe. This paper presents (a) ecological site descriptions from 30 Norwegian and Swedish sites, and (b) vegetation analyses from five Swedish populations of the closely related, alpine *P. straminea*, which enable some comparisons between taxa. A Detrended Correspondence Analysis ordination of vegetation data separated sites of *P. albida* rather well according to their geographical location. The Swedish south-west coast sites were particularly distinct. The Norwegian mid inland region constituted a transition zone between sites from the Norwegian west coast and sites from the Swedish eastern mountains. About 10 vascular plant species form a core group, common to nearly all sites. About 150 species occur in lower total frequencies than 50%. It is concluded that *P. albida* can occur in a wide array of plant communities. A Kendall correlation matrix for environmental variables for the *P. albida* sites and the site's scores along the three first axes in the DCA ordination showed significant correlations between altitude, soil-pH, grazing, precipitation, mowing, ignition loss, and soil-potassium, with vegetation clusters. © 2002 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2002, 139, 47–66

ADDITIONAL KEYWORDS: biodiversity – land use – regeneration niche – seminatural grasslands.

INTRODUCTION

The grassland orchid *Pseudorchis albida* (L.) Á. & D. Löve s.s. is classified as an endangered species in the main part of its European distribution area. All records of this species are from habitats of seminatural (anthropogenic) grasslands. In many European countries recent surveys of endangered vascular plant species have shown that the majority of such species belong to habitats within the agricultural landscapes,

and it is the seminatural grasslands that constitute the main parts of the threatened habitats in these types of landscapes. From Sweden, it is reported that 76% of the endangered and vulnerable vascular plant species belong to habitats within the agricultural landscapes (Naturvårdsverket, 1990). The threats affecting the largest number of species are changes in land management, cessation of grazing or mowing, fertilization, or ploughing (Stevenson & Thompson, 1993; Bernes, 1994; Blackstock *et al.*, 1995). This is a universal trend (van Dijk, 1991) along with the abandonment of traditional agricultural practices where the use of seminatural grassland was the key to the

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function of the preindustrial agro-ecosystems (Olsson, 1991). The purpose of this paper is to investigate the present distribution of *P. albida* s.s. in Scandinavia in relation to edaphic and biotic habitat characteristics. It is postulated that grassland management is one of the major factors for the maintenance of the populations of *P. albida* s.s.

The seminatural grasslands constituted the fodder areas already used by prehistoric farmers. The seminatural grasslands were utilized either by mowing for hay harvest and/or grazing by the live stock. Those practices shaped and maintained the seminatural grasslands initiated by the introduction of domestic stock grazing in Neolithic time, some 6000 years ago, followed by the introduction of hay harvesting by iron tools during the early Viking time, approx. 800 AD, until the industrial agriculture during the last century. The introduction of industrial agriculture led to use of artificial fertilizers, cultivation of leys, etc., and to substantially raised harvests. Those factors successively decreased or abolished the need for seminatural fodder areas (Olsson, 1991).

In the absence of management, these seminatural grasslands and heathlands reverted by natural succession to woodlands and forests, and the species richness of vascular plants declined dramatically (Londo, 1990). Many grassland species are short-statured annuals or biennials, which depend on minute, safe sites in the grass sward for their seedling recruitment. This feature was accomplished by traditional grassland use by the grazing and the trampling of the grazing stock – or by different combinations of mowing, grazing, and intermittent burning (Ekstam *et al.* 1988; Chapman *et al.* 1989; Londo, 1990; Milberg, 1992; Oostermeijer *et al.* 1994; Linusson *et al.* 1998). Today, in a changed land-use situation where many seminatural grasslands are either left without management, or subjected to changes in management, for example, lower grazing pressure, several grassland species can persist for some time in the grassland. This paper addresses the current situation for one of those grassland species which became endangered during the 20th century, probably due to land use changes. Comparison of the habitat characteristics of the closely related *P. straminea* (Fern.) Soó, occurring mainly in low alpine habitats in Scandinavia (Sivertsen, 1990; Nilsson, 1991; but see Reinhammar, 1998b), is also included in this paper.

MATERIAL AND METHODS

THE SPECIES COMPLEX *PSEUDORCHIS ALBIDA* S.L.

Pseudorchis albida was until the beginning of this century treated as one taxon. But when Fernald (1926)

described a new species, *Habenaria straminea*, based on material from Newfoundland and Greenland, this view was changed. Fernald's (1926) opinion that *H. straminea* was distinct enough to be treated as a species of its own, separated from *P. albida* s.s., was based on differences in floral parts, spike thickness, and bracts. Fernald (1933) also put forward the hypothesis that *P. straminea* was the North American vicariant to the European *P. albida* s.s. However, the distribution of Fernald's taxon has later been extended to Iceland (Löve, 1950) and to Scandinavia, when Hylander (1966) concluded that *Gymnadenia albida* f. *subalpina*, described by Neuman (1901) on the material from the province of Jämtland in Sweden, was identical to *H. straminea*. *P. straminea* was recently treated as a subspecies to *P. albida* s.s. (Reinhammar, 1998a, 1998b). In the present paper we will, for convenience, refer to them by their species names.

However, Klein (2000) recently suggested that material of *P. straminea* should be subdivided into two taxa, *P. albida* ssp. *tricuspis* and *P. albida* ssp. *straminea*. It should then be noted that, in the sense of Klein (2000), material here presented as *P. straminea*, may belong to two different taxa.

In Scandinavia, *P. albida* has a western distribution, with sites in Denmark, the western provinces of Sweden, and Norway (Mossberg *et al.* 1992). *P. albida* grows in Scandinavia only in seminatural grasslands such as hay meadows and pastures (Nilsson & Gustafsson, 1978; Ekstam *et al.*, 1988) and in *Calluna*-heaths (Damman, 1957). These habitats decreased dramatically during the 20th century (Damman, 1957; Bernes, 1994) and *P. albida* has become rare in Scandinavia, especially in Denmark (Løjtant, 1980; Wind, 1994) and in the south-west of Sweden (Nilsson & Gustafsson, 1978; Carlsson & Gustafsson, 1984), while the orchid has not suffered the same decrease in the central provinces of Norway and Sweden (cf. Danielsson, 1994; Reinhammar, 1995, 1998c; Sørmealand, 1996). In a wider geographical perspective, *P. albida* is registered as a threatened species in 13 European countries (Table 1). The main threat to *P. albida* is overgrowth of its habitats as a consequence of the abolishing of traditional agricultural practices like mowing and grazing (Nilsson & Gustafsson, 1978; Ekstam *et al.*, 1988; Olsson, 1994). However, grazing has also been considered as a threat since grazing cattle eat flowering stalks (Borg, 1982; Schwabe, 1990). Artificial fertilizing of meadows has also been mentioned as one of the reasons for the decline of *P. albida* (Nilsson & Gustafsson, 1978; Olsson, 1994).

P. straminea is widespread all along the Scandinavian mountain range (Sivertsen, 1990; Nilsson, 1991). It occurs in low alpine heaths and meadows, dwarf shrub areas, peatlands, rich fens, subalpine birch

Table 1. Status of *P. albida* in different European countries. Abbreviations: Ex = extinct, R = rare, E = endangered, V = vulnerable, and NT = not threatened

Country	Status	Habitats	Sources ^a
Austria	NT	poor grasslands, grazed lands, dwarfbush lands, on acid soil	1,17
The Balcan countries	R?	mountains, moist lawn, forests, juniper shrubs; alpine pastures	10,22
Belgium	R	heaths and grasslands (non amendées) on acid soil	5,16
Czechia	V	meadows	3,8
Denmark	R	haymaking meadows	33
France	V?	pastures (Nardion) and heaths (Vaccinio-Piceetalia) in mountains	6
Germany	V?	grasslands and grazed land in the mountains; soil often poor and acid; Nardion, Violion, <i>Juncus squarrosi</i>	15,17,20
Great Britain	NT	rough pastures and meadows, or grassy slopes and heaths; riverbanks under birch; lochside bog.	27,34
Ireland	V	rough pastures and meadows, or grassy slopes and heaths; riverbanks under birch; lochside bog.	2,26,34
Italy	NT?	meadows, pastures, shrublands; mostly subalpine; rarely in conifer forests and in the lowland	4
the Netherlands	Ex?	on dry, humus-rich hills (not reformed lately)	31
Norway	V	haymaking meadows, grazed lands, open forest	13,28
Poland	NT	mountain meadows (Nardetalia)	9,29,30
Romania	R	meadows, mountain forests, alpine areas (?)	21,25
Russia	?	boggy meadows and peat bogs	11
Slowakia	V	meadows	3,14
Spain	R	? (alpine)	15,32
Sweden	R	mown meadows and ditch-banks, grazed land, chalets, recently cleared land as power line gates and ski slopes; lowland to subalpine; indifferent to lime	18,19,23
Switzerland	NT	subalpine and alpine grasslands, meadows and grazing lands, open pineforests, heaths and moors; peat bogs and wet grasslands in deeper sites	7,12,24

^a Sources: 1 Adler *et al.* (1994); 2 Curtis & McGough (1988); 3 Dostál (1950); 4 Fiori (1923); 5 Goffart (1945); 6 Guinochet & Vilmorin (1978); 7 Heß *et al.* (1967); 8 Holub *et al.* (1979); 9 Ingelög *et al.* (1993); 10 Jordanov (1964); 11 Komarov (1935); 12 Landolt (1991); 13 Lid & Lid (1994), 14 Maglocky & Ferakova (1993); 15 Mossberg & Nilsson (1982), 16 Mullenders (1967); 17 H. Niklfeld, pers.comm., 18 Nilsson (1991), 19 Nilsson (1992), 20 Oberdorfer (1994); 21 Oltean *et al.* (1994); 22 Polunin (1980); 23 Reinhammar (1995), 24 Reinhard *et al.* (1991); 25 Savulescu (1972); 26 Scannell & Synnott (1987); 27 Stace (1991); 28 Størkersen (1992); 29 Szafer (1959); 30 Szafer *et al.* (1953); 31 Vermeulen (1958); 32 Willkomm (1893); 33 Wind (1994), 34 J. Wood, pers.comm.

forests, and coastal heaths (Sivertsen, 1990; Nilsson, 1991; Lid & Lid, 1994; T. Rytätari, pers. comm.), often on lime. *P. straminea* is rather common in all parts of its earlier known distribution (Hultén & Fries, 1986), except in Canada (Scoggan, 1978; Reinhammar, 1998b), the Faroes (Rasmussen, 1952) and Finland (Hämet-Ahti *et al.*, 1986). There is little information from Central Europe, due to a collective treatment with *P. albida*, but it seems that *P. straminea* is quite common in higher altitudes in at least Austria, Switzerland and Italy (Mossberg & Nilsson, 1982; Løjtnant, 1991; Klein & Kerschbaumsteiner, 1996; Reinhammar, 1998b; but see Klein, 2000). The taxon has also been identified in herbarium specimens from France, Poland, Slovakia and Macedonia

(Reinhammar, 1998b). A summary of frequency and habitat demands of *P. straminea* in European and North American countries is given in Table 2.

Reproduction in *P. albida* s.l. is reported to occur by sexual means only (Harmsen, 1943; Hagerup, 1951, 1952; Summerhayes, 1968). Müller (1881), Knuth (1899), and Ziegenspeck (1936) have, on base of floral morphology, suggested that *P. albida* s.s. should be pollinated by butterflies, and butterflies (Tineidae) have also been reported as visitors, along with solitary bees (Pijl & Dodson, 1966), 'other hymenopterous insects' (Summerhayes, 1968), and mosquitoes (Mossberg & Nilsson, 1982). However, there is no information on which breeding systems *P. albida* s.l. use, but both autogamy (e.g. Nilsson,

Table 2. Status of *P. straminea* in different European and North American countries. Abbreviations as in Table 1

Country	Status	Habitats	Sources ^a
Canada	R	hilly meadows and turfy or peaty places	10
The Faroes	R	mostly on humid grasslands	9
Finland	R	alpine (<i>Dryas</i> -)heaths and rich fens; forests; calciphilous	3,4,12
Greenland	NT	humid herb fields, willow shrublands	1
Iceland	NT	heaths, peatlands, grasslands	7
Norway	NT	subalpine birchforest, peatlands, meadows, and heaths on base-rich ground; coastal grassheaths on sand dunes	6,11
Russia	NT?	boggy meadows and peat bogs	5
Sweden	NT	<i>Dryas</i> -heaths and meadows, solifluction soil; mostly alpine but also subalpine; calciphilous, also on serpentine	2,8

^a Sources: 1 Bøcher *et al.* (1966); 2 Ericsson & Rune (1991), 3 Hämet-Ahti *et al.* (1986), 4 Ingelög *et al.* (1993); 5 Komarov (1935); 6 Lid & Lid (1994), 7 Löve 1977, 8 Nilsson (1991), 9 Rasmussen (1952), 10 Scoggan (1978), 11 Sivertsen (1990), 12 H. Väre & T. Rytteri, pers.comm.

1992) and outcrossing (e.g. Mossberg & Nilsson, 1982) have been suggested (see also Reinhammar, 1998a).

VEGETATION ANALYSES AND POPULATION PARAMETERS

Population and environmental data from 30 sites (for *P. albida*) from the province of Sør-Trøndelag in Central Norway (21 sites), from the provinces Halland and Västergötland in south-west Sweden (5), and from the provinces Härjedalen and Jämtland in Central Sweden (4), were collected during the summers of 1994 and 1995. The sites in south-western Sweden are situated at about 57–58°N, 13°E, while all other sites are found at 62–64°N, and 10–13°E.

The sites were divided into five regional groups, according to their geographical locations and altitudes. The five groups are the Swedish west coast, Norwegian west coast, Norwegian mid-inland region, Norwegian subalpine region, and finally, the Swedish subalpine region. Summary of site descriptions and their locations are given in Table 3 and Figure 1.

The vegetation of the sites was analysed using five squares of 1 m² per site (except at site no. 26, where only four squares were analysed). Each square was subdivided into 16 subsquares for frequency estimation of all vascular plant species. Presence of moss and lichen species was noted in each 1 m² square. The total number of sampled squares was 144. The nomenclature used follows Lid & Lid (1994) for vascular plants [although with one crucial exception: we use the generic name *Pseudorchis* instead of *Leucorchis*, following Reinhammar (1995)], Hallingbäck (1996) for mosses, and Moberg & Holmåsén (1984) for lichens.

We also included site data for *P. straminea* for comparison. Data for this taxon was collected at five sites,

studied 1990–97. Thirty-seven samples of 0.25 m² each were analysed, in which only presence of vascular plants was noted. The five sites are from the Swedish provinces Härjedalen (2), Jämtland (2), and Lappland (1). The sites are situated at 62–66°N, and 13–14°E (Table 3; Fig. 1).

ENVIRONMENTAL VARIABLES

For the ordination analyses, the variation in altitude between sites was scored as 1 when below 400 m, as 2 when between 400 and 700 m, and as 3, when the site was situated above 700 m. Exposition and inclination were estimated in the field, with the aid of a compass. Exposition and inclination at each site were combined into a single parameter, relative sun exposure, using a formula by Parker (1988), further developed by Myklebost (1996). Mean annual precipitation for the weather stations closest to the sites was included as a variable (data from Alexandersson *et al.* (1991) for Sweden, and from Det Norske Meteorologiske Institutt (1991a,b, 1996) for Norway) in the ordinations.

Soil samples were taken from all sites of *P. albida*, from the level 0–5 cm, and later analysed (at Lantbrukets analysesenter, Ås, Norway) for both physical and chemical parameters: pH, ignition loss (%), soluble phosphorus (P-AL, mg per 100 g), and soluble potassium (K-AL, mg per 100 g).

Tree canopy layer at each site was also estimated directly in the field, and assigned to any of the four classes: 0–25, 25–50, 50–75, and 75–100%. Assessment of land use for each site was based on land use in the five-year-period prior to our study. We distinguished three types of land use: mowing, grazing and 'clearance'. Clearance here means cutting of vegetation without removal of the cut biomass. Another dimen-

Table 3. Description of the sites studied. For Norway, see Sørmealand (1996). For Sweden, no precise site information is given, following recommendations given by Ingelög & Gransberg (1992). no. 1–30: sites for *P. albida*. A–E: sites for *P. straminea*. Abbreviations, provinces in Norway (N) and Sweden (S): ST = Sør-Trøndelag (No. 1–21), HI = Halland, Vg = Västergötland, Hrj = Härjedalen, Jmt = Jämtland, LyL = Lycksele Lappmark (Lappland)

Number	Locality name	Land use	Assignment	Region	Altitude (m)
1	Åfjord, Grønolia, ST, N	grazing	outfield	NW-coast	180
2	Åfjord, Momyr, ST, N	grazing	outfield	NW-coast	260
3	Osen, Rørvatnet, ST, N	grazing	outfield	NW-coast	200
4	Rissa, Helset, ST, N	grazing	infield	NW-coast	300
5	Hemne, Hollbusetra, ST, N	grazing	infield	NW-coast	330
6	Midtre Gauldal, Telnesvollen, ST, N	mowing	infield	NM-region	460
7	Melhus, Balltjønn, ST, N	grazing	outfield	NM-region	540
8	Melhus, Åsali, ST, N	grazing	infield	NM-region	500
9	Midtre Gauldal, Stolvollen, ST, N	mowing	infield	NM-region	440
10	Midtre Gauldal, Røsløkken, ST, N	mowing	infield	NM-region	510
11	Røros, Johannesvollen, ST, N	grazing	outfield	W mountains	710
12	Røros, Svarthammeren, ST, N	grazing	outfield	W mountains	820
13	Røros, Gaukvollen, St, N	grazing	infield	W mountains	790
14	Holtålen, Nordaune, ST, N	grazing	infield	NM-region	540
15	Tydal, Nedalen, ST, N	grazing	outfield	W mountains	750
16	Tydal, Hertjønn, ST, N	grazing	outfield	W mountains	570
17	Selbu, Volavollen, ST, N	grazing	outfield	W mountains	630
18	Midtre Gauldal, Bakkløkken, ST, N	grazing	infield	NM-region	500
19	Midtre Gauldal, Enli, ST, N	mowing	infield	NM-region	550
20	Midtre Gauldal, Enlidgårdene, ST, N	grazing	infield	NM-region	330
21	Midtre Gauldal, Ranstad, ST, N	grazing	infield	NM-region	490
22	Våxtorp, HI, S	mowing	infield	SW-coast	40
23	Ölsremma, Vg, S	grazing	infield	SW-coast	300
24	Fivlered, Vg, S	none	infield	SW-coast	250
25	Sandhem, Vg, S	grazing	infield	SW-coast	270
26	Liared, Vg, S	mowing	infield	SW-coast	320
27	Tännäs South, Hrj, S	mowing	infield	E mountains	810
28	Tännäs North, Hrj, S	clearing	infield	E mountains	800
29	Åre North, Jmt, S	mowing	infield	E mountains	600
30	Åre South, Jmt, S	clearing	outfield	E mountains	600
A	Tännäs South, Hrj, S	–	–	–	1100
B	Storsjö, Hrj, S	–	–	–	1050
C	Åre, Jmt, S	–	–	–	870; 1000
D	Hotagen, Jmt, S	–	–	–	720
E	Tärna, LyL, S	–	–	–	900

sion of land use is the assignment of each site into one of the traditional land use categories ‘infield area’ or ‘outfield, commons’. Traditional land use of grasslands within infields implied haymaking (mowing), while most grasslands in the commons were used for grazing, although exceptions occurred (Olsson, 1991).

DEMOGRAPHIC STUDIES

At two sites, nos. 22 and 27 in Table 3, the populations were followed annually from 1991 to 1997. At each site, every plant was permanently marked with a

metal pin bearing an individual number, enabling records of the fate of each individual. In one site, no. 27 in Table 3, one part of the site was mowed while the other part was not managed at all. In these separate parts, one permanent square, 3 × 3 metres, was established in each in order to compare which effects the two management regimes eventually would have.

DATA ANALYSIS

For the analysis of vegetation data, a DCA (Detrended Correspondence Analysis) ordination was performed

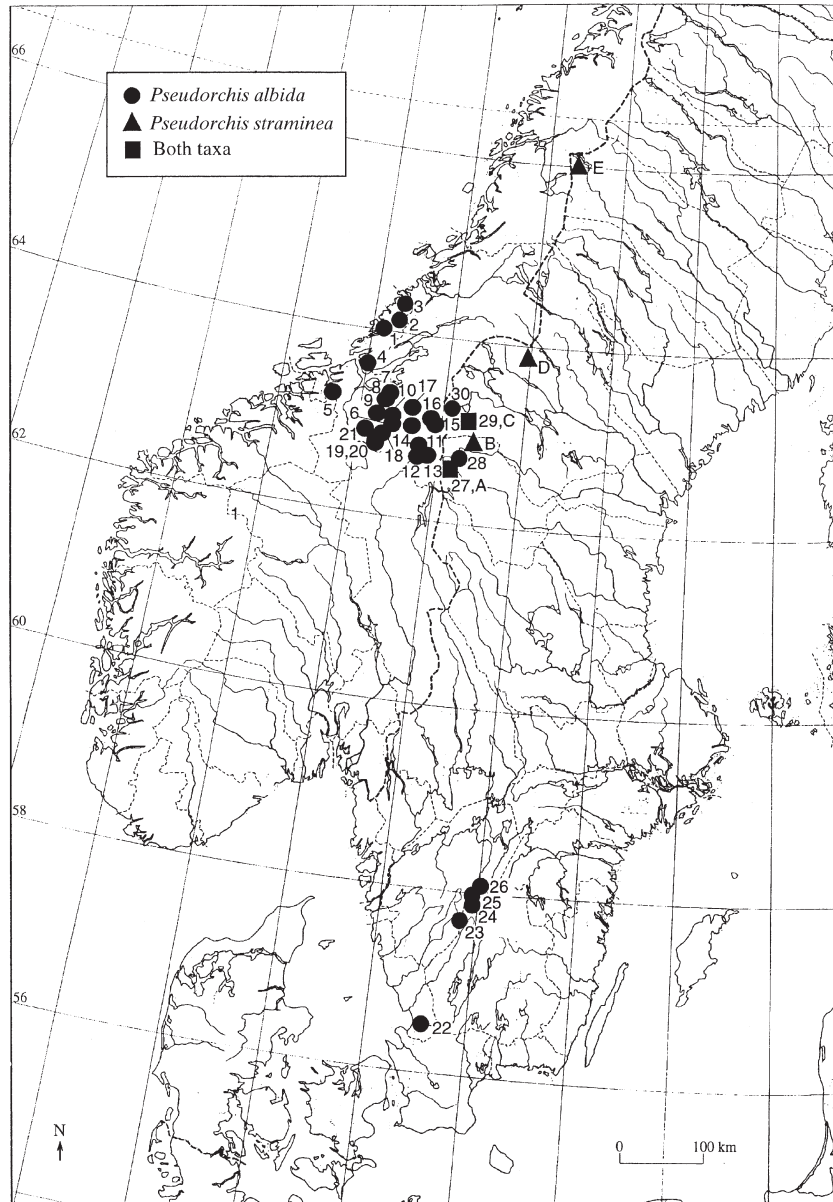


Figure 1. Map showing the geographical positions of the study sites (see also Table 3). Symbols: Sites 1–30 *P. albida*-circles. Sites A–E *P. straminea*-triangles. The two squares represent positions where one site of *P. albida* and one of *P. straminea* were closely situated (Sites 27 and A, and 29 and C, respectively).

in order to summarize major trends in the vegetation data (ter Braak, 1995). Species with few occurrences were down-weighted in the analysis to avoid distortions. The ordinations method was applied through the computer program CANOCO (ter Braak, 1987, 1990a,b).

A Kendall correlation (Kendall, 1938) was used to estimate intercorrelation between environmental variables, and correlation between environmental variables and plot scores on the DCA-axes.

The statistical calculations were focused on the investigations of possible relations between population parameters and environmental variables (including land use). The parameter orchid population size was used as a response variable in a multiple regression analysis, where soil pH, ignition loss, phosphorus, and potassium were used as explanatory variables (all parameters were log-transformed prior to the regression). Analysis of variance (ANOVA) was used to compare influence of land use, geographical location

(climatic region), and vegetation diversity, on the population parameters. Vegetation diversity was expressed as Shannon's diversity index (H' ; Pielou, 1969), and species richness. A Student's t -test was performed to check for any significant differences between the land use categories infield and outfield.

RESULTS

SPECIES COMPOSITION IN SITES OF *P. ALBIDA*

In total, 210 species were found in the 144 squares analysed at 30 sites. Of those species 168 were vascular plants, 35 mosses, and seven lichens. *Potentilla erecta* is the most common vascular plant species. As can be seen in Table 4, there is a core of rather few vascular plant species that frequently (>50% total frequency) occur together with *P. albida*, but there is a wide range of other species, which occur more rarely (see Appendix 1). This indicates that *P. albida* is a rather tolerant species that is not connected to any particular plant community. There are also differences between the five regions (Fig. 2A) and in land use (Fig. 2B).

VEGETATION PATTERN AND ENVIRONMENTAL VARIABLES

The DCA ordinations of sites (Fig. 2A,B) and of species (Fig. 3) display a pattern supporting the interpretation given above, with a central group of sites originating from different regions, and with small groupings at the margin of the central group. This central group is characterized by high frequencies of the core species mentioned above, which are common to most *P. albida* habitats.

In the DCA ordination of sites (Fig. 2A), the sites from the Swedish south-west coast constitute the most easily identified group. Unique species for this group (Fig. 3) such as *Arnica montana*, *Pedicularis sylvatica*, *Galium saxatile*, *Carex panicea*, *C. montana* and *Veronica spicata*, are among those that contribute to this separation. The other regional groups are somewhat more difficult to recognize. The Norwegian west coast sites are found in the left end corner of the DCA-diagram (Fig. 2A). Bog and wetland species, such as *Carex pauciflora*, *Trichophorum cespitosum*, *Eriophorum angustifolium*, *Drosera rotundifolia* and *Narthecium ossifragum*, occur in high frequencies at those sites (Fig. 3). The Norwegian mountain sites tend to group in the lowermost left corner (Fig. 2A). Alpine or calciphilous species, for example, *Pedicularis oederi*, *Bartsia alpina*, *Coeloglossum viride*, *Thalictrum alpinum*, *Tofieldia pusilla*, *Carex capillaris* and *C. lepidocarpa*, are among those that contribute to this location (Fig. 3). The Swedish mountain sites

Table 4. Survey of the most frequent vascular plant species in the sites of *P. albida* (50% of sample squares; vascular plant frequency values).

Species	% Appearance in the complete material
<i>Potentilla erecta</i>	92.0
<i>Vaccinium myrtillus</i>	78.5
<i>Solidago virgaurea</i>	75.2
<i>Trientalis europaea</i>	73.2
<i>Deschampsia flexuosa</i>	71.1
<i>Anemone nemorosa</i>	63.1
<i>Anthoxanthum odouratum</i>	61.7
<i>Nardus stricta</i>	58.4
<i>Bistorta vivipara</i>	55.0
<i>Hieracium</i> spp.	53.7
<i>Vaccinium vitis-idaea</i>	50.3

constitute a quite clear group in the centre of the DCA diagram (Fig. 2A), although there is an overlap with sites from the Norwegian mountain and mid-inland regions. Common companion species (many of which also are the core-species mentioned above; Table 4) such as *Vaccinium myrtillus*, *Potentilla erecta*, *Deschampsia flexuosa* and *Solidago virgaurea* contribute to this pattern (Fig. 3). Furthermore, there is a tendency for Norwegian mid-inland sites to group in the DCA diagrams lowermost right corner (Fig. 2A), characterized by grassland species such as *Hypericum maculatum*, *Prunella vulgaris*, *Alchemilla vulgaris* coll., *Leucanthemum vulgare* and *Festuca rubra* (Fig. 3). The conclusion from the DCA ordinations (Figs 2, 3), is thus that *P. albida* occurs in a wide array of habitats.

An interpretation of the DCA ordination (Figs 2, 3) in relation to recorded environmental variables (Table 5A,B) indicates that the first axis might be a combination of humidity (precipitation and soil organic matter) and land use ranging from the dry sites managed by mowing (sometimes by clearing only) in the right part of the diagram to humid and wet sites mostly managed by grazing in the left part of the diagram (Figs 2, 3; Table 5B). The second axis could also be an expression of humidity according to Table 5B ranging from dry sites at the top, to wet at the negative side of axis 2 (Figs 2, 3; Table 5B). Table 5A shows intercorrelations among the environmental variables and, as expected, precipitation is highly intercorrelated with soil organic matter (loss of ignition) and content of soil potassium. The land use variables grazing, mowing and clearing are mutually exclusive, i.e. mowed sites are seldom grazed and thus significantly negatively intercorrelated (Table 5A):

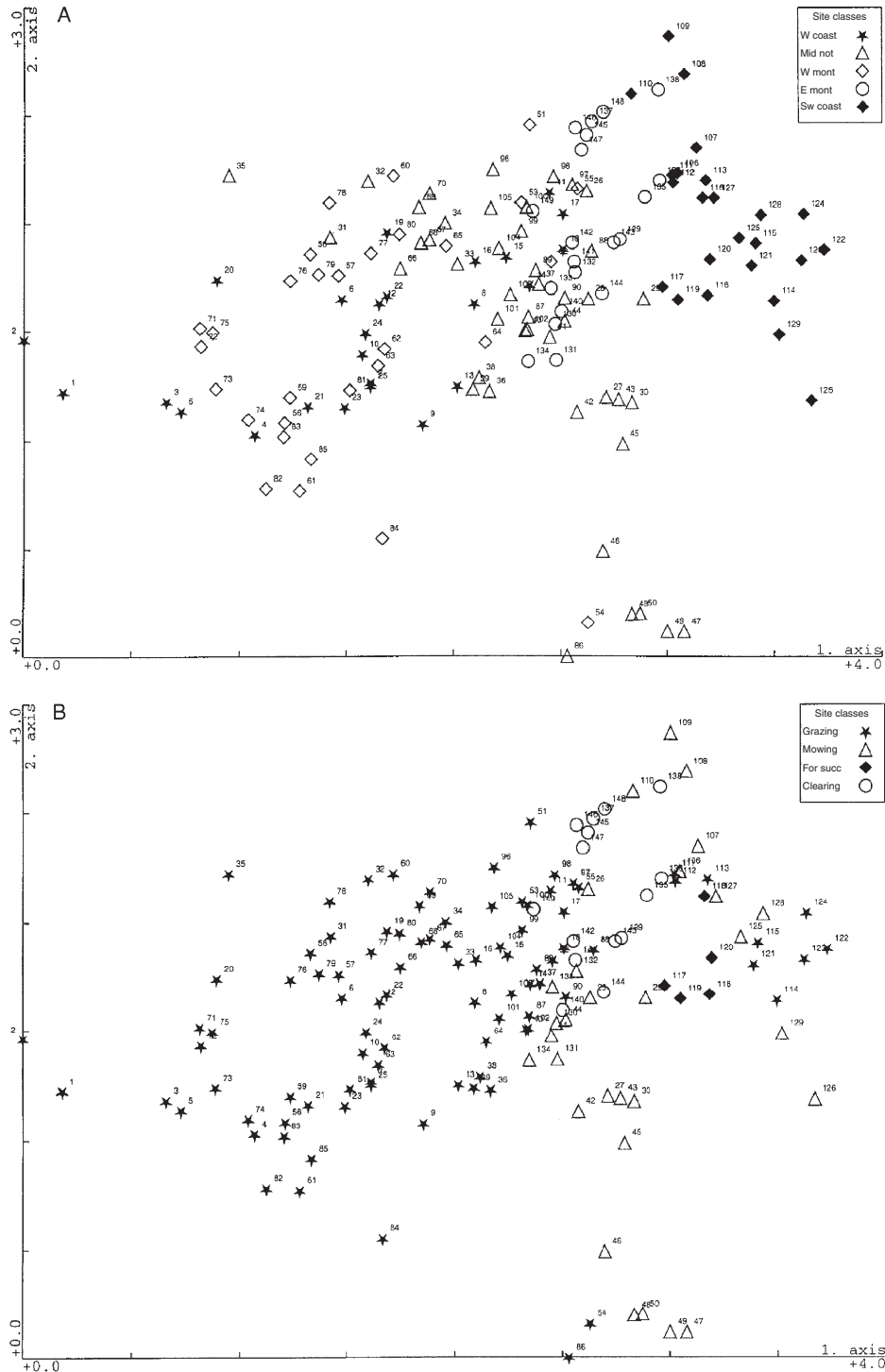


Figure 2. (A) Detrended correspondence analysis (DCA ordination) of vegetation data from 30 sites of *P. albida*. The symbols refer to classification of sites into regional groups: SW coast = South Swedish west coast; W coast = Mid Norway west coast; Mid Nor = Mid Norway inland sites; W mont = Mid Norway inland mountains; E mont = Mid Swedish mountains (see also Figure 1). Eigenvalue of DCA-axis 1 = 0.408; DCA-axis 2 = 0.288; DCA-axis 3 = 0.237; DCA-axis 4 = 0.184 (axes 3 and 4 not shown). (B) Detrended correspondence analysis (DCA ordination) of vegetation data from 30 sites of *P. albida*. The symbols refer to the classification of land use at the different sites; Grazing = presently grazed by domestic livestock; Mowing = presently used for hay making; Clearing = presently mowed, but no removal of cut biomass; For succ = presently no management – ongoing forest succession.

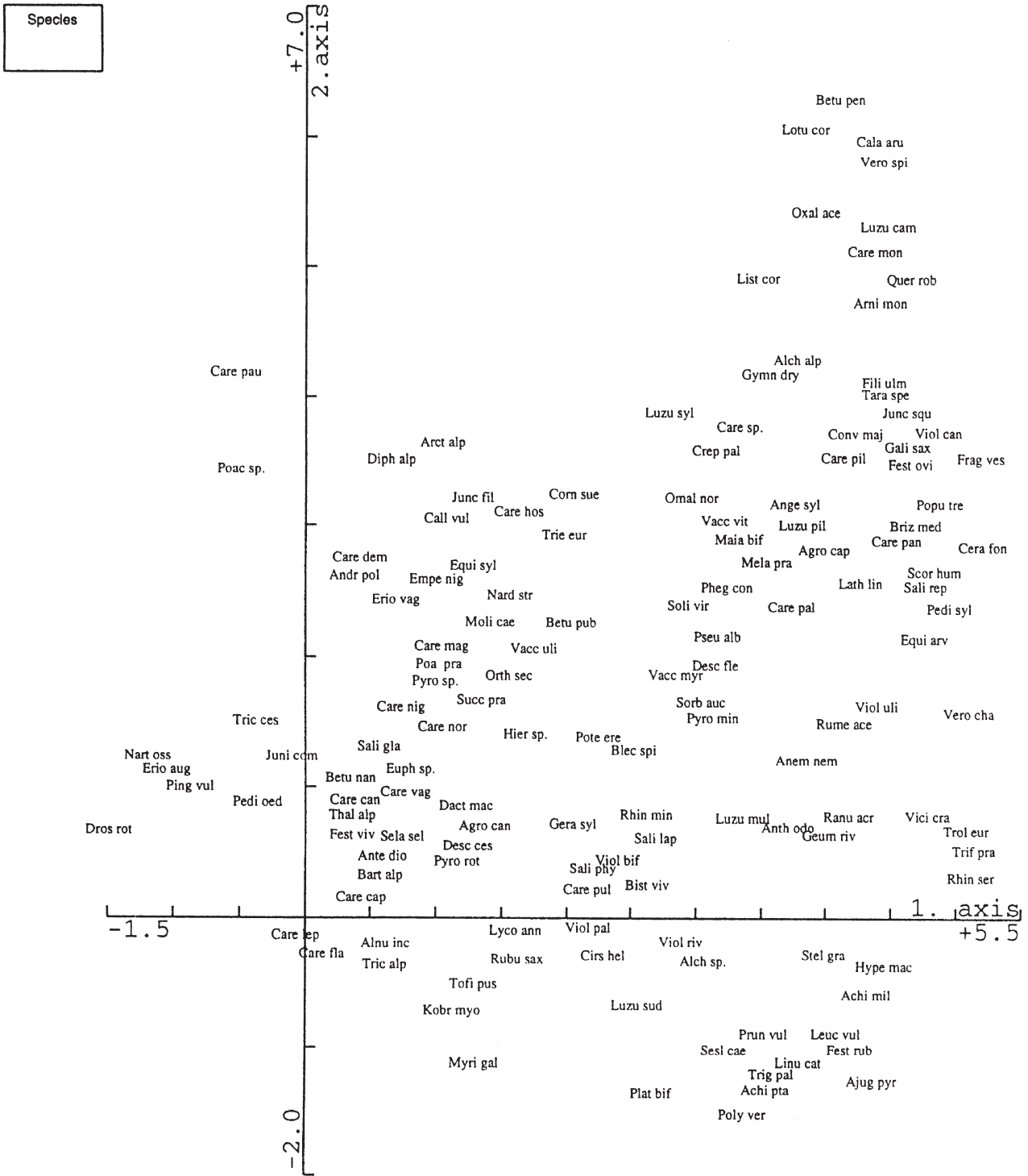


Figure 3. Detrended correspondence analysis (DCA ordination) of vegetation data from 30 sites of *P. albida*. Species ordination.

The conclusion from the ordination of sites of *P. albida*, along with the wide amplitude of the soil parameters studied (Table 6) indicates that *P. albida* can occur along a wide ecological gradient.

The large variation of environmental variables is shown explicitly in Table 6. There is a strong climatic gradient from the humid Mid-Norwegian west coast (>1200mm precipitation per year) to the drier inland

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Table 5A. Correlation matrix for environmental variables for the *Pseudorchis albida* sites. The table shows Kendall's correlation coefficients and *P*-values; n.s. = *p* > 0.05. Significant intercorrelations are printed in bold. Graz = grazing; Mowi = mowing; Clear = mowing without clearing of biomass; Cano = tree canopy cover; Expo = combined value of exposition and inclination; Alti = altitude, m above sea level; Prec = mean annual precipitation; Loss = soil loss of ignition; K = soil potassium content; P = soil phosphorus content; pH = soil pH. See also Table 6 and Methods

L. use	Graz	1.000																		
L. use	Mowi	-0.703 0.000	1.000																	
L. use	Clear	-0.468 0.000	-0.175 0.036	1.000																
	Cano	0.210 0.008	-0.280 0.000	-0.010 n.s.	1.000															
Topo	Expo	0.107 n.s.	-0.095 n.s.	-0.076 n.s.	0.144 n.s.	1.000														
Topo	Alti	-0.032 n.s.	-0.089 n.s.	0.293 0.000	0.046 n.s.	-0.046 n.s.	1.000													
Topo	Prec	0.184 0.009	0.049 n.s.	-0.264 0.000	0.001 n.s.	-0.223 0.000	-0.376 0.000	1.000												
Soil	Loss	0.303 0.000	-0.092 n.s.	-0.268 0.000	0.164 0.012	-0.179 0.002	-0.055 n.s.	0.301 0.000	1.000											
Soil	K	0.218 0.001	-0.120 n.s.	-0.181 0.008	0.132 0.043	-0.219 0.000	-0.072 n.s.	0.233 0.000	0.707 0.000	1.000										
Soil	P	-0.109 n.s.	0.183 0.008	-0.082 n.s.	0.098 n.s.	-0.062 n.s.	0.007 n.s.	0.066 n.s.	0.362 0.000	0.384 0.000	1.000									
Soil	pH	-0.094 n.s.	-0.028 n.s.	0.155 n.s.	-0.122 n.s.	-0.116 n.s.	0.134 0.024	0.066 n.s.	0.067 n.s.	0.098 n.s.	-0.31 n.s.									
Graz	Mowi	Clear	Cano	Expo	Alti	Prec	Loss	K	P											

mountains in Norway and Sweden. The Swedish south-west coast sites belong to the dry part of the gradient.

ORCHID POPULATION PARAMETERS IN RELATION TO LAND USE AND ENVIRONMENTAL VARIABLES

There was no significant difference in number of orchid individuals at sites classified as infields or outfields: ($P = 0.85$; infield, $n = 20$, $\bar{x} = 37.5$, $SD = \pm 69.0$; Outfield, $n = 10$, $\bar{x} = 20.8$, $SD = \pm 14.3$). A multiple regression showed no significant relation between number of orchid individuals per site against the explanatory variables pH, amount phosphorus, amount potassium, and ignition loss. Ranges, mean values and standard deviations for the explanatory variables areas are presented in Table 6.

DEMOGRAPHY

At site no. 27 (Table 3), where different parts of the site were subjected to different managements, i.e.

mowing vs. no management (i.e. ongoing forest succession), there is a difference in the development in the permanent plots in the years 1991–97 (Fig. 4A, B). In the mowed plot, the number of new individuals appearing annually is quite large and stable (Fig. 4A). Furthermore, the turnover with new and disappearing plants is apparent, with no new individuals at all occurring in the last 2 years (Fig. 4B). This plot shows a static and nondynamic pattern where old plants can persist and survive for years despite forest succession, but with no or little recruitment.

The flowering frequency varies quite a lot between years, especially in the Halland (no. 22, Table 3) population (Fig. 5A). The Härjedalen population seems to be more stable, perhaps because this site is more humid (Fig. 5B). The difference in numbers between years in recorded individuals can thus be substantial which is especially evident in the Halland population (Fig. 5A). Further results of flowering frequency in *P. albida* at these sites will be presented later (L.G. Reinhammar, unpublished results).

Table 5B. Correlation matrix for environmental variable for the *Pseudorchis albida* sites and the site's scores along the three first axes in the DCA ordination. The table shows Kendall's correlation coefficients and *P*-values; n.s. = *P* > 0.05. Graz = grazing; Mowi = mowing; Clear = mowing without clearing of biomass; Cano = tree canopy cover; Expo = combined value of exposition and inclination; Alti = altitude, m above sea level; Prec = mean annual precipitation; Loss = soil loss of ignition; K = soil potassium content; P = soil phosphorus content; pH = soil pH. See also Table 6 and Methods

		Axis 1	Axis 2	Axis 3
L. use	Graz	-0.530 0.000	-0.083 n.s.	0.121 n.s.
L. use	Mowi	0.384 0.000	-0.115 n.s.	-0.001 n.s.
L. use	Clear	0.191 0.005	0.265 0.000	-0.117 n.s.
	Cano	-0.153 0.019	0.082 n.s.	-0.147 0.025
Topo	Expo	0.024 n.s.	0.189 0.001	0.033 n.s.
Topo	Alti	-0.180 0.002	-0.026 n.s.	0.337 0.000
Topo	Prec	-0.221 0.000	-0.271 0.000	-0.102 n.s.
Soil	Loss	-0.450 0.000	-0.220 0.000	0.034 n.s.
Soil	K	-0.345 0.000	-0.169 0.003	-0.020 n.s.
Soil	P	-0.026 n.s.	0.045 n.s.	-0.093 n.s.
Soil	pH	-0.205	-0.336	0.164
001	0.000	0.005		

Table 6. Mean values, standard deviations (SD) and range of selected environmental variables for the sites of *P. albida*: soil pH, soil phosphorus (mg P per 100 g soil), soil potassium (mg K per 100 g soil), loss of ignition (% organic content in soil), and mean annual precipitation (mm)

Variable	Mean	SD	Range
pH	5.1	0.4	4.5–7.2
Phosphorus	4.2	3.8	0.4–20.6
Potassium	25.0	17.1	4.0–112.0
Loss of Ignition	26.2	21.1	4.3–89.4
Precipitation	958.7	402.7	628–2010

COMPARISON OF THE HABITATS OF *P. ALBIDA* AND *P. STRAMINEA*

The vegetation composition in sites for *P. albida* and *P. straminea*, respectively, shows clear differences (Fig. 6, Appendix 1). In total, 206 vascular plant species were found in the investigated sample square. Of those, 38 (18.4%) were found only in squares with *P. straminea*, 39 (18.9%) were common to both orchid taxa, while 129 (62.6%) were associated only with *P. albida*. However, the number of sites studied for *P. straminea* is too few, and the difference in the area investigated for each orchid taxon is too large to give statistically relevant information. Of more interest,

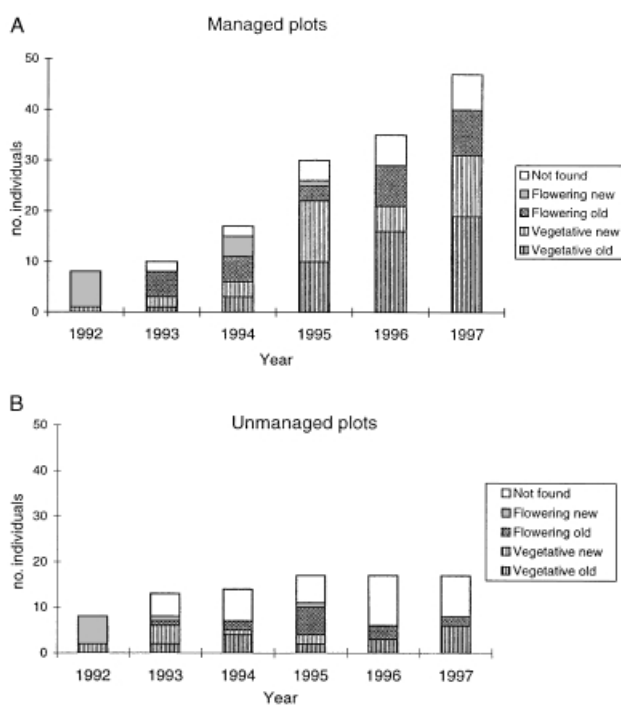


Figure 4. (A,B) Population dynamics of *P. albida* over a 6-year period in one managed (mowed) grassland (above), and one unmanaged grassland (ongoing forest succession; below) plot, respectively (Site 27, Table 3). Population registrations performed in one permanent 9 m² sample square in each plot, respectively. All individuals were permanently marked.

however, is to compare the species composition. A classification of Norwegian mountain plants presented in Austrheim *et al.* (1999), was applied to the species data in this paper with some modifications (Fig. 6). In the *P. albida* sites, the companion plants are mainly grassland plants along with species belonging to the group indifferent plants. In contrast, the

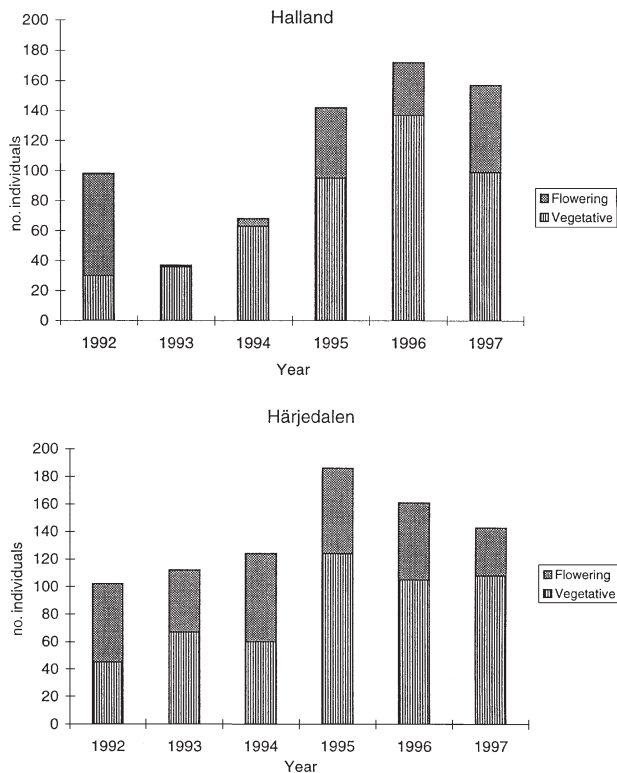


Figure 5. Population dynamics of *P. albida* over a 6-year period in two managed (mowed or grazed) grasslands (Sites 22 – above, and 27 – below, Table 3). Population registrations performed in permanently ~200 m² squares in each plot, respectively. All individuals were permanently marked.

P. straminea-sites are characterized by alpine species (some of them favoured by grassland management), and to a lower extent also by grassland and indifferent species. The most common companion vascular plant species to *P. albida* have previously been presented (Table 4). A corresponding presentation for *P. straminea* is given in Table 7. It is obvious that *Dryas*-heaths communities are characteristic for the *P. straminea* habitats.

DISCUSSION

OCCURRENCE OF *P. ALBIDA* IN RELATION TO LAND USE AND ENVIRONMENTAL VARIABLES

All the investigated habitats of *P. albida* consist of seminatural grasslands, although with variation in species composition. However, in considering companion plants, there is obviously a core of about 10 vascular plant species that are very common (a total frequency >50%) in the squares analysed (Table 4). The wide amplitude in companion species (Appendix 1) and the pattern seen in the ordinations

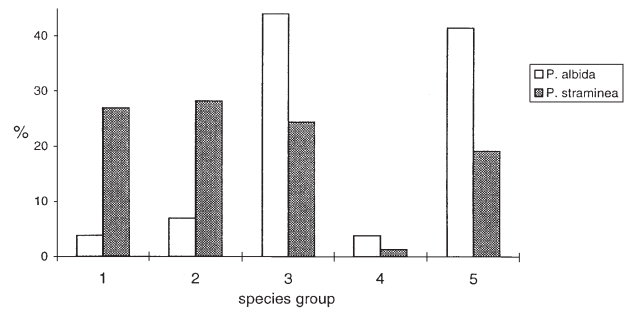


Figure 6. Comparison of field layer vegetation at sites of *P. albida* and *P. straminea*, respectively. The classification of plant species is a modification from Austrheim *et al.* (1994). 1 = alpine species; 2 = alpine species favoured by grassland management; 3 = grassland species; 4 = weeds, nitrophytes and ley species; 5 = indifferent species, not favoured by grassland management.

Table 7. Survey of the most frequent vascular plant species in the sites of *P. straminea* (50% in the studied 0.25 m² squares; presence data)

Species	% Appearance in the complete material
<i>Dryas octopetala</i>	86.5
<i>Bistorta vivipara</i>	81.8
<i>Vaccinium uliginosum</i>	78.4
<i>Empetrum nigrum</i>	64.9
<i>Pinguicula vulgaris</i>	56.8
<i>Thalictrum alpinum</i>	54.1
<i>Tofieldia pusilla</i>	51.4
<i>Vaccinium vitis-idaea</i>	51.4

(Figs 2, 3) indicate that *P. albida* is not bound to any particular plant community. This fact, together with the wide amplitude in soil chemistry parameters (Table 6), indicates that *P. albida* is a tolerant plant, and rather indifferent to, e.g. lime (cf. Nilsson, 1991) and soil humidity. This observation is also confirmed by two other recent studies of plant composition at *P. albida* sites. Dierschke (1994) and Sortland (1996; cf. Reinhammar, 1998c) reported from studies in North Germany and North Norway, respectively, the occurrence of frequent companion plant species in concordance with our results as given in Table 4. A common denominator for all sites in our study is that they have in some way been subject to human grassland management (or other human activities). Therefore, an assumption relating the occurrence of *P. albida* to the presence or absence of traditional agricultural practices, such as mowing and/or grazing, seems plausible.

However, we find no correlation between the occurrence of *P. albida* and land use (grassland management) in the 5-year-period prior to this study. But, it should be kept in mind that this orchid is a long-lived perennial (which may attain an age of at least 30 years; Summerhayes, 1968), and it possibly needs at least 3 years just to appear above ground (Summerhayes, 1968). The time span of 5 years, used in this study for this particular orchid, is probably too short to reflect the influence of land use. *P. albida* can obviously be present quite a long time after cessation of traditional grassland management. On the other hand, the establishment of new individuals (seed plant recruitment) is obviously low in sites where such agricultural practices have ended. Data from one of the Swedish sites included here (Fig. 4), show that recruitment is absent when no grassland management occurs. Obviously, the main threat to *P. albida* is the abolishment of traditional practices such as haymaking and moderate grazing (Schwabe, 1990), leading to forest succession. This change of agricultural practices has occurred later in the provinces of Sør-Trøndelag (Sørmeland, 1996), Jämtland and Härjedalen (see Rosander, 1968; Rindberg, 1981), than in southern Scandinavia. Also, considering that forest succession is slower here than in the southern provinces of Scandinavia, it is not surprising that the northern provinces today provide more suitable habitats for this orchid.

Demographic studies might give the critical information to explain the decline of *P. albida*. Very few such studies exist for orchids in European grasslands. Hutchings (1987a,b) work on the lime-demanding *Ophrys sphegodes* in England, showed that a very hard grazing pressure can have devastating effects on population density of *O. sphegodes*. At hard grazing pressure most flowers are eaten, inhibiting seed set and seed plant recruitment, an observation that has also been reported for *P. albida* (Borg, 1982; Schwabe, 1990). Furthermore, Hutchings (1987a) and Waite & Hutchings (1991) showed that the intensity and time for grazing are important factors for the establishment of *O. sphegodes* and that conservation schemes must aim at creating conditions positive for the flowering, seed set and seed plant recruitment of *O. sphegodes*. McKendrick (1995), studying *Dactylorhiza praetermissa* in England, found that the location of the orchid plants in relation to surrounding habitats was an important factor for the survival and growth of this species. The creation of open spots, e.g. from land use and flooding, lead to the increase of populations of *D. praetermissa*. Tamm (1972) reported that seed propagation in orchids is slow in a closed sward. Willems (1982) and Willems & Bik (1991), studying *Orchis simia* in the Netherlands, noted that nearly all new juvenile plants appeared in the open grassland,

while only a few appeared below a nearby *Crataegus* shrub. Similar sensitivity to shrubs and trees of orchid seedlings was reported by Farrell (1991) in her study on *Orchis militaris* in England. Kull (1998) noted that in populations of *Cypripedium calceolus*, shortness of suitable microsites was the limiting factor for the regeneration of this species in Estonia. Bateman & Farrington (1989) and Qamaruz-Zaman *et al.*, (1998) found in *O. simia* in England, that populations of this species have been through a genetic bottleneck due to anthropogenic influences. Furthermore, it has been found that large fluctuations between years are common, for example in *Herminium monorchis*, although it is not a general rule for all orchid species (Wells, 1981). This means that one single census year can give a totally erroneous estimation of an orchid population size (cf. Tamm, 1972; Wells & Cox, 1991). The difference in numbers between 'good' and 'bad' years in recorded individuals can be substantial, which is evident for two Swedish populations of *P. albida* (Fig. 5; see also Løjtant, 1991).

Oostermeijer *et al.* (1994) found in a demographic study on *Gentiana pneumonanthe*, a perennial grassland herb, that populations tended to become 'senile' when traditional land use ceased, with overgrowth as a consequence. 'Senile' means that the share of young plants and seedlings is low in unmanaged sites, compared to managed ones. The same pattern is evident in the comparison between managed and nonmanaged sites of *P. albida* in this study (Fig. 4). There is a substantially higher recruitment in the well-managed site, compared to the site subjected to forest succession. If the demographic structure had been available for all sites studied here, significant correlations with land use would probably have been found.

Comparing the results presented in the above mentioned studies (Tamm, 1972, 1991; Wells, 1981; Willems, 1982; Hutchings, 1987a,b; Bateman & Farrington, 1989; Willems & Bik, 1991; Oostermeijer *et al.*, 1994; McKendrick, 1995; Kull, 1998; Qamaruz-Zaman *et al.*, 1998) with our results, support is given to our interpretation of the importance of the 'regeneration niche' (cf. Grubb, 1977) for *P. albida*. Clearly, *P. albida* is not especially demanding as regards plant communities and soil chemistry parameters, but it seems to require small open patches for regeneration. This is especially evident as the species today often occur on paths or other disturbed areas (Reinhammar, 1995; Sørmeland, 1996). It is also obvious that the taxon is not very demanding on traditional grassland management like mowing or grazing which is evident from the occurrence of *P. albida* in recently cleared areas as power line gates and alpine ski slopes (Reinhammar, 1995). As has been pointed out earlier, the use and management of seminatural grasslands has decreased substantially during the last century

(Bernes, 1994), and thus also the area of potential habitats for this species. Even if new habitats are created by other means (see above) it is unclear if the existing populations will be large enough in number and size to be able to disperse to such new habitats.

Detailed knowledge of the reproduction biology of *P. albida* and on the role of mycorrhizae would have been desirable for a more complete insight into limiting factors for its distribution and survival.

DIFFERENTIATION BETWEEN *P. ALBIDA* AND *P. STRAMINEA*

The vegetation analyses reveal that *P. albida* and *P. straminea* occupy quite different habitats, and thus can be said to be ecologically separated in Scandinavia as is illustrated in Figure 6 and Appendix 1. It is interesting that both taxa have a large, and rather similar, degree of companion plants that are grassland species (Fig. 6). The two species are certainly sister taxa, and they have perhaps even more similar habitat demands than indicated here, since open grasslands and heaths are the most prominent habitats for both taxa.

P. straminea grows in lime- or base-rich habitats, mainly alpine, such as *Dryas*-heaths and serpentine soils (Sivertsen, 1990; Ericsson & Rune, 1991; Nilsson, 1991) in Scandinavia. *P. albida* on the other hand, is apparently indifferent to lime (Nilsson, 1991), and occurs from the lowlands up to the subalpine level. This taxon occurs only in seminatural grasslands such as haymaking meadows and grazing lands. *P. albida* starts flowering earlier, and also flowers during a shorter time period, than *P. straminea* in the areas of sympatry in central Sweden (L.-G. Reinhammar, pers. observ.). This difference in phenology is perhaps an adaptation in *P. albida* to the selection pressure to human land use impacts such as summer farm practices in the Swedish provinces Härjedalen and Jämtland (i.e. the area of sympatry in Sweden; Hultén & Fries 1986, Reinhammar, 1995). Similar phenomena have been observed in early flowering *Euphrasia* spp. (Karlsson, 1984) and *Gentianella* spp. (Lennartsson, 1997).

An interesting fact is that for plant species occurring with both taxa (Appendix 1), some species are common in different habitats in the alpine area, but in the Scandinavian lowlands, they only occur in the seminatural grasslands. Today, many of those species are disappearing from their lowland habitats due to the abolishing of grassland management. Examples of such plants are *Bistorta vivipara*, *Botrychium lunaria*, *Carex capillaris* and *Selaginella selaginoides* (Ekstam *et al.*, 1988; Gjørevoll, 1992). The dependence on lime-rich habitats at higher altitudes may in lowland habitats be compensated by mowing and/or grazing which change the competition conditions.

P. straminea occupies arctic-alpine habitats which are not dependent on human disturbance, and this taxon is probably not as vulnerable as *P. albida*. The influence of grazing from reindeer and voles in Scandinavian alpine habitats, and its role for regulating vegetation pattern is still poorly understood (Skogland, 1984; Oksanen, 1990; Oksanen & Ranta, 1992; Oksanen & Moen, 1994; Väre *et al.* 1995). In addition, the long-term grazing influence from domestic herbivores, today mainly sheep, must be considered in the alpine areas of Norway (E. G. A. Olsson *et al.*, unpubl. data).

In a study of allozyme variation (Reinhammar & Hedrén, 1998) in Swedish material of *P. albida* and *P. straminea* virtually no genetic variation was found in *P. albida* in 15 enzyme systems studied, while some genetic variation was found in *P. straminea*. The two taxa were fixed for different alleles at one locus. These data suggest that *P. albida* and *P. straminea* started to diversify well before the Weichselian glaciation. It was also hypothesized that *P. albida* and *P. straminea* may have immigrated into Scandinavia at different times (Reinhammar & Hedrén, 1998). *P. straminea* was suggested to have immigrated soon after the ice had retreated, whereas *P. albida* was suggested to have colonized Scandinavia later on, perhaps as late as when human agricultural methods first were introduced in Scandinavia some 5000 years ago (Ekstam *et al.*, 1988; Olsson, 1991; Reinhammar & Hedrén, 1998). Such a scenario finds some further support in the vegetation data presented in this paper. A number of common companion plants to *P. straminea* were present in icefree areas in Central Europe during the Weichselian glaciation maximum including *Dryas octopetala*, *Bistorta vivipara* and *Loiseleuria procumbens* (Gjørevoll, 1992; but note that *B. vivipara* may also be common at *P. albida* sites as well).

CONCLUSIONS AND IMPLICATIONS FOR THE CONSERVATION OF *P. ALBIDA*

From the present study, some universal characteristics for the sites of *P. albida* are evident. Firstly, *P. albida* is apparently indifferent to the measured soil chemistry parameters, and can occur in a wide array of plant communities. Secondly, according to available demographic and microhabitat data, *P. albida* seems to demand a short grass sward, a thin litter layer, and some disturbance that creates open patches for seed plant recruitment (Reinhammar, 1995; unpubl. observ., Sørmealand, 1996; cf. Willems & Melser, 1998; concerning the close relative *Coeloglossum viride*).

Thirdly, the present occurrence of *P. albida* is in all registered sites seminatural habitats, such as (former) meadows and pastures. We could not show any rela-

tionship between land use during the last 5 years and the occurrence of *P. albida*. The time period of 5 years for recording land use employed in the present study is apparently too short to give any significant impact of different land use practices, as *P. albida* is a long-lived, perennial plant.

A management scheme for the remaining sites of *P. albida* must consider all those facts. Mowing is important in keeping the sward short. Extensive grazing (after flowering; Borg, 1982; Hutchings, 1987a; Schwabe, 1990; McKendrick, 1995) creates open spots in the sward, which evidently is important for establishment of new plants. Burning of old grasslands, a traditional land use form in south-west Sweden, seems to have an effect similar to mowing (Ekstam *et al.*, 1988). Restoration of old, not presently managed seminatural grasslands, closely situated to extant populations, may increase the area of suitable habitats for this species and would hopefully make new colonization possible.

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REFERENCES

Adler W, Oswald K, Fischer R. 1994. *Exkursionsflora Von Österreich*. Wien: Eugen Ulmer GmbH.
Alexandersson H, Karlström C, Larsson-McCann S. 1991. *Temperaturen Och Nederbörden I Sverige 1961–90 Referensnormaler*. Norrköping: SMHI Meteorologi no. 81.

Austrheim G, Olsson EGA, Grøntvedt E. 1999. Land-use impact on plant communities in semi-natural sub-alpine grasslands of Budalen, central Norway. *Biological Conservation* **87**: 360–379.
Bateman RM, Farrington OS. 1989. Morphometric comparison of populations of *Orchis simia* Lam. (Orchidaceae) from Oxfordshire and Kent. *Botanical Journal of the Linnean Society* **100**: 205–218.
Bernes C. 1994. *Biological diversity in Sweden – a country study*. Solna: Swedish Environmental Protection Agency.
Blackstock TH, Stevens JP, Howe EA, Stevens DP. 1995. Changes in the extent and fragmentation of heathland and other semi-natural habitats between 1920 and 22 and 1987–88 in Llyn peninsula, Wales, UK. *Biological Conservation* **72**: 33–44.
Bøcher TW, Holmen K, Jakobsen K. 1966. *Grønlands Flora*. København: P. Haase & Söns Forlag.
Borg B. 1982. Vityxnen och betesdjuren. *Skaraborgs Natur*. **19**: 47–50.
ter Braak CJF. 1987. CANOCO – a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis. *Principal Components Analysis and Redundancy Analysis*, Version 2.1. Wageningen: TNO Institute of Applied Computer Science.
ter Braak CJF. 1990a. *CANOCO*, Version 3.10. Wageningen: Agricultural Mathematics Group.
ter Braak CJF. 1990b. *Update notes: Canoco, version 3.10*. Wageningen: Agricultural Mathematics Group.
ter Braak CJF. 1995. Ordination. In: Jongman RHG, ter Braak CJF, van Tongeren OFR, eds. *Data analysis in community and landscape ecology*, 3rd edn. Cambridge: Cambridge University Press, 91–173.
Carlsson Å, Gustafsson L-Å. 1984. Vityxne – en hotad slätterängsart. *Svensk Botanisk Tidsskrift* **78**: 117–128.
Chapman SB, Rose RJ, Clarke RT. 1989. The behaviour of populations of the marsh gentian (*Gentiana pneumonanthe*): a modelling approach. *Journal of Applied Ecology* **26**: 1059–1072.
Curtis TGF, McGough HN. 1988. *The Irish red data book 1: vascular plants*. Dublin: Wildlife Service Ireland.
Damman AWH. 1957. The south-Swedish *Calluna*-heath and its relation to the *Calluna-Genistetum*. *Botaniska Notiser* **110**: 363–398.
Danielsson B. 1994. *Härjedalens Kärlväxtflora*. Lund: SBT-förlaget.
Det Norske Meteorologiske Institutt. 1991a. *Nedbørsnormaler 1961–90*. Oslo: Klimaavdelingen, stencil.
Det Norske Meteorologiske Institutt. 1991b. *Temperaturnormaler 1961–90*. Oslo: Klimaavdelingen, stencil.
Det Norske Meteorologiske Institutt. 1996. *Nedbør-og temperaturnormaler for 1994*. Oslo: Klimaavdelingen, stencil.
Dierschke H. 1994. Die Weissunge (*Pseudorchis albida* [L.] Á. & D. Löve) im Harz wiedergefunden. *Tuexenia* **14**: 399–402.
van Dijk G. 1991. The status of semi-natural grasslands in Europe. In: Gourop PD, Batten LA, Norton JA, eds. *The*

- conservation of lowland dry grassland birds in Europe. The Hague: Joint Nature Conservation Committee. 15–36.
- Dostál J. 1950.** *Kvetena CSR a Ilustrovany Kl'ck Urcen Vsech Cevnatych Rostlin, Na Územ Aeskolslovensko Plane Ros-touc'ch Nebo Bezne Pestovanych.* Prague: Prirodovedecké nakladatelství.
- Ekstam U, Aronsson M, Forshed N. 1988.** *Ängar Om Naturliga Slättermarker I Odlingslandskapet.* Stockholm: LTs förlag.
- Ericsson S, Rune O. 1991.** Ny svensk sydgräns för lapsk alprots *Rhododendron lapponicum* – en isolerad förekomst på serpentinen. *Svensk Botanisk Tidskrift* **85**: 71–80.
- Farrell L. 1991.** Population changes and management of *Orchis militaris* at two sites in England. In: Wells TCE, Willems JH, eds. *Population ecology of terrestrial orchids.* The Hague: SPB Publishing bv, 463–468.
- Fernald ML. 1926.** Two summers of botanizing in Newfoundland. *Rhodora* **28**: 174–175.
- Fernald ML. 1933.** Recent discoveries in the Newfoundland flora. *Rhodora* **35**: 237–239.
- Fiori A. 1923.** *Nuova Flora Analitica d'Italia Contenente la Descizione Delle Piante Vascolari Indigene Inselvatiche E Largamente Coltivate in Italia, I (3).* Firenze: Tipografia di M. Ricci.
- Gjærevoll O. 1992.** *Plantegeografi* 2nd edn. Tapir: Tapir Forlag.
- Goffart J. 1945.** *Flora de Belgique et Des Regions Limitrophes.* Liège: Éditions Desoer.
- Grubb PJ. 1977.** The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Review* **52**: 107–145.
- Guinochet M, de Vilmorin R. 1978.** *Flore de France Fascicule 3.* Paris: Éditions du centre de la recherche scientifique.
- Hagerup O. 1951.** Pollination in the Faroes – in spite of rain and poverty in insects. *Danske Biologiske Meddelelser* **18**: 1–48.
- Hagerup O. 1952.** Bud autogamy in some northern orchids. *Phytomorphology* **2**: 51–60.
- Hallingbäck T. 1996.** *Ekologisk Katalog Över Mossor.* Uppsala: ArtDataBanken, Sveriges Lantbruksuniversitet.
- Hämet-Ahti L, Suominen J, Ulvinen T, Uotila P, Vuokko S. 1986.** *Retkeilykasvio*, 3rd edn. Suomen Luonnonsuojelun Tuki Oy.
- Harmen L. 1943.** Studies on the cytology of arctic plants. II. *Habenaria Meddelelser Om Grönland* **131**: 1–15.
- Heß HE, Landolt E, Hirzel R. 1967.** *Flora der Schweiz und Angrenzender Gebiete Bind 1.* Basel: Birkhäuser-Verlag.
- Holub J, Procházka F, Cerovsky J. 1979.** Seznam vykynul-nych, endemických a ohrozených taxonů vyssich rostlin kveteny CSR (1. verze). *Preslia* **51**: 213–237.
- Hultén E, Fries M. 1986.** *Atlas of North European vascular plants*, Vol. I. Königstein: Koeltz Scientific Books.
- Hutchings M. 1987a.** The population biology of the early spider orchid, *Ophrys sphegodes* Mill. I. A demographic study from 1975 to 1984. *Journal of Ecology* **75**: 711–727.
- Hutchings M. 1987b.** The population biology of the early spider orchid, *Ophrys sphegodes* Mill. II. Temporal patterns in behaviour. *Journal of Ecology* **75**: 729–742.
- Hylander N. 1966.** *Nordisk Kärnväxtflora II.* Stockholm: Almqvist & Wiksell.
- Ingelög T, Andersson R, Tjernberg M. 1993.** *Red data book of the Baltic region. Part 1. Lists of threatened vascular plants and vertebrates.* Uppsala: Swedish Threatened Species Unit.
- Ingelög T, Gransberg M. 1992.** Rekommendationer med anledning av ökat hot om illegal insamling av hotade väx-tarter. *Svensk Botanisk Tidskrift* **86**: 60.
- Jordanov D. (Ed.) 1964.** *Flora Reipublicae Popularis Bulgaricae.* Vol. II. Sofia: Aedibus Academiae Scientiarum Bulgaricae.
- Karlsson T. 1984.** Early-flowering taxa of *Euphrasia* (Scrophulariaceae) on Gotland, Sweden. *Nordic Journal of Botany* **4**: 303–326.
- Kendall MG. 1938.** A new measure of rank correlation. *Biometrika* **30**: 81–93.
- Klein E. 2000.** *Pseudorchis albida* subsp. *tricuspis* (BECK) KLEIN stat. nov., eine weitgehend übersehene, calcicole, alpsich-boreale Sippe (Orchidaceae – Orchideae). *Phyton* **40**: 141–159.
- Klein E, Kerschbaumsteiner H. 1996.** *Die Orchideen der Steiermark.* Graz: Landesdruckerei.
- Knuth P. 1899.** *Handbuch der Blütenbiologie, II.* Leipzig: Engelmann.
- Komarov VL. 1935.** *Flora of the USSR. IV. Liliiflorae and Microspermae.* Jerusalem: Israel Program for Scientific Translations 1968.
- Kull T. 1998.** Fruit-set and recruitment in populations of *Cypripedium calceolus* L. in Estonia. *Botanical Journal of the Linnean Society* **126**: 27–38.
- Landolt E. 1991.** *Rote Liste – Gefährdung der Farn- und Blütenpflanzen in der Schweiz.* Bern: Bundesamt für Umwelt, Wald und Landschaft.
- Lennartsson T. 1997.** Seasonal differentiation – a conserva-tive reproductive barrier in two grassland *Gentianella* (Gentianaceae) species. *Plant Systematics and Evolution* **208**: 45–69.
- Lid J, Lid DT. 1994.** *Norsk Flora 6. utgave.* Oslo: Det Norske Samlaget.
- Linusson AC, Bergin G, Olsson EGA. 1998.** Reduced community diversity in semi-natural meadows in southern Sweden, 1965–90. *Plant Ecology* **136**: 77–94.
- Løjtnant B. 1980.** Status over den danske flora. Miljøministeriet, Fredningstyrelsen. In: *Status Over Den Danske Plante-Og Dyreverden.* København: Stougaard Jensen, 327–340.
- Løjtnant B. 1991.** Overvågning af orchidéer 1987–89. *Flora Og Fauna* **97**: 63–121.
- Londo G. 1990.** Conservation and management of semi-natural grasslands in Northwestern Europe. In: Bohn U, Neuhäusl R, eds. *Vegetation and Flora of Temperate Zones.* The Hague: Academic Publishing, 69–77.
- Löve Á. 1950.** Some innovations and nomenclatural suggestions in the Icelandic flora. *Botaniska Notiser* **103**: 24–60.
- Löve Á. 1977.** *Íslensk ferð aflora 2. útgáfa.* Reykjavík: Almenna bókafélagið.

- Maglocky S, Ferakova V. 1993.** Red list of ferns and flowering plants (Pteridophyta and Spermatophyta) of the flora of Slovakia (the second draft). *Biologia* **48**: 361–385.
- McKendrick SL. 1995.** The effects of herbivory and vegetation on laboratory-raised *Dactylorhiza praetermissa* (Orchidaceae) planted into grassland in southern England. *Biological Conservation* **73**: 215–220.
- Milberg P. 1992.** Seed bank in a 35-year-old experiment with different treatments of a semi-natural grassland. *Acta Oecologia* **13**: 743–752.
- Moberg R, Holmåsén I. 1984.** *Lavar En Fälthandbok 2: a upplagan*. Stockholm: Interpublishing.
- Mossberg B, Nilsson S. 1982.** *Orkidéer Europas Vildväxande Arter*. Turnhout: Wahlström & Widstrand.
- Mossberg B, Stenberg L, Ericsson S. 1992.** *Den Nordiska Floran*. Turnhout: Wahlström & Widstrand.
- Mullenders W. 1967.** *Flore de la Belgique, Du Nord de la France et Des Regions Voisines*. Liège: Éditions Desoer.
- Müller H. 1881.** *Alpenblumen, Ihre Befruchtung durch Insekten und Ihre Anpassungen an Dieselben*. Leipzig: Engelmann.
- Myklebost HE. 1996.** En populasjons- og vegetasjonsøkologisk undersøkelse av *Pedicularis oederi* (gullmyrklegg) langs to transekter i Grødalen, Sunndal kommune. Trondheim: MSc-thesis.
- Naturvårdsverket. 1990.** *Hotade Arter – Långsiktig Handlingsprogram*. Solna: Naturvårdsverket.
- Neuman LM. 1901.** *Sveriges Flora*. Lund: C.W.K. Gleerups förlag.
- Nilsson Ö. 1991.** *Nordisk Fjällflora*, 3rd edn. Bonnier: Fakta Bokförlag AB.
- Nilsson Ö. 1992.** *Pseudorchis albida* ssp. *albida* – vityxne. In: Ingelög T, Thor G, Hallingbäck T, Andersson R, Aronsson M, eds. *Floravård I Jordbrukslandskapet Skyddsvärda Växter*. Lund: SBT-förlaget. 266–267.
- Nilsson Ö, Gustafsson LÅ. 1978.** Projekt Linné rapporterar 64–79. *Svensk Botanisk Tidskrift* **72**: 1–24.
- Oberdorfer E. 1994.** *Pflanzensociologische Exkursions Flora*, 7th edn. Stuttgart: Eugen Ulmer GmbH.
- Oksanen L. 1990.** Predation, herbivory, and plant strategies along gradients of primary productivity. In: Grace JB, Tilman D, eds. *Perspectives of plant competition*. San Diego: Academic Press, 445–474.
- Oksanen L, Moen J. 1994.** Species-specific plant responses to exclusion of grazers in three Fennoscandian tundra habitats. *Ecoscience* **1**: 31–39.
- Oksanen L, Ranta E. 1992.** Plant strategies along mountain vegetaion gradients-test of 2 theories. *Journal of Vegetation Science* **3**: 175–186.
- Olsson EGA. 1991.** Agro-ecosystems from Neolithic time to present. In: Berglund B, ed. *The cultural landscape during 6000 years in southern Sweden*. Sweden: Ecological Bulletins, 293–314.
- Olsson EGA. 1994.** Samuels dagböcker och den biologiska mångfalden – aspekter på odlingslandskapet i Västergötland. *Västergötlands Fornminnesförenings Tidskrift 1993–94*: 59–64.
- Olsson EGA, Austrheim G, Grenne SN. 2000.** Landscape change patterns in mountains, land use and environmental diversity, Mid-Norway 1960–1993. *Landscape Ecology* **15**: 155–170.
- Oltean M, Negrean G. 1994.** Lista roie a plantelor superioare din România. *Studii Sintenze, Documentatii de Ecologie I Bucuresti* **52**: 52.
- Oostermeijer JGB, Veer R, den van't Nijs JCM. 1994.** Population structure of the rare, long-lived perennial *Gentiana pneumonanthe* in relation to vegetation and management in the Netherlands. *Journal of Applied Ecology* **31**: 428–438.
- Parker KC. 1988.** Environmental relationships and vegetation associates of columnar cacti in northern Sonoran desert. *Vegetatio* **78**: 125–140.
- Pielou EC. 1969.** *An introduction to mathematical ecology*. New York: Wiley.
- van der Pijl L, Dodson CH. 1966.** *Orchid flowers, their pollination and evolution*. Coral Gables: University of Miami Press.
- Polunin O. 1980.** *Flora of Greece and the Balkans*. Oxford: Oxford University Press.
- Qamaruz-Zaman F, Fay MF, Parker JS, Chase MW. 1998.** The use of fingerprinting in conservation genetics: a case study of *Orchis simia* (Orchidaceae). *Lindleyana* **13**: 125–133.
- Rasmussen R. 1952.** *Føroya Flora*, 2nd edn. Tórshavn: Skúlabókagrunnur Løgtingsins.
- Reinhammar LG. 1995.** Evidence for two distinct species of *Pseudorchis* (Orchidaceae) in Scandinavia. *Nordic Journal of Botany* **15**: 469–481.
- Reinhammar LG. 1998a.** Variation in *Pseudorchis albida* s.l. (Orchidaceae) and *Carex capitata* s.l. (Cyperaceae). Morphology, genetic diversity, ecology and systematics. Acta Universitatis Upsaliensis. *Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology* **343**: 1–42.
- Reinhammar LG. 1998b.** Systematics of *Pseudorchis albida* s.l. (Orchidaceae) in Europe and North America. *Botanical Journal of the Linnean Society* **126**: 363–382.
- Reinhammar LG. 1998c.** Kommentarer om vit- och fjällyxne (kvit- og fjellkurle – *Pseudorchis albida* s.lat., Orchidaceae) i Nordnorge. *Polarflokken* **22**: 139–145.
- Reinhammar LG, Hedrén M. 1998.** Allozyme differentiation between lowland and alpine populations of *Pseudorchis albida* s.l. (Orchidaceae) in Sweden. *Nordic Journal of Botany* **18**: 7–14.
- Reinhard HR, Gözl P, Reudi P, Wildermuth H. 1991.** *Die Orchideen der Schweiz und Angrenzender Gebiete Egg bei*. Zürich: Fotorotar.
- Rindberg L. 1981.** Vad ger fåboden? *Föreningen Heimbygdas Årsbok 1982 Jämten* **75**: 11–16.
- Rosander G. 1968.** Fåboddriften i Jämtlands län 1967. *Föreningen Heimbygdas Årsbok 1968 Jämten* **62**: 121–137.
- Savulescu T. 1972.** *Flora Republicii Socialiste România*, Vol. XIII. Editura Academici Republicii Socialiste România.
- Scanell MJP, Synnott DM. 1987.** *Census Catalogue of the Flora of Ireland*, 2nd edn. Dublin: The Stationery Office.

- Schwabe A. 1990.** Syndymanische Prozesse in Borstgrasrasen: Reaktionsmuster von Brachen nach erneuter Rinderbeweidung und Lebensrhythmus von *Arnica montana* L. *Carolinaea* **48**: 45–68.
- Scoggan HJ. 1978.** *The Flora of Canada Part 2 Pteridophyta, Gymnospermae, Monocotyledonae*. Ottawa: National Museum of Natural Sciences.
- Sivertsen S. 1990.** *Leucorchis straminea* (Fern.) Á. Löve. In: Gjærevoll O, ed. *Maps of distribution of Norwegian vascular plants*, Vol. II *alpine plants*. Trondheim: Tapir Publishers, 73–74.
- Skogland T. 1984.** Wild reindeer foraging-niche organization. *Holarctic Ecology* **7**: 345–379.
- Sørmealand E. 1996.** Hvitkurle (*Pseudorchis albida* (L.) Á. & D. Löve, Orchidaceae) – en truet grasmarksart. Utbredelse og populasjonsstatus i Sør-Trøndelag fylke. Trondheim: MSc-thesis.
- Sortland AB. 1996.** Kvitkurle (*Leucorchis albida* ssp. *albida*) i Lofoten. *Polarflokken* **20** (2): 121–128.
- Stace CA. 1991.** *New Flora of the British Isles*. Bury St. Edmunds, Suffolk: Cambridge University Press.
- Stevenson AC, Thompson DBA. 1993.** Long-term changes in the extent of heather moorland in upland Britain and Ireland: palaeoecological evidence for the importance of grazing. *Holocene* **3**: 70–76.
- Størkersen ØR. 1992.** Truede arter i Norge. Norwegian Red List. *DN-rapport* 1992–6.
- Summerhayes VS. 1968.** *Wild orchids of Britain*, 2nd edn. London: Collins.
- Szafer W. 1959.** *Szata Roslinna Polski Tom 1*. Warszawa: Panstowe Wydawnictwo Naukowe.
- Szafer W, Kulczynski S, Pawlowski B. 1953.** *Rósliny Polski*. Warszawa: Panstowe Wydawnictwo Naukowe.
- Tamm CO. 1972.** Survival and flowering of some perennial herbs. II. The behaviour of some orchids on permanent plots. *Oikos* **23**: 23–28.
- Tamm CO. 1991.** Behaviour of some orchid populations in a changing environment. Observations on permanent plots, 1943–1990. In: Wells TCE, Willems JH, eds. *Population ecology of terrestrial orchids*. The Hague: SPB Publishing bv, 1–13.
- Väre H, Ohtonen R, Oksanen J. 1995.** Effects on reindeer grazing on understory vegetation in dry *Pinus sylvestris* forests. *Journal of Vegetation Science* **6**: 523–530.
- Vermeulen P. 1958.** *Orchidaceae*. In: Weevers T, Danser BH, Heimans J, eds. *Flora Neerlandica, deel I, aflevering. 5*. Amsterdam: Koninklijke Nederlandse Botanische Vereniging.
- Waite S, Hutchings MJ. 1991.** The effects of different management regimes on the population dynamics of *Ophrys sphegodes*: Analysis and description using matrix models. In: Wells TCE, Willems JH, eds. *Population ecology of terrestrial orchids*. The Hague: SPB Publishing bv, 161–175.
- Wells TCE. 1981.** Population ecology of terrestrial orchids. In: Syngé H, ed. *The biological aspects of rare plant conservation*. Chichester: Wiley, 281–295.
- Wells TCE, Cox R. 1991.** Demographic and biological studies on *Orchis apifera*: some results from a 10 year study. In: Wells TCE, Willems JH, eds. *Population ecology of terrestrial orchids*. The Hague: SPB Publishing bv, 47–61.
- Willems JH. 1982.** Establishment and development of a population of *Orchis simia* Lamk. in the Netherlands, 1972–81. *New Phytologist* **91**: 757–765.
- Willems JH, Bik L. 1991.** Long-term dynamics in a population of *Orchis simia* in the Netherlands. In: Wells TCE, Willems JH, eds. *Population ecology of terrestrial orchids*. The Hague: SPB Publishing bv, 33–45.
- Willems JH, Melser C. 1998.** Population dynamics and life-history of *Coeloglossum viride* (L.) Hartm. & endangered species in the Netherlands. *Botanical Journal of the Linnean Society* **126**: 83–93.
- Willkomm W. 1893.** *Supplementum Prodrumi Florae Hispanicae*. Stuttgart: Sumtibus E. Scheizerbart (E. Koch).
- Wind P. 1994.** Fredede arter i Danmark 8. *Urt* **18**: 43–52.
- Ziegenspeck H. 1936.** *Orchidaceae*. In: von Kirchner, O, Loew, E, Schröter, C, eds. *Lebensgeschichte der Blütenpflanzen Mitteleuropas*, Vol. I no. 4. Stuttgart: Verlagsbuchhandlung Eugen Ulmer. 1–840.

APPENDIX 1

A comparison of vascular plant species found in squares for *P. albida* and *P. straminea*, respectively. The material of *P. albida* comprises 144 squares of 1 m² each where frequencies of each species were estimated, while the material of *P. straminea* is based on presence-absence data in 37 squares of 0.25 m². The localities studied are given in Table 3 and Fig. 1. Nomenclature follows Lid & Lid (1994) for vascular plants, Hallingbäck (1996) for mosses, and Moberg & Holmåsén (1984) for lichens.

A. PLANT SPECIES THAT OCCUR ONLY WITH

P. STRAMINEA

Agrostis mertensii
Astragalus alpinus
Astragalus norvegicus
Botrychium lunaria
Carex atrata
Carex atrofusca
Carex bigelowii
Carex glacialis
Carex rupestris
Cerastium alpinum
Chamorchis alpina
Diapensia lapponica
Dryas octopetala
Equisetum variegatum
Erigeron uniflorus
Gentiana nivalis
Gentianella amarella
Hieracium Sect. Alpina
Juncus trifidus
Loiseleuria procumbens
Luzula spicata
Oxyria digyna
Pedicularis lapponica

Phleum alpinum
Poa alpina
Potentilla crantzii
Sagina saginoides
Salix hastata ssp. *alpestris*
Salix lanata
Salix myrsinites
Salix phylicifolia
Salix reticulata
Saussurea alpina
Saxifraga aizoides
Silene acaulis
Taraxacum Sect. *Crocea*
Trisetum spicatum
Veronica alpina

B. PLANT SPECIES THAT OCCUR WITH BOTH
P. ALBIDA AND *P. STRAMINEA*

Andromeda polifolia
Antennaria dioica
Anthoxanthum odoratum
Arctostaphylos alpinus
Bartsia alpina
Betula nana
Bistorta vivipara
Calluna vulgaris
Campanula rotundifolia
Carex capillaris
Carex dioica
Carex vaginata
Coeloglossum viride
Crepis paludosa
Empetrum nigrum
Euphrasia frigida
Festuca ovina
Festuca vivipara
Geranium sylvaticum
Juniperus communis
Lotus corniculatus
Luzula multiflora ssp. *frigida*
Luzula sudetica
Omalotheca norvegica
Parnassia palustris
Pedicularis oederi
Phyllodoce caerulea
Pinguicula vulgaris
Ranunculus acris
Rhinanthus minor
Rumex acetosa
Selaginella selaginoides
Solidago virgaurea
Thalictrum alpinum
Tofieldia pusilla
Vaccinium myrtillus
Vaccinium uliginosum
Vaccinium vitis-idaea
Viola biflora

C. PLANT SPECIES THAT OCCUR ONLY WITH *P. ALBIDA*

Achillea millefolium
Achillea ptarmica

Agrostis canina
Agrostis capillaris
Ajuga pyramidalis
Alchemilla alpina
Alchemilla glaucescens
Alchemilla subcrenata
Alchemilla subglobosa
Alchemilla vulgaris coll.
Alchemilla wichurae
Alnus incana
Alopecurus pratensis
Anemone nemorosa
Angelica sylvestris
Arnica montana
Betula pendula
Betula pubescens
Blechnum spicant
Briza media
Calamagrostis arundinacea
Carex canescens
Carex demissa
Carex flava
Carex hostiana
Carex lepidocarpa
Carex magellanica
Carex montana
Carex nigra
Carex norvegica
Carex pallescens
Carex panicea
Carex pauciflora
Carex pilulifera
Carex pulicaris
Cerastium fontanum
Cirsium helenioides
Convallaria majalis
Cornus suecica
Dactylis glomerata
Dactylorhiza maculata
Danthonia decumbens
Deschampsia cespitosa
Deschampsia flexuosa
Diphasiastrum alpinum
Drosera rotundifolia
Eleocharis quinqueflora
Equisetum arvense
Equisetum sylvaticum
Eriophorum angustifolium
Eriophorum vaginatum
Euphrasia hyperborea
Festuca rubra
Filipendula ulmaria
Fragaria vesca
Galium boreale
Galium saxatile
Galium uliginosum
Geum rivale
Gymnocarpium dryopteris
Hieracium auriculatum
Hieracium Sect. *Nigrescentia*
Hieracium pilosella
Hieracium Sect. *Rigida*
Hieracium Sect. *Vulgata*
Hypericum maculatum

Juncus filiformis
Juncus squarrosus
Knautia arvensis
Kobresia myosuroides
Lathyrus linifolius
Leontodon autumnalis
Leontodon hispidus
Leucanthemum vulgare
Linum catharticum
Listera cordata
Luzula campestris
Luzula multiflora ssp. *multiflora*
Luzula pilosa
Luzula sylvatica
Lycopodium annotinum
Maianthemum bifolium
Melampyrum pratense
Melampyrum sylvaticum
Melica nutans
Molinia caerulea
Myrica gale
Nardus stricta
Narthecium ossifragum
Orthilia secunda
Oxalis acetosella
Pedicularis sylvatica
Phegopteris connectilis
Picea abies
Plantago lanceolata
Platanthera bifolia
Poa pratensis
Polygonatum verticillatum
Populus tremula
Potentilla erecta
Prunella vulgaris
Pyrola minor
Pyrola rotundifolia
Quercus robur
Rhinanthus serotinus
Rubus saxatilis
Salix glauca
Salix lapponum
Salix repens
Scorzonera humilis
Sesleria caerulea
Sorbus aucuparia
Stellaria graminea
Succisa pratensis
Taraxacum Sect. *Spectabilia*
Trichophorum alpinu
Trichophorum caespitosum
Trientalis europaea
Trifolium pratense
Trifolium repens
Triglochin palustris

Trollius europaeus
Veronica chamaedrys
Veronica officinalis
Veronica spicata
Vicia cracca
Viola canina
Viola palustris
Viola riviniana

D. MOSS SPECIES THAT OCCUR WITH *P. ALBIDA*

Barbilophozia barbata
Barbilophozia floerkei
Barbilophozia lycopodioides
Bryum pseudotriquetrum
Chiloscyphus coadunatus
Chiloscyphus pallescens
Cirriphyllum piliferum
Dicranum fuscescens
Dicranum majus
Dicranum scoparium
Dicranum sp.
Hylocomiastrum umbratum
Hylocomium splendens
Hypnum cupressiforme
Lophozia ventricosa
Lophozia sp.
Mylia taylorii
Plagiochila asplenioides
Plagiomnium affine
Plagiomnium elatum
Plagiomnium sp.
Pleurozium schreberi
Polytrichum commune
Ptilidium ciliare
Ptilidium sp.
Ptilium crista-castrensis
Rhytidiadelphus loreus
Rhytidiadelphus squarrosus
Sanionia uncinata
Scapania sp.
Sphagnum cuspidatum
Sphagnum girgensohnii
Sphagnum imbricatum
Sphagnum riparium

E. LICHEN SPECIES THAT OCCUR WITH *P. ALBIDA*

Cladina arbuscula
Cladina rangiferina
Cladonia furcata
Cladonia sp.
Hypogymnia physodes
Peltigera praetextata
Peltigera rufescens