K.W. Dixon, S.P. Kell, R.L. Barrett and P.J. Cribb (eds) 2003. *Orchid Conservation*. pp. 137–158.

Chapter 8

DEMOGRAPHIC STUDIES AND LIFE-HISTORY STRATEGIES OF TEMPERATE TERRESTRIAL ORCHIDS AS A BASIS FOR CONSERVATION

Dennis F. Whigham
Smithsonian Environmental Research Center, Box. 28, Edgewater, MD 21037, USA.

Jo H. Willems
Plant Ecology Group, Utrecht University, PO Box 800.84, NL 3508 Utrecht, The Netherlands.

"Our knowledge about the lives of individual plants and of their persistence in plant communities is very incomplete, however, especially when perennial herbs are concerned" - C.O. Tamm, 1948.

Terrestrial orchids represent a wide diversity of species that are characterised by an equally diverse range of life history attributes. Threatened and endangered species of terrestrial orchids have been identif ed on all continents where they occur and conservation plans have been developed for some species. Even though there is a considerable amount of information on the ecology of terrestrial orchids, few species have been studied in detail and most management plans focus on habitat conservation. In this paper, we consider the diversity of terrestrial orchids and summarise information on threatened and endangered species from a global perspective. We also describe approaches to the conservation and restoration of terrestrial orchids and develop the argument that much information is needed if we are to successfully conserve this diverse group of plant species.

1. Introduction

Terrestrial orchids represent a wide variety of life history types, from autotrophic evergreen to completely myco-heterotrophic species that obtain most of their resources from a mycobiont. Life history characteristics of terrestrial orchids are generally well known (e.g. Dixon, 1991; Rasmussen, 1995) but detailed ecological data are available for relatively few species (e.g. Hutchings, 1987a; b; Inghe and Tamm, 1988; Mehrhoff, 1989b; Wells and Willems, 1991; Sieg and King, 1995; Gill, 1996; Hutchings, Mendoza and Havers, 1998; Primack and Stacy, 1998; Willems and Melser, 1998; Shefferson *et al.*, 2001; Kindlmann *et al.*, 2002). Most ecological studies have focused on pollination biology and, to a lesser degree, population dynamics. Few *in situ* ecological studies have considered the dynamics of seeds and protocorms, two important life history stages (Dixon, 1989; Johansen and Rasmussen, 1992; Rasmussen and Whigham, 1993; 1998a; Masuhara and

Katsuya, 1994; Perkins, Masuhara and McGee, 1995; Rasmussen, 1995; Stoutamire, 1996; Zelmer, Cuthbertson and Currah, 1996; Zettler, 1996; Peterson, Ueteke and Zelmer, 1998; McKendrick, Leake and Read, 2000; McKendrick *et al.*, 2000; Zettler *et al.*, 2001).

Successful conservation and management of terrestrial orchids are also impacted by the paucity of ecological information on life histories. Many terrestrial orchid species have declined in abundance; typically, declining populations are associated with human activities such as habitat loss and over-collection (Drayton and Primack, 1996; Arft and Ranker, 1998). Terrestrial orchids are also indirectly impacted by anthropogenic activities such as changing environmental conditions (Dijk and Eck, 1995; Dijk, Willems and van Andel, 1997) or changes in land management (Mehrhoff, 1989b; Seig and King, 1995; Parks and Wildlife Service Tasmania, 1998; Anonymous, 1999; Willems, 2002).

Terrestrial orchids are increasingly being listed as endangered (i.e. in danger of extinction) or threatened (i.e. likely to become endangered in the future) at national levels. For example, sixteen species of terrestrial orchids have been listed as endangered or threatened in the U.S. (USFWS, 2001) and Canada (COSEWIC, 2001). Endangered and threatened terrestrial orchids are conspicuous components of some national lists of threatened taxa. For example, terrestrial orchid genera comprise the largest family of plants designated as critically endangered for the orchid rich zone of south-west Western Australia (Atkins, 2001).

How are threatened and endangered orchids managed? In this chapter we attempt to discuss issues related to the conservation of terrestrial orchids and recommend future research that will benefit conservation efforts. We begin the paper with a description of the life history strategies found in terrestrial orchids to demonstrate that we have critical life history information for relatively few species.

2. Life-history classes in terrestrial orchids

Terrestrial orchid species comprise a wide variety of plant characteristics. The most striking developments have been the evolution of completely saprophytic protocorms in the early stages of germination and seedling development with some species that are saprophytic for their complete life cycle, some even remaining below-ground during their entire life cycles (Dixon and Pate, 1984; Dixon, Pate and Kuo, 1990). Well known and widely spread northern hemisphere saprophytes include *Neottia nidus-avis*, *Epipogium aphyllum, Corallorhiza trifida*, and *Limodorum abortivum*, all species which retain a strongly mycotrophic phase during their life cycle (Ziegenspeck, 1936; Rose, 1981). Most holo-mycotrophic orchid genera are represented by only a few species with the holo-mycotrophic habit having arisen throughout a number of phylogenetic lineages in the Orchidaceae, from the Diurideae to Cymbidieae (see Chase *et al.*, this volume). This pattern is in contrast to many genera (e.g. *Orchis* and *Ophrys*) of terrestrial orchids that include tens of species.

There is a large variety in underground organs among terrestrial orchids, e.g. several types of persisting rhizomes with roots or small bulb-like tubers, which may be either persistent or renewed yearly (Wells, 1981). Some species predominantly multiply by vegetative means (Dixon, Buirchell and Collins, 1989). *Hammarbya (Malaxis) paludosa*, for example, produces bulbils, a specialised form of vegetative reproduction (Kreutz and Dekker, 2000). Some species invest in clonal spread by producing plants at the end of rather long underground runners, e.g. *Herminium monorchis* and *Goodyera repens* (Grubb, 1990; Wells, 1994). Other species produce asexual corms or branching rhizomes, which eventually fragment into separate individuals (Kull, 1997).

The above-ground phase of terrestrial orchids is also highly variable and ranges from evergreen genera (e.g. *Goodyera*) to herbaceous perennial species which have leaves that are above-ground for only a short time, viz. in spring and early summer (e.g. *Listera ovata*, *Orchis purpurea*, and *Dactylorhiza fuchsii*). Still other species produce leaves early in the growing season and persist until freezing temperatures return (e.g. species of *Cypripedium*). Cool temperate wintergreen species such as *Spiranthes spiralis*, *Aceras anthropophorum*, and *Tipularia discolor* are above-ground for the greater part of the year, viz. 7-9 months (Wells, 1981; Whigham, 1984; Willems and Lahtinen, 1997). Many terrestrial orchids (e.g. *Galearis spectabilis*, *Cypripedium calceolus*) flower soon after emergence in the spring (Kull, 1987) but some genera have species that flower in mid-summer (e.g. *Goodyera*) or autumn (e.g. *Corallorhiza*). In *Leporella fimbriata* and *Genoplesium* spp. (Fig. 1) from the summer-dry mediterranean type climate of southern Australia, precocious flowering ensures that ripened seeds are produced in concert with breaking rains. In the Western Australian underground orchid (*Rhizanthella gardneri*), the seven month long seed maturation period is supported by the full period of winter rains prior to plant senescence in late spring.

Figure 1. *Leporella fimbriata* is a clonal species that releases seed mid-way through the growing season (L). *Genoplesium nigricans* is a precocious flowering and seeding species often completing both phases just prior to the start of the growing season (R). (Photos: M.C. Brundrett (L); G. Brockman (R))

Flowering in many orchids is determined by the resource status of plants, which in turn is influenced by habitat management, climatic conditions, or patterns of herbivory. Among wintergreen species, for example, there are important differences in timing and frequency of flowering. *Spiranthes spiralis* flowers in August-September and the number of flowering plants is largely determined by the plant's performance during the previous year. Plant performance is mostly determined by site management. For plants to flower, the sward has to be very low and open during the greater part of the above-ground phase of the species, enabling the plants to store sufficient carbohydrates to support the flowering stalk the next growing season (Willems, Balounova and Kindlmann, 2001). In contrast, flowering in *Aceras anthropophorum* takes place at the end of the above-ground phase of the plants, viz. in June, and is controlled primarily by environmental conditions (e.g. precipitation) during the same growing season, rather than habitat management (Wells, 1981). A significant number of terrestrial taxa from arid-tropical (*Eulophia bicallosa* from northern Australia) to dry mediterranean species (*Caladenia reptans, Leporella fimbriata*, *Leptoceras menziesii*, *Pyrorchis nigricans* (Fig. 2) and others) have highly synchronised flowering in the wet season following a fire.

The literature contains few data on the longevity of individuals in populations of terrestrial orchids. Tamm (1972) and Inghe and Tamm (1988) showed that individuals of some species live for several decades or even more than a century. Long-term population studies have also demonstrated that clonal and non-clonal species in *Cypripedium* can also be long-lived (Gill, 1996; Kull, 1997). Such life spans are in sharp contrast with short-lived species, such as *Ophrys sphegodes* with an average age of about 2 years (Hutchings, 1987a; b) and *Coeloglossum viride* (Fig. 2) of only 1.5 years (Willems and Melser, 1998). Long-term populations studies have also demonstrated that individuals can remain below-ground for several years, a situation that may be important in considering the rare, threatened, or endangered status of terrestrial orchids (Shefferson *et al.*, 2001; Willems, 2002). Also, little is known about the life-span of individual plants and their performance over time. Individuals of the long-lived Lady's tresses (*Spiranthes spiralis*) from northern Europe

Figure 2. *Pyrorchis nigricans* is a relatively long-lived, clonal species with prolific flowering following fire (L). *Coeloglossum viride* represents one of the shortest documented life-cycles in a terrestrial orchid of just 1.5 years (R). (Photos: R.L. Barrett (L); D.T. Ettlinger (R))

showed no decrease in seed production some 20 years after attaining flowering maturity for the first time (Willems and Dorland, 2000). Plant longevity data are of great importance in order to devise appropriate conservation measures. For short-lived species, yearly seed production is a prerequisite for their preservation, whereas for long-lived species, habitat management for survival of individual plants may be more important. Although detailed long-term studies are rather rare, provisional data suggest that both *r*- and *K*-strategists (*sensu* MacArthur and Wilson, 1967) can be distinguished in terrestrial orchids (Hutchings, 1989; Willems and Melser, 1998; Roberts, this volume).

The subterranean life phase (prior to the first appearance above-ground as an autotrophic plant) of terrestrial orchids is rarely investigated (Rasmussen, 1995; 2002). In spite of this, it is obvious from present knowledge that the duration of the underground phase varies from very short (a matter of months or less) to at least 15 years (Hutchings, 1989; Rasmussen, 1995; Wells, 1981). In *Orchis simia*, it was observed under field conditions that the duration of the protocorm stage (i.e. between seed germination and appearance of the first green leaves) lasted at least 3-4 years, whereas another 3 year period was required to achieve first flowering (Willems, 1982). The highly variable duration of the subterranean life phase needs to be carefully evaluated in the derivation of management measures at a given site and for particular species.

Pollination is another aspect that varies among terrestrial orchids in the temperate zone and is discussed in detail by Roberts (this volume). Successful pollination can result from autogamy or cleistogamy but most species require insects (i.e. entomogamy) for successful pollination. A large variety of insect pollinators have been identified and they can be attracted by either smell or shape of the flower, e.g. mimicking sexual partners for groups of insects like bees, bumble bees or flies (Darwin, 1888; Nilsson, 1992; van der Cingel, 1995). Pollinator limitation may be a factor influencing the geographical distribution of an orchid species, especially near the margins of distribution (Sipes and Tepedino, 1995).

3. Distribution, threats and status of terrestrial orchids

In this section, we review global patterns of taxonomic diversity among terrestrial orchids with an emphasis on the temperate zone, especially in Europe. We also consider the range of threats to terrestrial orchids and approaches that are used to identify and protect species that are threatened or endangered. The Orchidaceae comprises some 25,000 species that grow in various habitats, and with life forms ranging from underground to epiphytic. Most species occur in the tropics and subtropics, and an estimated 75-80% are epiphytic (A. Pridgeon, pers. comm.).

3.1 Canada and the United States

Canada and the U.S. have about 190 orchid species, including approximately 60 subtropical terrestrial and epiphytic species mainly restricted to Florida and nearby (Hágsater and Dumont, 1996). Many of the terrestrial genera in the U.S. and Canada are widespread and species diversity is lowest in arid areas such as the desert southwest and drier portions of the western mountains. Threats to orchids in the U.S. and Canada include widespread direct and indirect loss of habitat caused by expanding human activities and more localised activities such as pollution, over-collection, and threats from invasive species. More information on threatened and endangered terrestrial orchids in the U.S. and Canada is provided in section 5.

3.2 Australasia

Australasia, including Australia and New Zealand, has a rich and diverse orchid flora (Hágsater and Dumont, 1996). Terrestrial orchids are especially diverse in southwest Australia and Victoria, each with more than 300 taxa, many of them endemic (Dixon, 1989; Backhouse and Jeanes 1995; Hopper and Brown 2001). New Zealand has more than a hundred species with a number of intriguing contemporary rarities or 'vagrant' species believed to be recent, natural introductions from Australia (St George and McCrae, 1990). Threats to terrestrial orchids throughout Australasia include direct and indirect loss of habitat, over-collection and the widespread and pervasive impact of weeds, feral animals, salinisation, pests and diseases (Cropper, 1993; Dixon and Hopper 1996). Terrestrial orchids of conservation concern in Australia and New Zealand are listed in Table 1 below.

3.3 North Asia

North Asia (Siberia, Korean Peninsula, Ryukyu Islands, eastern part of mainland China) and Japan also have a rich orchid flora (Hágsater and Dumont, 1996) and most of the estimated 400 species are terrestrial. Geographically, the diversity of terrestrial orchids is high in Japan (approximately 225 species) compared to the Korean Peninsula (40 species). Only two species of terrestrial orchids (*Liparis elliptica*, *Cypripedium macranthos* var. *speciosum*) are nationally protected in Japan. China also has a diverse orchid flora and include horticulturally significant and ethnobotanical taxa which are threatened because of over-collection and illegal export (P. Cribb, pers. comm.).

3.4 Europe

Countries in Europe, North Africa, and the Near East have over 300 species of terrestrial orchids (Hágsater and Dumont, 1996). This region, including more than 50 countries, and represents a region of environmental complexity and includes habitats distributed over five floristic regions (mediterranean, sub-mediterranean, temperate, boreal, arctic). Many countries in the region share common genera and species, and a relatively large number of species are of conservation concern because of a long history of human impact, including extensive land clearing, grazing and ethnobotanical use. Many of the terrestrial orchids in this region have adapted to the wide range of human activities and conservation often involves active management (Reinhard *et al.*, 1991).

In 1992, a well-documented publication on the conservation of European orchids appeared as a report of the Council of Europe (Stewart, 1992). Approximately 200 species native to that area (at that time western Europe), had decreased, both in the number of recorded sites and population size. The primary cause for this decline was habitat degradation stemming from altered agricultural practices half a century earlier. Semi-natural habitats, with their rich and highly diverse orchid flora, have decreased over much of Europe. For example, in the United Kingdom only 5% of the traditional hay-lands survive, and chalk grasslands and natural or traditionally managed woodlands have decreased by 20% and 60%, respectively (Rackham, 1980; Stewart, 1992). Similar data can be obtained from other orchid habitats in the Mediterranean area, where the highest diversity of species is found. About 90% of the total number of European orchid species occur in the Mediterranean region, including species with spectacular pollination syndromes including a number of endemic species (Polunin and Walters, 1985). Noteworthy are the islands in the eastern part of the Mediterranean area, with calcareous soils, which support a very diverse orchid flora, including many endemic species. For example, on Cyprus, the easternmost island, 40 species of terrestrial orchids can be encountered, including 3 endemic species (Wood, 1985).

In many parts of Europe, the diversity of orchid species is related to the large variation in geomorphology, especially in limestone areas (Bournérias, 1998). In Cyprus, the highest peaks of the Troödos Mountains are almost 2,000 m; the island has as many native orchids as The Netherlands, even though it is only about a quarter of the size. Switzerland, with mountains of over 4,000 m has about 70 native orchids compared to 40 taxa in The Netherlands, a country of approximately the same size. Turkey has 148 orchid species (Kreutz, 1998) with wild orchid tubers and roots collected every year to produce "salep" which is used to flavour ice cream and as a drink. Some 60-100 tons of underground organs are "harvested" from natural populations (Voth, 1973; Kreutz, 1998). In particular, the genera *Anacamptis*, *Ophrys*, *Orchis*, *Serapias* and *Spiranthes* are collected (Stewart, 1992). The impact of this traditional extractive practice on the conservation status of the harvested species requires investigation.

Figure 3. Widespread habitat loss has resulted in *Liparis loeselii* (L) and *Hammarbya (Malaxis) paludosa* (R) becoming endangered in northern Europe. (Photos: RBG Kew)

Apart from locally threatened species, few terrestrial orchids are severely endangered in the majority of the 20 countries of the European Community. *Cypripedium calceolus*, *Hammarbya (Malaxis) paludosa,* and *Liparis loeselii* are noteworthy exceptions. *Cypripedium calceolus* is a species that was once widespread in Europe and occupied many different habitats. However, due to the large and attractive flowers, this species was a clear target for plant collectors and has been extirpated from smaller countries like Luxemburg and Belgium (De Langhe *et al.*, 1983; Bournérias, 1998) with a single wild plant in the United Kingdom (Wood, 1989; Stewart, 1992; Ramsey and Stewart, 1998). *Liparis loeselii* and *Hammarbya (Malaxis) paludosa* (Fig. 3), both species with inconspicuous flowers and existing mainly in northern European countries, are endangered by drainage and eutrophication of their wetland habitats, oligotrophic bogs and fens (Géhu and Wattez, 1971; Adema, 1985; Weeda, 1985; Stewart, 1992; Wheeler, Lambley and Geeson, 1998).

4. International and national standards for orchid conservation

Legislation for the conservation of terrestrial orchids exist in many countries and there are also international agreements regulating the trade in orchid species.

IUCN-The World Conservation Union is the leading international organisation devoted to the conservation of 'the integrity and diversity of nature'. IUCN actively encourages member states, agencies, non-government organisations, and affiliates to identify resources that are threatened and endangered.

The Species Survival Commission (SSC) is one of six volunteer commissions of IUCN, and consists of a network of 125 taxonomic and regional Specialist Groups. The Orchid Specialist Group of the SSC was established in 1984 and is an international network of professional and non-professional volunteers who are committed to the conservation and sustainable utilisation of orchid species and their habitats.

The IUCN Species Survival Commission maintains a Web site (IUCN, 2001) that can be used to search for information on threatened species. Currently, there are few orchid species listed; this does not, however, reflect current trends or our status of knowledge; rather it is the result of the implementation of a new Red Listing process using the revised criteria, which will involve several years of work for the Orchidaceae.

World trade in plants, including orchids, and animals is largely regulated by CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora). The Convention entered into force in 1975 and there are currently 152 Parties (CITES, 2001). In addition to CITES, many States have further legislation regulating trade in orchids, e.g. European regulations, as well as procedures for listing species requiring protection.

In the US, listing endangered or threatened species is mandated under the Endangered Species Act (1996). The US Fish and Wildlife Service currently lists 7 species of terrestrial orchids (Table 1), and one species (*Platanthera integrilabia)* is proposed for listing. Eight terrestrial orchids have been listed for Canada (Table 1) and two (*Isotria medeoloides*, *Platanthera praeclara*) are also on the US list. Australia and New Zealand are examples of two countries in the southern hemisphere that share common genera and have extensive legislative mechanisms for the protection of terrestrial orchids. Two genera (*Prasophyllum*, *Pterostylis*) have been listed in both Australia and New Zealand (Table 1) but the species differ. Australia has many listed species, most likely the result of a relatively high level of endemism and species diversity and a number of comprehensive modern treatments of the orchid flora compared to other countries listed in Table 1.

Almost all Red Data Lists of European countries contain a number of orchid species that require protection from habitat destruction or by abating the causes of decline by appropriate management measures. The British Red Data Book for vascular plants includes 14 orchid species, which is 28% of the total number listed (Perring and Farrell, 1983; Wood, 1989). Sometimes it is difficult, especially for non-botanists, to recognise protected species, especially for *Dactylorhiza* and *Ophrys*. Accordingly, Stewart (1992) recommended that governments put all native orchid species on the Red Data List to avoid difficulties with identification of the species, whether or not they are protected (Ludwig and Schnittler, 1996). This has already been realised in The Netherlands, where all 38 species are protected by law; although two, *Listera ovata* and *Epipactis helleborine*, are neither threatened nor rare in the country. Most countries in northern Europe have regulations to protect terrestrial orchids and in some countries the percentage of terrestrials that are protected is quite high. In Norway, for example, 49% of the 39 terrestrial orchid species have protected status. The 1979 Convention on the Conservation of European Wildlife and Natural Habitats (Berne Convention) also provides a mechanism for protecting terrestrial orchids; however, among the 119 plant species listed, there is only one orchid species, viz. *Ophrys kotschyi* (Table 1), one of three endemic orchids from Cyprus (Stewart, 1992).

5. Management of terrestrial orchids

5.1 Approaches to management in Europe and the United States

In the previous section, we demonstrated that considerable effort has been made in some parts or the world to identify terrestrial orchids that are threatened or endangered. How are species of threatened terrestrial orchids managed, and is ecological information used in the development of management plans?

Terrestrial orchids typically become the focus of conservation efforts following documentation that populations have been reduced to the point where extirpation is a distinct possibility. The typical action plan for conservation of terrestrial orchids involves protection of remaining populations through habitat management. Ecological studies, however, are usually initiated only after recognition that a species has declined and there are concerns about extinction or the loss of genetic variability (e.g. Hutchings, 1987a; Mehrhoff, 1989a; b; Farrell, 1991; Sipes and Tepedino, 1995; Sun, 1996; Arft and Ranker, 1998; Willems and Melser, 1998).

In Europe, active means of vegetation management are often used to sustain and increase populations of terrestrial orchids. Many European species occur in grasslands or wetlands and populations decline following invasion of woody species or following changes in grazing and mowing practices. For example, Willems (1989) found that populations of the endangered *Spiranthes spiralis* (Fig. 4) decreased dramatically in the Limburg area of the Netherlands from about 50 sites before 1950 to only one site at present. The decline of this species was the direct result of increased shading following grassland abandonment. Reintroduction of grazing and removal of invading woody species has led to an increase in population size of *S. spiralis*. *Ophrys sphegodes*, a rare species in the United Kingdom, is also sensitive to shading (Hutchings, 1987a), and habitat management is essential to sustain the remaining populations. In the case of *O. sphegodes*, however, care must be taken in determining which animals are used in management, as sheep are beneficial while cattle grazing is detrimental (Waite and Hutchings, 1991).

In the US, management plans are developed for endangered species that have been officially recognised under the Endangered Species Act. *Isotria medeoloides*, a terrestrial orchid in eastern North America, was listed as an endangered species in 1982 and the status was changed to threatened in 1994 because the number of known populations had increased significantly (e.g. Sperduto and Congalton, 1996). A national recovery plan was developed for *I. medeoloides* (von Oettingen, 1992) based, in part, on results of ecological studies. Mehrhoff (1989a; b) examined several populations of *I. medeoloides* and found that it is a mid-successional species that declines in response to increased shading and competition from surrounding plants. Mehrhoff (1989a) suggested that it would not be possible to conserve populations of *I. medeoloides* by site acquisition alone, but that active site management would be required. Some populations of *I. medeoloides* have been protected by site-

Figure 4. *Spiranthes spiralis* is endangered in the Netherlands where grazing or mowing is required to ensure that plants are not over-shaded. (Photos: P.J. Cribb (L); J. Delamain (R))

specific purchases but the long-term viability of the species is not assured because populations on private land could be lost to development or negatively impacted by logging (NatureServe, 2001).

Like *Isotria medeoloides, Platanthera praeclara* is an endangered North American species that had declined substantially before ecological studies had been initiated. *Platanthera praeclara* was originally common in wetland habitats throughout much of the tallgrass prairie, but conversion of native grassland to agricultural production reduced the species distribution to areas in Minnesota and North Dakota in the U.S., and Manitoba in Canada (Sieg and King, 1995). A Recovery Plan was developed for the species in 1996 (USFWS, 2002) and detailed Management Guidelines were written for a population in the Sheyenne National Grassland in North Dakota (Anon., 1999). The Management Guidelines were based on a metapopulation approach using life history and population data published by Sieg and King (1995). One goal of the Management Guidelines was to establish core areas that would be managed to protect plants during their period of reproduction (late April to mid-September). The population size of *P. praeclara* has increased substantially in the Sheyenne National Grassland. While management, especially autumn burning, seems to have had a significant and positive impact, much of the success may be due to changing weather conditions (B. Stotts, pers. comm.). The Sheyenne population declined during a drought in the 1980s and in the 1990s, a period of high precipitation, has increased just as rapidly as the previous decline occurred.

In the U.S., there are also examples of management plans that have been developed for species that have not been given national protection. Similar to management plans for species given national recognition, the three examples of regional management plants that we present were each developed with little ecological knowledge. The Bureau of Land Management (BLM) manages extensive areas in the western U.S. and they are required to develop management plans for species of conservation concern that occur on lands that they manage. Three terrestrial orchids of conservation concern (*Cypripedium fasciculatum*, *C. montanum*, *Platanthera orbiculata*) occur

Table 1. Threatened and endangered species of terrestrial orchids in two countries in the northern hemisphere (US and Canada), Europe, and two countries in the southern hemisphere (Australia and New Zealand). Sources of information are: US (USFWS, 2001) Canada (COSEWIC, 2001), New Zealand (HOS, 2001), Australia (ANOS, 2001). Status (refer to Web sites for each country for definitions): Critical = C, Endangered = EN, Extinct = EX, Special Concern = SC, Threatened = T, Vulnerable = V.

Species	Status	Country
Bulbophyllum globuliforme	V	Australia
Caladenia arenaria	EN	Australia
Caladenia concolor	EN	Australia
Caladenia rosella	EN	Australia
Caladenia tessellata	V	Australia
Cephalanthera austiniae	SC	Canada
Chiloglottis formicifera	EX	New Zealand
Cryptostylis hunteriana	V	Australia
Cypripedium candidum	EN	Canada
Diuris aequalis	V	Australia
Diuris arenaria	EN	Australia
Diuris disposita	EN	Australia
Diuris flavescens	EN	Australia
Diuris pedunculata	EN	Australia
Diuris praecox	V	Australia
Diuris shaeffiana	V	Australia
Diuris venosa	V	Australia
Epipactis gigantea	SC	Canada
Genoplesium plumosum	EN	Australia
Genoplesium rhyoliticum	EN	Australia
Isotria medeoloides	EN	United States, Canada
Liparis liliifolia	EN	Canada
Microtis angusii	EN	Australia
Ophrys kotschyi	EN	Europe
Phaius australis	EN	Australia
Phaius tankervilleae	EN	Australia
Platanthera leucophaea	T (US), SC (Canada)	United States, Canada
Platanthera praeclara	T (US), EN (Canada)	United States, Canada
Platanthera holochila	EN	United States
Prasophyllum affine	EN	Australia
Prasophyllum aff. *patens*	V	New Zealand
Prasophyllum fuscum	V	Australia
Prasophyllum morganii	V	Australia
Prasophyllum petilum	EN	Australia
Prasophyllum uroglossum	EN	Australia
Pterostylis cobarensis	V	Australia
Pterostylis cucullata	V	Australia
Pterostylis micromega	T	New Zealand
Pterostylis nigricans	V	Australia
Pterostylis nutans	EX	New Zealand
Pterostylis pulchella	V	Australia
Pterostylis gibbosa	EN	Australia
Pterostylis saxicola	EN	Australia
Pterostylis sp. Botany Bay	EN	Australia

Table 1. continued.

Species	Status	Country
Sarcochilus hartmannii	V	Australia
Sarcochilus weinthalii	V	Australia
Spiranthes delitescens	EN	United States
Spiranthes diluvialis	T	United States
Spiranthes parksii	EN	United States
Thelymitra matthewsii	C	New Zealand
Triphora trianthophora	EN	Canada

in BLM lands in California, Oregon and Washington. *Cypripedium fasciculatum* and *C. montanum* have many features in common and management recommendations are very similar. Both have been identified as species of conservation concern and both species have long-lived individuals in forests over a wide range of altitudes (300-2,150 m). The greatest threat to both species appears to be the loss of small isolated populations through activities that disturb the soil and litter layers, or decrease canopy cover below 60% (Seevers and Lang, 1998a; b). To our knowledge, there have not been any detailed population studies of either species, and knowledge about their ecology and biology is limited (Seevers and Lang, 1998a; b). Given the lack of knowledge about the species, suggested management plans focus on avoidance of large-scale and intense anthropogenic activities that would negatively impact existing populations. The management recommendation documents for both species, not surprisingly, contain long lists of research questions and gaps in information. There are no data, for example, on the level of disturbance that plants can sustain before they die. There have not been any published studies of the mycobionts, pollinators, or ecological requirements of various life cycle stages (e.g. seeds to protocorms) for either species.

More taxonomic and ecological information is available for *Platanthera orbiculata*, a species that is more common and widespread in eastern North America (Currah, Smreciu and Hambleton, 1990; Reddoch and Reddoch, 1993). In the western U.S., it is also more common than *Cypripedium fasciculatum* and *C. montanum* (Lesher and Henderson, 1998). Management recommendations for *P. orbiculata* were developed because it has a limited distribution on the western slopes of the Cascade Mountains and it is rare in some locations. Additionally, populations tend to be small and the species may be vulnerable to herbivory (Lesher and Henderson, 1998). Compared with the other two species, management recommendations for *P. orbiculata* focus mostly on avoiding the use of herbicides that might affect pollinators, and management of forested landscapes. The plan included recommendations that the status of the species be assessed in areas that have been proposed for land conversion (i.e. logging), and that conservation plans be developed for areas in which the species occurs. Recommendations in the plan mostly focus on the management of forested landscapes to include stands in all ages of succession, thus increasing the possibility that some populations of the orchid will be able to persist.

With the exception of *Isotria medeoloides*, all the examples that we have provided for terrestrial orchids in the U.S. demonstrate that management decisions were made with minimal ecological information on population dynamics, habitat requirements, and basic life history data. It is also noteworthy that none of the management plans described in this section included plans to restore species through the introduction of seeds, protocorms, or fungi required by the orchids. The assumption for all management plans was that habitat protection and management were the first levels of defence to avoid extinction. Management plans were also based on the assumption that species would be able to recover naturally if populations were protected.

5.2 Effectiveness of management plans

Bearing in mind that current management plans are often developed with little knowledge about species ecology, have they resulted in increases in the number of populations, the number of individuals within populations, and in the genetic diversity of the species being managed? Most management plans dedicated to orchid conservation are relatively recent (<15 years) and it is probably too early to determine if the habitat approach to management has been successful in releasing species from the threat of extirpation. In some instances, habitat-environmental interactions may be very complex and it will be difficult to develop suitable management plans without additional long-term population studies (e.g. Sieg and King, 1995). There are, however, a few success stories. *Platanthera praeclara* has increased substantially at a North Dakota site due to a combination of effective management of grazing and a natural shift to wetter climatic conditions. Others are *Coeloglossum viride* and *Spiranthes spiralis* which, in the Netherlands, have benefited from management plans that controlled the timing of mowing, removal of the mowed biomass, and eliminated application of fertiliser (Willems and Lahtinen, 1997; Willems and Melser, 1998). Restriction of sheep grazing to winter periods has also benefited *Ophrys sphegodes*, a rare terrestrial orchid in the United Kingdom (Hutchings, 1987a).

Research-based management has lead to the stabilisation and restoration of populations in 10 out of 32 endangered orchid species in northern Switzerland. This has led to the introduction of the so-called Blue List in Switzerland (Gigon *et al.*, 2000) which contains a number of orchid species no longer threatened and able to be removed from the Red List. The Blue List clearly demonstrates that conservation successes result from the application of appropriate management practices, and reinforces to the general public that biodiversity can be successfully sustained.

We expect that there have been other success stories related to habitat management but most of them probably do not result in readily accessible publications. If habitat management is the best approach available given limitations on ecological information, what role can population, ecological, and genetic studies play in increasing the chances that threatened and endangered species will survive and flourish? Also, can management of terrestrial orchids benefit from studies of orchid-mycorrhiza interactions?

6. Augmentation of conservation efforts

6.1 Population studies

Population monitoring is an essential element of studies of threatened and endangered terrestrial orchids. Without an adequate monitoring program, it would not be possible to follow the responses of populations to natural and anthropogenic changes to their habitats. Population studies are also important because they are required to elicit patterns and processes that are easily overlooked. For example, naturalists have known for decades that there is annual variability in the numbers of flowering plants in orchid populations and many long-term data sets on flowering exist, e.g. 20 successive years of monitoring *Spiranthes spiralis* in Germany (Salkowski, 1990) and almost 60 years for *Anacamptis pyramidalis* in The Netherlands (Kreutz and Dekker, 2000). Efforts have been made to link the yearly fluctuating numbers of flowering plants with external and environmental factors, e.g. variation in climatic conditions. However, such long-term data series on flowering contribute little to an understanding of population dynamics as many individuals, probably the majority, do not flower regularly and individuals may not appear above-ground annually.

Irregular flowering of some orchid species was the incentive for an investigation, started in 1942, designed to follow the fate of individual plants in permanently marked plots in Sweden (Tamm, 1948; 1991). One of Tamm's research questions was whether non-flowering plants were absent or present above-ground. Tamm monitored yearly populations of different herbs, including some orchids, for several decades, and expressed the results in conveniently arranged life line diagrams. From these figures, not only the fate of individuals became clear (e.g. flowering frequency), but also important population characteristics, such as recruitment, flowering percentage and mortality. The ability of individuals to persist below-ground for one or more years was first shown by Tamm (1948).

Wells (1967) also found this pattern during a monitoring study of individuals of *Spiranthes spiralis*. Long-term monitoring in combination with phenological observations of the whole plant, including the underground parts, revealed new information on population dynamics of terrestrial orchids. Wells and others have demonstrated that the percentage of temporarily absent aerial plants can account for >50% of the total population (e.g. Wells, 1981; 1994; Willems and Bik, 1991). It is now widely recognised that individual plants can remain dormant for one or more years (Hutchings, 1987a; Mehrhoff, 1989b; Gill, 1996; Hutchings, Mendoza and Havers, 1998; Willems and Melser, 1998) even though the causes of dormancy are not understood.

A recent paper by Shefferson *et al.* (2001) demonstrates the importance of obtaining data on individual plants from long-term monitoring studies. They monitored *Cypripedium calceolus* ssp. *parviflorum (C. parviflorum)*, an endangered species in most states in the U.S. where it occurs, in eight patches for five years and applied mark-recapture statistics to estimate annual probabilities of dormancy. Their results showed that dormancy was influenced by spring frost days, precipitation, and mean spring temperatures. They also demonstrated that dormancy patterns differed among patches, a finding that suggests the importance of monitoring more than one patch or population.

Population monitoring data can also be used to develop survivorship curves of plant cohorts, thus estimating the longevity of individuals, and to develop age structure diagrams of populations; the latter being an important tool to gain insight into population performance (Willems and Bik, 1991; Vakhrameeva and Tatarenko, 1998; Tali, 2002). Population monitoring is also useful for other reasons. The impacts of altering management practices or changing climatic conditions can be analysed through the use of transition matrix models that simulate population processes (Waite, 1989; Gregg, 1991; Waite and Hutchings, 1991). Matrix models are considered more extensively by Tremblay and Hutchings (this volume).

6.2 Genetic studies

The genetic diversity of rare and threatened species has been recognised to be important because small and isolated populations either have or potentially have limited genetic diversity (Karron, 1991). Patterns of genetic diversity in rare and threatened terrestrial orchids, however, remain virtually unknown, as few species have been studied (e.g. Arft and Ranker, 1998; Ehlers and Pedersen, 2000; Sun, 1996; 1997; Wong and Sun, 1999). The few studies that have been carried out suggest that general patterns are not likely to be easily identified and that management for purposes of conserving or increasing genetic diversity is likely to require information about each species of concern. The following examples demonstrate the possible range of patterns of genetic diversity among terrestrial orchid species. The same studies also demonstrate that genetic studies, and other studies of reproductive biology, can provide valuable information for development of management strategies.

Individual populations of *Spiranthes diluvialis*, a rare allopolyploid species in western North America, were shown to contain most of the within-species genetic variability and a high degree of inter-population gene flow was also suggested (Arft and Ranker, 1998). Sipes and Tepedino (1995) found that species of *Bombus* were required for pollination of *S. diluvialis*. These two studies of *S. diluvialis* collectively demonstrate that species conservation should be based on habitat management with multiple goals. In addition to direct protection of orchid habitat, management activities need to assure that the primary pollinator has adequate ecological protection and that *S. diluvialis* habitats should have a high diversity of flowering species to meet the energetic and nutritional requirements of the pollinator.

Genetic studies of terrestrial orchids in Hong Kong also offer guidance for conservation and management (Sun, 1996; 1997; Wong and Sun, 1999). Sun (1997) found low levels of within and between population genetic diversity in three common colonising species of terrestrial orchids (*Eulophia sinensis*, *Spiranthes hongkongensis* (= *S. sinensis*), *Zeuxine strateumatica*) with very different life history strategies. Sun and colleagues also examined two rare species (*Spiranthes sinensis*, *Goodyera procera*) and found differing genetic patterns (Sun, 1996; Wong and Sun, 1999). *Goodyera procera* had low levels of genetic diversity and limited gene flow between populations. In contrast, *Spiranthes sinensis* had high levels of genetic variation but the amount of genetic diversity within a population was less in smaller populations (Sun, 1996). Sun suggested that genetic diversity of *Spiranthes sinensis* could be conserved by protection of large and small populations. Small populations are important because they are genetically distinct from one another, and their conservation has the potential to preserve the most genetic diversity, including rare alleles.

6.3 Re-establishment of rare and threatened species

Habitat management has the potential to maintain and enhance populations of threatened and endangered terrestrial orchids (e.g. Hutchings, 1987a; Farrell, 1991; Willems and Lahtinen, 1997; Willems and Melser, 1998). Until recently, very little attention has been given to development of techniques that can be used to reintroduce plants into native or restored habitats, even though considerable success has been made germinating seeds and growing and propagating terrestrial orchids symbiotically (Clements and Ellyard, 1979; Rasmussen, 1995; Allen, 1996). Terrestrial orchids potentially could be reintroduced as seeds, protocorms, seedlings, or juvenile and adult plants and recent research is demonstrating the value of artificial processes in orchid establishment and conservation (Dixon, 1989). We now consider these life history stages in the context of reintroduction of terrestrial orchids into native or restored habitats.

With the exception of studies of Australian terrestrial orchids (Batty, Dixon and Sivasithamparam, 2000; Batty *et al.*, 2001; 2002), seeds and protocorms have been difficult to work with *in situ*. The development of *in situ* techniques to retain orchid seeds and protocorms in mesh bags offers considerable promise for understanding the dynamics of early life history stages (e.g. Rasmussen and Whigham, 1993). The technique, which involves placing seeds into small mesh-nylon netting which is secured in a plastic slide that can be placed into the soil (Rasmussen and Whigham, 1993), can be used to examine spatial patterns of germination (Masuhara and Katsuya, 1994; Rasmussen and Whigham, 1998b; McKendrick *et al.*, 2000; Batty *et al.*, 2001). The technique can also be used as a source of protocorms from which mycorrhiza can be isolated and identified (Masuhara and Katsuya, 1994; Perkins and McGee, 1995; Zelmer, Cuthbertson and Currah, 1996; McKendrick, Leake and Read, 2000; McKendrick *et al.*, 2000). Spatial patterns of fungal distribution can also be evaluated using this technique (Masuhara and Katsuya, 1994, McKendrick *et al.*, 2000; Batty *et al.*, 2001; Whigham et al., 2002) and it potentially can be used to reintroduce orchid-fungi into native and restored habitats. Publications by McKendrick and colleagues (McKendrick, Leake and Read, 2000; McKendrick *et al.*, 2000) are especially noteworthy because they demonstrate how effectively the slide frames technique can be applied. They evaluated three-way interactions between orchids, orchid-fungi, and other green plants. They demonstrated that *Corallorhiza trifida* protocorms developed ectomycorrhizal relationships with *Betula pendula* and *Salix repens* but not with *Pinus sylvestris*. This type of information could prove invaluable when restoration requires successful establishment of orchids and their ectomycorrhizal hosts.

Laboratory studies also provide useful information on approaches that can be used to artificially propagate threatened and endangered terrestrial orchids prior to planting them into native or restored habitats (Batty *et al.*, 2002; Debeljak *et al.*, 2002). Zettler *et al.* (2001) were able to successfully germinate seeds of *Platanthera leucophaea* following stratification and exposure to fungi collected from adult plants of the orchid. They grew protocorms infected with mycorrhiza into leaf-bearing seedlings that could potentially be reintroduced into native habitats. Zettler and colleagues also found a wide range of germination responses when they exposed seeds from different source plants to two of the mycorrhiza that they had isolated. Anderson (1996) successfully transplanted laboratory grown *Platanthera ciliaris* into the field. These two studies support the results of other investigators by demonstrating that it is important to conduct detailed studies of each orchid species and its attendant mycobiont.

Some orchid-mycorrhiza interactions are very specific (e.g. Warcup, 1981) while in other instances fungi may support seed germination but not protocorm growth (e.g. Masuhara and Katsuya, 1994). Ongoing research in our laboratory at the Smithsonian demonstrates that *Liparis liliifolia* germination and protocorm growth is supported by one fungus over the sampled range of distribution of the orchid (unpublished data). In contrast, germination and protocorm growth of *Goodyera pubescens* are supported by a range of fungal types.

The general consensus of most authors is that restoration by transplanting adult plants is not desirable, especially for threatened and endangered species that typically have small populations with few individuals. In addition, it is now illegal to collect terrestrial orchids in many countries. For many species, transplanting individuals that have been grown from seeds offers greater possibilities, especially when the seeds are germinated symbiotically and plants develop appropriate mycorrhizas (Anderson, 1996; Zettler *et al.*, 2001) or when they are sufficiently mature to have less stringent mycorrhizal requirements (Malmgren, 1996). A web page authored by Marilyn Light (Light, 1998) and papers in Allen (1996) offer interesting commentaries on the propagation of terrestrial orchids in the northern hemisphere.

7. Conclusions

Terrestrial orchids represent a widespread group of plants that have attracted considerable interest from a conservation perspective. Terrestrial orchids encompass a wide range of life history strategies and have a relationship with fungi that is unique in the plant kingdom. Adult orchids almost always have mycorrhiza but some species can survive without mycorrhiza. Many species have become rare, threatened or endangered and international rules and regulations have been developed to protect them. Many species of terrestrial orchids are endangered because of direct and indirect changes in habitat, or exploitation by plant collectors. Few species have been studied in detail; long-term studies of the demographics of individual plants are especially lacking and there is even less information on the importance of orchid-fungal interactions. The lack of detailed ecological information of terrestrial orchids has precluded specific management strategies. Most management strategies thus are focused less on the ecological and biological requirements of the endangered species and more on habitat management. Habitat management appears to be a viable approach for the conservation and reestablishment of threatened and endangered terrestrial orchids but other information is needed if management outcomes are to be interpreted in an ecological sense. Management of terrestrial orchids would especially benefit by additional long-term population studies, studies of the genetic characteristics of populations, experiments and studies of orchid-fungal interactions, and studies of plant-pollinator interactions.

Acknowledgements

The authors would like to recognise Jay O'Neill, Melissa McCormick and Dan Sloan for helpful comments on earlier drafts of the manuscript. Terrestrial orchid research in one of our laboratories (DFW) has been supported by the Environmental Sciences Program and Scholarly Studies programs of the Smithsonian Institution. The contributions of Hanne Rasmussen, Bruce Caldwell and Tim Daniell to the Smithsonian efforts are greatly appreciated.

Literature cited

Adema, F. (1985). *Hammarbya paludosa* (L.) O.Kuntze. In Mennema, J., Quené-Boterenbrood, A.J. and Plate, C.L. eds. *Atlas van de Nederlandse flora 2. Zeldzame en vrij zeldzame planten*. pp. 166. Bohn, Scheltema & Holkema, Utrecht.

Allen, C. (ed.) (1996). *North American native terrestrial orchids - propagation and production*. The North American Native Orchid Alliance, Germantown, MD.

Anderson, A.B. (1996). The reintroduction of *Platanthera ciliaris* in Canada. In Allen, C. ed. *North American native terrestrial orchids - propagation and production*. pp. 73–76. The North American Native Terrestrial Orchid Conference, Germantown, MD.

Anonymous. (1999). Management guidelines for the Western Prairie fringed orchid on the Sheyenne National Grassland, Dakota Prairie Grasslands. http://www.fs.fed.us/r2/nebraska/gpng/orchid_guide.html

Arft, A.M. and Ranker, T.A. (1998). Allopolyploid origin and population genetics of the rare orchid *Spiranthes diluvialis*. *American Journal of Botany* **85**: 110–122.

Atkins, K.J. (2001). *Declared rare and priority flora list*. Department of Conservation and Land Management, Como.

Australian Native Orchid Society (ANOS) (2001). http://www.anos.org.au/conservation/conservationframe.html

Backhouse, G.N. and Jeanes, J.A. (1995). *The orchids of Victoria*. Melbourne University Press, Carlton.

Batty, A.L., Dixon, K.W. and Sivasithamparam, K. (2000). Soil seed bank dynamics of terrestrial orchids. *Lindleyana* **15**: 227–236.

____, _____, Brundrett, M.C. and Sivasithamparam, K. (2001). Constraints to symbiotic germination of terrestrial orchid seed in a mediterranean bushland. *New Phytologist* **152**: 511–520.

_____, _____. _____, and _____. (2002). Orchid conservation and mycorrhizal associations. In: Sivasithamparam, K., Dixon, K.W. and Barrett, R.L. eds. *Microorganisms in plant conservation and biodiversity*. pp. 195-226. Kluwer Academic Publishers, Dordrecht.

Bournérias, M. (1998). *Les orchidées de France, Belgique et Luxembourg*. Parthénope Collection, Montpellier.

Chase, M.W., Cameron, K.M., Barrett, R.L. and Freudenstein, J.V. (2003). DNA data and Orchidaceae systematics: a new phylogenetic classification. In Dixon, K.W., Kell, S.P., Barrett, R.L. and Cribb, P.J. eds. *Orchid conservation*. pp. 69–89. Natural History Publications, Kota Kinabalu, Sabah.

Clements, M.A. and Ellyard, R.K. (1979). The symbiotic germination of Australian terrestrial orchids. *American Orchid Society Bulletin* **48**: 810–816.

Convention on International Trade in Endagered Species of Wild Fauna and Flora (CITES) (2001). http://www.cites.org/CITES/eng/index.html

Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (2001). http://www.cosewic.gc.ca

Cropper, S.C. (1993). *Managment of endangered plants*. CSIRO, East Melbourne, Victoria.

Currah, R.S., Smreciu, E.A. and Hambleton, S. (1990). Mycorrhiza and mycorrhizal fungi of boreal species of *Platanthera* and *Coeloglossum* (Orchidaceae). *Canadian Journal of Botany* **68**: 1171–1181.

Darwin, C. (1888). *Fertilisation of orchids: The various contrivances by which orchids are fertilised by insects*. 2nd edn. Murray, London.

Debeljak, N., Dixon, K.W., Regvar, M. and Sivasithamparam, K. (2002). The effects of sucrose, jasmonic acid and paclobutrazol on tuber formation in an Australian terrestrial orchid *Pterostylis sanguinea*. *Plant Growth Regulation* **36**: 253–260.

De Langhe, J.E., Delvosalle, L., Duvigneaud, J. Lambino, J. and Vandenberghen, C. (1983). *Flora van België, het Groothertogdom Luxemburg, noord-Frankrijk en de aangrenzende gebieden*. Nationale Plantentuin van België, Meise-Brussel.

Dijk, E. and Eck, N.D. (1995). Effects of mycorrhizal fungi on *in vitro* nitrogen response of some Dutch indigenous orchid species. *Canadian Journal of Botany* **73**: 1203–1211.

_____, Willems, J.H. and van Andel, J. (1997). Nutrient responses as a key factor to the ecology of orchid species. *Acta Botanica Neerlandica* **46**: 339–363.

Dixon, K.W. (1989). Seed propagation of ground orchids. In Dixon, K.W., Buirchell, B.J. and Collins, M.T. eds. *Orchids of Western Australia*. pp. 18–26. Western Australian Native Orchid Study and Conservation Group Inc., Victoria Park.

_____ (1991). Seeder/clonal concepts in Western Australian orchids. In Wells, T.C.E. and Willems, J.H. eds. *Population ecology of terrestrial orchids*. pp. 111–124. SPB Academic Publishing, The Hague.

_____, Buirchell, B.J. and Collins, M.T. (eds) (1989). *Orchids of Western Australia*. Western Australian Native Orchid Study and Conservation Group Inc., Victoria Park.

_____ and Hopper, S.D. (1996). Australia. In Hágsater, E. and Dumont, V. eds. *Orchids – status, survey and conservation action plan*. pp. 109–115. IUCN, Gland and Cambridge.

_____ and Pate, J.S. (1984). Biology and distributional status of *Rhizanthella gardneri* Rogers (Orchidaceae), the Western Australian underground orchid. *Kings Park Research Notes* **9**: 1–54.

_____, _____ and Kuo, J. (1990). The Western Australian fully subterranean orchid *Rhizanthella gardneri*. In Arditti, J. ed. *Orchid biology reviews and perspectives, V*. pp. 37–62. Timber Press, Portland, Oregon.

Drayton, B. and Primack, R.B. (1996). Plant species lost in an isolated conservation area in metropolitan Boston from 1894-1993. *Conservation Biology* **10**: 30–39.

Ehlers, B.K. and Pedersen, H.Æ. (2000). Genetic variation in three species of *Epipactis* (Orchidaceae): geographic scale and evolutionary inferences. *Biological Journal of the Linnean Society* **69**: 411–430.

Farrell, L. (1991). Population changes and management of *Orchis militaris* at two sites in England. In Wells, T.C.E. and Willems, J.H. eds. *Population ecology of terrestrial orchids*. pp. 63–68. SPB Academic Publishing bv, The Hague.

Géhu, J.M. and Wattez, J.R. (1971). *Liparis loeselii* (L.) Rich. Dans le Nord de la France; ses stations anciennes et son maintien actuel. *Bulletin de la Société Botanique de France* **118**: 801–812.

Gigon, A., Langenauer, R., Meier, C. and Nievergelt, B. (2000). Blue lists of threatened species with stabilized or increasing abundance: a new instrument for conservation. *Conservation Biology* **14**: 402–413.

Gill, D.E. (1996). The natural population ecology of temperate terrestrials: pink lady's-slippers, *Cypripedium acaule*. In Allen, C. ed. *North American native terrestrial orchids - propagation and production*. pp. 91–106. The North American Native Orchid Alliance, Germantown.

Gregg, K.B. (1991). Reproductive strategy of *Cleistes divaricata* (Orchidaceae). *American Journal of Botany* **78**: 350–360.

Grubb, P.J. (1990). Demographic studies on the perennials in chalk grassland. In Hillier, S.H., Walton, D.W.H. and Wells, D.A. eds. *Calcareous grasslands. Ecology and management*. pp. 93–99. Bluntisham Books, Bluntisham.

Hágsater, E. and Dumont, V. (eds) (1996). *Orchids – status, survey and conservation action plan*. IUCN, Gland and Cambridge.

Hardy Orchid Society (HOS) (2001). http://www.drover.demon.co.uk/HOS

Hopper, S.D. and Brown, A.P. (2001). Contributions to Western Australian orchidology: 2. New taxa and circumscriptions in *Caladenia* (spider, fairy and dragon orchids of Western Australia). *Nuytsia* **14**: 27–314.

Hutchings, M.J. (1987a). The population biology of the early spider orchid, *Ophrys shegodes* Mill. I. a demographic study from 1975 to 1984. *Journal of Ecology* **75**: 711–727.

_____. (1987b). The population biology of the early spider orchid, *Ophrys sphegodes* Mill. II. Temporal patterns in behaviour. *Journal of Ecology* **75**: 729–742.

_____. (1989). Population biology and conservation of *Ophrys sphegodes* Mill. pp. 101–116 in Pritchard, H.W. ed. *Modern methods in orchid conservation. The role of physiology, ecology and management.* Cambridge University Press, Cambridge.

_____, Mendoza, A. and Havers, W. (1998). Demographic properties of an outlier population of *Orchis militaris* L. (Orchidaceae) in England. *Botanical Journal of the Linnean Society* **126**: 95–107.

Inghe, O. and Tamm, C.O. (1988). Survival and flowering of perennial herbs. V. Patterns of flowering. *Oikos* **51**: 203–219.

IUCN, The World Conservation Union (2001). Redlist of threatened species. http://www.redlist.org

Johansen, B. and Rasmussen, H.N. (1992). *Ex situ* conservations of orchids. *Opera Botanica* **113**: 43–48.

Karron, J.D. (1991). Patterns of genetic variation and breeding systems in rare plant species. In Falk, D.A. and Holsinger, K.E. eds. *Genetics and conservation of rare plants*. pp. 87–98. Oxford University Press, New York.

Kindlmann, P., Willems, J.H. and Whigham, D.F. (eds) (2002). *Trends and fluctuations and underlying mechanisms in terrestrial orchid populations.* Backhuys Publishers, Leiden.

Kreutz, C.A.J. (1998). *Die orchideen der Türkey*. Beschreibing, Öcologie, Verbreitung, gefährdung, Schutz. Selbstverlag, Landgraaf-Raalte.

_____ and Dekker, H. (2000). *De orchideeën van Nederland*. Ecologie, verspreiding, bedreiging, beheer. B.J. Seckel & C.A.J. Kreutz, Raalte-Landgraaf.

Kull, T. (1987). Population ecology of *Cypripedium calceolus* L. In Laasimer, L. and Kull, T. eds. *The plant cover of the Estonian SSR: flora, vegetation and ecology*. pp. 77–83. Valgus, Tallinn.

_____. (1997). Populations dynamics in *Cypripedium calceolus* L. Tartu University Press, Tartu.

Lesher, R.D. and Henderson, J.A. (1998). Management recommendations for Large Round-leaved orchid (*Platanthera orbiculata* (Pursh) Lundl.) [syn. *Habenaria orbiculata* (Push) Torr.]. http://www.or.blm.gov/surveyandmanage/MR/VascularPlants/section12.html

Light, M.H.S. (1998). Temperate terrestrial orchids. http://www.geocities.com/~marylois/archiv80.html

Ludwig, G and Schnittler, M. (1996). *Rote liste gefährdeter pflanzen Deutschlands*. Bundesambt für Naturschutz, Bonn-Bad Godesberg.

MacArthur R.H. and Wilson, E.O. (1967). *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey.

Malmgren, S. (1996). Orchid propagation: theory and practice. In Allen, C. ed. *North American native terrestrial orchids - propagation and production*. pp. 63–72. The North American Native Terrestrial Orchid Conference, Germantown, MD.

Masuhara, G. and Katsuya, K. (1994). *In situ* and *in vitro* specificity between *Rhizoctonia* spp. and *Spiranthes sinensis* (Persoon) Ames. var. *amoena* (M. Bieberstein) Hara (Orchidaceae). *New Phytologist* **127**: 711–718.

McKendrick, S.L., Leake, J.R. and Read, D.J. (2000). Symbiotic germination and development of myco-heterotrophic plants in nature: transfer of carbon from ectomycorrhizal *Salix repens* and *Betula pendula* to the orchid *Corallorhiza trifida* through shared hyphal connections. *New Phytologist* **145**: 539–548.

_____, _____, Taylor, D.L. and Read, D.J. (2000). Symbiotic germination and development of myco-heterotrophic plants in nature: ontogeny of *Corallorhiza trifida* and characterization of its mycorrhizal fungi. *New Phytologist* **145**: 523–537.

Mehrhoff, L.A. (1989a). Reproductive vigor and environmental factors in populations of an endangered North American orchid, *Isotria medeoloides* (Pursh) Rafinesque. *Biological Conservation* **47**: 281–296.

_____. (1989b). The dynamics of declining populations of an endangered orchid, *Isotria medeoloides*. *Ecology* **70**: 783–786.

NatureServe: An online encyclopedia of life [web application]. (2001). *Isotria medeoloides* (Pursh) Raf. Small Whorled Pogonia. http://www.natureserve.org/

Nilsson, L.A. (1992). Orchid pollination biology. *Trends in Ecology and Evolution* **7**: 255–259.

Parks and Wildlife Service, Tasmania. (1998). Gaping leek orchid (*Prasophyllum correctum*). http://

www.parks.tas.gov.au/esl/glorchid.html

Perkins, A.J., Masuhara, G. and McGee,P.A. (1995). Specificity of the associations between *Microtis parviflora* (Orchidaceae) and its mycorrhizal fungi. *Australian Journal of Botany* **43**: 85–91.

_____ and McGee, P.A. (1995). Distribution of the orchid mycorrhizal fungus, *Rhizoctonia solani*, in relation to its host, *Pterostylis acuminata* in the field. *Australian Journal of Botany* **43**: 565–575.

Perring, F.H. and Farell, L. (1983). *British red data book 1: vascular plants*. 2nd edn. Royal Society for Nature Conservation, Lincoln.

Peterson, R.L., Uetake, Y. and Zelmer, C. (1998). Fungal symbioses with orchid protocorms. *Symbiosis* **25**: 29–55.

Polunin, O. and Walters, M. (1985). *A guide to the vegetation of Britain and Europe*. Oxford University Press, New York.

Primack, R. and Stacy, E. (1998). Cost of reproduction in the pink lady's slipper orchid (*Cypripedium acaule*, Orchidaceae): an eleven-year experimental study of three populations. *American Journal of Botany* **85**: 1672–1679.

Rackham, O. (1980). *Ancient woodlands, its history, vegetation and uses in England*. Arnold Publishers, London.

Rasmussen, H.N. (1995). *Terrestrial orchids from seed to mycotrophic plant*. Cambridge University Press, Cambridge.

_____. (2002). Recent developments in the study of orchid mycorrhiza. *Plant and Soil* **244**: 149–163.

_____ and Whigham, D.F. (1993). Seed ecology of dust seeds *in situ*: a new study technique and its application in terrestrial orchids. *American Journal of Botany* **80**: 1374–1378.

_____ and _____. (1998a). The underground phase: a special challenge in studies of terrestrial orchid populations. *Botanical Journal of the Linnean Society* **126**: 49–64.

_____ and _____. (1998b). Importance of woody debris in seed germination of *Tipularia discolor* (Orchidaceae). *American Journal of Botany* **85**: 829–834.

Reddoch, A.H. and Reddoch, J.M. (1993). The species pair *Platanthera orbiculata* and *P. macrophylla* (Orchidaceae): taxonomy, morphology, distributions and habitats. *Lindleyana* **8**: 171–187.

Ramsey, M.M. and Stewart, J. (1998). Re-establishment of the lady's slipper orchid (*Cypripedium calceolus* L.) in Britain. *Botanical Journal of the Linnean Society* **126**: 173–181.

Reinhard, H.R., Gölz, P., Peter, R. and Wildermuth, H.R. (1991). *Die orchideen de Schweiz und angrenzender Gebiete*. Fotorotar AG, Druck und Verlag, Egg.

Rose, F. (1981). *The wild flower key; British islands and N.W. Europe*. Frederick Warne, Ltd. London.

Salkowski, H.-E. (1990). 20 Jahre *Spiranthes spiralis* (L.) Chevall. im Rabengrund bei Wiesbaden. *Berichten Arbeitskreis Heimischer Orchideen* **7**: 73–76.

Seevers, J. and Lang, F. (1998a). Management recommendations for Clustered Lady slipper orchid (*Cypripedium fasciculatum* Kellogg ex S. Watson). http://www.or.blm.gov/surveyandmanage/MR/VasccularPlants/section9.htm

_____ and _____. (1998b). Management recommendations for Mountain Lady's-slipper (*Cypripedium montanum* Douglas ex Lindley). http:www.or.blm.gov/surveyandmanage/MR/VascularPlants/section10.html

Shefferson, R.P., Sandercock, B.K., Proper, J. and Beissinger, S.R. (2001). Estimating dormancy and survival of a rare herbaceous perennial using mark-recapture models. *Ecology* **82**: 145–156.

Sieg, C.H. and King, R.M. (1995). Influence of environmental factors and preliminary demographic analyses of a threatened orchid *Platanthera praeclara*. *American Midland Naturalist* **134**: 307–323.

Sipes, S.D. and Tepedino, V.J. (1995). Reproductive biology of the rare orchid, *Spiranthes diluvialis*: breeding system, pollination, and implications for conservation. *Conservation Biology* **9**: 929–938.

Sperduto, M.B. and Congalton, R.G. (1996). Predicting rare orchid (small whorled Pogonia) habitat using GIS. *Photogrammetric Engineering and Remote Sensing* **62**: 1269–1279.

Stewart, J. (1992). *The conservation of European orchids*. Nature and Environment 57. Council of Europe, Strasbourg.

St George, I. and McCrae, D. (1990). *The New Zealand orchids: natural history and cultivation*. The New Zealand Native Orchid Group, Dunedin.

Stoutamire, W. (1996). Seeds and seedlings of *Platanthera leucophaea* (Orchidaceae). In Allen, C. ed. *North American native terrestrial orchids - propagation and production*. pp. 55–62. North American Native Terrestrial Orchid Conference, Germantown, MD.

Sun, M. (1996). Effects of population size, mating system, and evolutionary origin on genetic diversity in *Spiranthes* *sinensis* and *S. hongkongensis*. *Conservation Biology* **10**: 785–795.

____. (1997). Genetic diversity in three colonizing orchids with contrasting mating systems. *American Journal of Botany* **84**: 224–232.

Tali, K. (2002). Dynamics of Orchid ustulata populations in Estonia. In Kindlmann, P., Willems, J.H. and Whigham, D.F. eds. *Trends and fluctuations and underlying mechanisms in terrestrial orchid populations*. pp. 33–42. Backhuys Publishers, Leiden.

Tamm, C.O. (1948). Observations on reproduction and survival of some perennial herbs. *Botaniska Notiser* **3**: 305–321.

____. (1972). Survival and flowering of some perennial herbs. II. The behaviour of some orchids on permanent plots. *Oikos* **23**: 23–28.

____. (1991). Behaviour of some orchid populations in a changing environment: observations on permanent plots, 1943-1990. In Wells, T.C.E. and Willems, J.H. eds. *Population ecology of terrestrial orchids*. pp. 1–14. SPB Academic Publishing bv, The Hague.

United States Fish and Wildlife Service (USFWS). (2001). http://endangered.fws.gov/wildlife.html

____. (2002). Western Prairie Fringed Orchid. http://ecos.fws.gov/servlet/SpeciesProfile?spcode=Q2YD

Vakhrameeva, M.G. and Tatarenko, I.V. (1998). Age structure of population of orchids with different life forms. *Acta Universitatis Wratislaviensis* **2037**: 129–139.

van der Cingel, N.A. (1995). *An atlas of orchid pollination. European orchids*. Balkema, Brookfield and Rotterdam.

von Oettingen, S.L. (1992). *Small Whorled Pogonia* (Isotria medeoloides) *recovery plan*. First revision. U.S. Fish and Wildlife Service, Newton Corner, Massachusetts.

Voth, W. (1973). Salep im Türkischen Speiseeis. *Orchidée* **24**: 29–31.

Waite, S. (1989). Predicting population trends in *Ophrys sphegodes* Mill. In Pritchard, H.W. ed. *Modern methods in orchid conservation: the role of physiology, ecology and management*. pp. 117–126. Cambridge University Press, Cambridge.

____ and Hutchings, M.J. (1991). The effects of different management regimes on the population dynamics of *Ophrys sphegodes*: analysis and description using matrix models. In Wells, T.C.E. and Willems, J.H. eds. *Population ecology of terrestrial orchids*. pp. 161–175. SPB Academic Publishing bv, The Hague.

Warcup, J.H. (1981). The mycorrhizal relationships of Australian orchids. *New Phytologist* **87**: 371–381.

Weeda, E.J. (1985). *Liparis loeselii* (L.) Rich. In Mennema, J., Quené-Boterenbrood, A.J. and Plate, C.L. eds. *Atlas van de Nederlandse flora 2. Zeldzame en vrij zeldzame planten*. pp. 197. Bohn, Scheltema & Holkema, Utrecht.

Wells, T.C.E. (1967). Changes in a population of *Spiranthes spiralis* (L.) Chevall. at Knocking Hoe National reserve, Bedfordshire, 1962-65. *Journal of Ecology* **55**: 83–99.

____. (1981). Population ecology of terrestrial orchids. In Synge, H. ed. *The biological aspects of rare plant conservation*. pp. 281–295. John Wiley & Sons, Chichester.

____. (1994). Population ecology of British terrestrial orchids. In Pridgeon, A.M. ed. *Proceedings of the 14th World Orchid Conference*. pp. 170–175. H.M.S.O. Edinburgh.

____ and Willems, J.H. (eds) (1991). *Population ecology of terrestrial orchids*. SPB Academic Publishing, bv, The Hague.

Wheeler, B.D., Lambley, P.W. and Geeson, J. (1998). *Liparis loeselii* (L.) Rich. In eastern England; constraints on distribution and population development. *Botanical Journal of the Linnean Society* **126**: 141–158.

Whigham, D.F. (1984). Biomass and nutrient allocation patterns in *Tipularia discolor*. *Oikos* **42**: 303–313.

____, O'Neill, J., McCormick, M., Smith, C., Rasmussen, H., Caldwell, B. and Daniell, T. (2002). Interactions between decomposing wood, mycorrhizas, and terrestrial orchid seeds and protocorms. In Kindlmann, P., Willems, J.H. and Whigham, D.F. eds. *Trends and fluctuations and underlying mechanisms in terrestrial orchid populations*. pp. 117–132. Backhuys Publishers, Leiden.

Willems, J.H. (1982). Establishment and development of a population of *Orchis simia* (Lamk.) in The Netherlands, 1972 to 1981. *New Phytologist* **91**: 757–765.

____. (1989). Population dynamics of *Spiranthes spiralis* in South-Limburg. *Mémoires de la Société Royale Botanique Belgique* **11**: 115–121.

____. (2002). A founder population of *Orchis simia* in the Netherlands: a 30-year struggle for survival. In Kindlmann, P., Willems, J.H. and Whigham, D.F. eds. *Trends and fluctuations and underlying mechanisms in* *terrestrial orchid populations*. pp. 23–32. Backhuys Publishers, Leiden.

_____, Balounova, S. and Kindlmann, P. (2001). The effect of experimental shading on seed production and plant survival in the threatened species *Spiranthes spiralis* (L.) Chevall. (Orchidaceae). *Lindleyana* **16**: 31–37.

_____ and Bik, L. (1991). Long-term dynamics in a population of *Orchis simia* in The Netherlands. In Wells, T.C.E. and Willems, J.H. eds. *Population ecology of terrestrial orchids*. pp. 33–45. SPB Academic Publishing, bv, The Hague.

_____ and Dorland, E. (2000). Flowering frequency and plant performance and their relation to age in the perennial orchid *Spiranthes spiralis* (L.) Chevall. *Plant Biology* **2**: 344–349.

_____ and Lahtinen, M.-L. (1997). Impact of pollination and resource limitation on seed production in a border population of *Spiranthes spiralis* (Orchidaceae). *Acta Botanica Neerlandica* **46**: 365–375.

_____ and Melser, C. (1998). Population dynamics and life-history of *Coeloglossum viride* (L.)Hartm.: an endangered orchid species in The Netherlands. *Botanical Journal of the Linnean Society* **126**: 83–93.

Wong, K.C. and Sun, M. (1999). Reproductive biology and conservation genetics of *Goodyera procera* (Orchidaceae). *American Journal of Botany* **86**: 1406–1413.

Wood, J.J. (1985). Orchidaceae. In Meilke, R.D. ed. *Flora of Cyprus*. Vol. 2. pp. 1491–1558. Bentham Moxon Trust, Kew.

_____. (1989). British orchids in their European context. In Pritchard, H.W. ed. *Modern methods in orchid conservation. The role of physiology, ecology and management*. pp. 141–146. Cambridge University Press, Cambridge.

Zelmer, C.D., Cuthbertson, L. and Currah, R.S. (1996). Fungi associated with terrestrial orchid mycorrhizas, seeds and protocorms. *Mycoscience* **37**: 439–448.

Zettler, L.W. (1996). Symbiotic seed germination of terrestrial orchids in North America during the last decade - a progress report. In Allen, C. ed. *North American native terrestrial orchids - propagation and production*. pp. 43–53. The North American Native Orchid Alliance, Germantown.

_____, Steward, S.L., Bowles, M.L. and Jacobs, K.A. (2001). Mycorrhizal fungi and cold-assisted symbiotic germination of the federally threatened Eastern Prairie Fringed orchid, *Platanthera leucophaea* (Nuttall) Lindley. *American Midland Naturalist* **145**: 168–175.

Ziegenspeck, H. (1936). *Orchidaceae*. Lebensgeschichte der Blütenpflanzen Mitteleuropas. Band 1, Abteilung 4. Ulmer Verlag, Stuttgart.