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Long-term dynamics and population viability in one of the last populations of the endangered *Spiranthes spiralis* (Orchidaceae) in the Netherlands

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ABSTRACT

During the last decades, most orchid species in much of Western Europe have suffered significant declines and the long-term survival of the remaining populations remains to a large extent uncertain. In particular, populations at range margins may be more prone to extinction than more central populations, as the former tend to be small and isolated, occur in ecologically marginal habitats and have a lower per-capita reproductive rate. In this study, we investigated the long-term dynamics and population viability of a population at the margin of its range of *Spiranthes spiralis* in the Netherlands. At present, only 2 out of 40 previously known populations persist. Individual plants were monitored for 24 years and their life span, flowering frequency and vegetative growth were determined. Individual plants showed large temporal variation in sexual and vegetative growth among years. The proportion of flowering plants varied from 0 (no plants were flowering) to 100 (all plants were flowering). Vegetative growth, on the other hand, increased when the number of individuals decreased. Dormancy was present, but occurred only in a few individuals. Using a non-structured population viability model, future prospects of this species were assessed. Calculation of extinction probabilities and estimated times to extinction using the diffusion approximation model showed that the species had a relatively high probability (79%) of surviving the next 20 years, whereas the median time to extinction was forty years. However, because 95% confidence intervals of the population growth included 1, we suggest that continued monitoring and additional genetic research are needed to assess the long-term viability of this species.

1. Introduction

During the last decades, most orchid species in much of Western Europe have suffered significant declines, most likely as a result of land use changes, habitat deterioration and fragmentation (e.g. Jacquemyn et al., 2005a; Kull and Hutchings, 2006), whereas the viability of the remaining populations remains to a large extent uncertain. In particular, populations at range margins may be more prone to extinction than central populations because they tend to be small and isolated, often occur in ecologically marginal habitats and have a low per-capita reproductive rate (Lawton, 1993; Hoffman and Blows, 1994; Lesica and Allendorf, 1995; Sagarin and Gaines, 2002). At range margins, adequate

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management is therefore most of the times a prerequisite to maintain viable plant populations (see for example Oostermeijer et al., 2003).

The long-term survival of plant populations is determined by their vital rates, i.e. reproduction, recruitment, growth, and survival. However, the relative importance of these rates may differ in different environments. Under unfavorable conditions, individual plants may invest relatively more resources into clonal growth as a means to survive unfavorable habitat conditions (Jacquemyn et al., 2005b, 2006). Under such harsh conditions, sexual recruitment may be suppressed, locally less adapted genotypes may be outcompeted by better-adapted genotypes (Hartnett and Bazzaz, 1985), and only one or a few genotypes may survive (Schaal and Leverich, 1996; Klein and Steinger, 2002).

Sexual reproduction and seedling recruitment, on the other hand, are accompanied by genetic recombination and hence by the addition of new genotypes, which may allow adaptation to changing environmental conditions (Wise et al., 2002). Additionally, seed dispersal allows a species to travel greater distances and thus to escape unfavorable habitat conditions and to occupy a wider range of suitable microsites than dispersal by vegetatively produced propagules (Loehle, 1987; Gardner and Mangel, 1999; van Kleunen et al., 2001).

Most terrestrial orchid species possess the capability to reproduce sexually as well as clonally (Klimeš et al., 1997), although little is known about the relative importance of clonal growth and sexual reproduction in determining demography and population viability of orchid species. The few available studies indicate that sexual recruitment is prevalent among orchid species (but see Brzosko et al., 2002; Machon et al., 2003; Chung et al., 2004). This is surprising because most orchids are pollinator limited, recruitment through sexual reproduction is very unpredictable due to symbiosis with fungi and because sexual reproduction may come at a fitness cost (e.g. Snow and Whigham, 1989; Primack and Hall, 1990). In case trade-offs between fruit set and flowering frequency constrain the lifetime fitness of orchid populations (Calvo, 1993), clonal growth may be an efficient means to survive unfavorable habitat conditions.

In this study, we investigated the long-term dynamics and population viability in a population at the margin of its range of the extremely rare, long-lived, perennial orchid *Spiranthes spiralis* in the Netherlands. Despite the fact that appropriate management has prevented extinction during the last 25 years, the long-term survival largely remains uncertain. The aims of this study were, firstly, to provide insights in the demography of this species, and secondly, to assess its future prospects. The meet these aims, demographic data were collected for 24 years in a large permanent plot. More specifically, we investigated how clonal growth and sexual reproduction varied among years, and how clonal growth affected survival. Finally, a population viability analysis using the diffusion approximation (Dennis et al., 1991) was performed to assess future prospects of the species and to estimate extinction probabilities of the studied population within specific time horizons.

2. Material and methods

2.1. Species

Spiranthes spiralis (L.) Chevall. is a small, long-lived perennial orchid that is widely distributed in Southern Europe, in the Mediterranean region and in coastal areas of North Africa (Ziegenspeck, 1936; Tutin et al., 1980). The species reaches the limits of its northwestern distribution in the southern part of the United Kingdom and The Netherlands. The species has suffered significant declines in much of Western Europe, most likely being the result of habitat loss and deterioration (Jacquemyn et al., 2005a; Kull and Hutchings, 2006). In the Netherlands, *S. spiralis* is listed as endangered: out of around 40 populations that were present before 1950, only two still exist today (Willems and Lahtinen, 1997; see also Kreutz and Dekker (2000) for past and present distribution maps).

S. spiralis typically occurs in relatively dry, nutrient-poor meadows or calcareous grassland (Weeda et al., 1994; Kreutz and Dekker, 2000). It typically occurs in open grazed situations with a constant land-use. Individual plants survive during many years and may consist of several rosettes and one or several small belowground tubers per plant (Wells, 1967; Willems and Lahtinen, 1997; Machon et al., 2003). New tubers are formed during the winter and spring, and leaves as well as inflorescences emerge in late summer. Leaves are small (between 1 and 5 cm long and 0.5 and 1.5 cm wide) and die off in late spring or early summer. *S. spiralis* flowers in August and September. The height of the inflorescence varies between 5 and 25 cm and it may bear up to 25, small, white flowers that are arranged in a spiral on the upper half of the flowering stalk. Flowers are self-compatible, produce nectar and are mainly pollinated by bumblebees and bees (van der Cingel, 1995; Willems and Lahtinen, 1997). Spontaneous self-pollination does not occur. In October to November the capsules become ripe. Fruit set varies between 0% and 78% (mean: 35%) (Willems and Lahtinen, 1997). The seeds are wind-dispersed, but most seeds fall in the direct neighborhood of the mother plant (Machon et al., 2003). Vegetative multiplication occurs by the growth of a lateral bud on the underground stem, the new plant forming its own tubers, and eventually the connection between the mother plant and vegetatively produced plants withers away (Wells, 1967). In this way, small groups of plants are formed, which are easily distinguished from plants that have arisen from seed.

2.2. Study site

This study was conducted from 1981 to 2004 in the Berghofweide Nature Reserve in the Netherlands (50°50′N; 5°53′E). This site is a species-rich calcareous grassland located on a south-facing slope (inclination 15°, altitude 170 m). The subsoil consists of a mixture of gravel deposits and weathered chalk products. The pH of the loamy topsoil is high (6.0–7.5). Before 1980, both manure and artificial fertilizer were applied yearly to the site, but in limited quantities. From 1980 onwards, this practice was abandoned and management nowadays consists of yearly mowing and hay removal in summer (July) and grazing in late autumn or early winter by sheep.