# Trends and fluctuations and underlying mechanisms in terrestrial orchid populations

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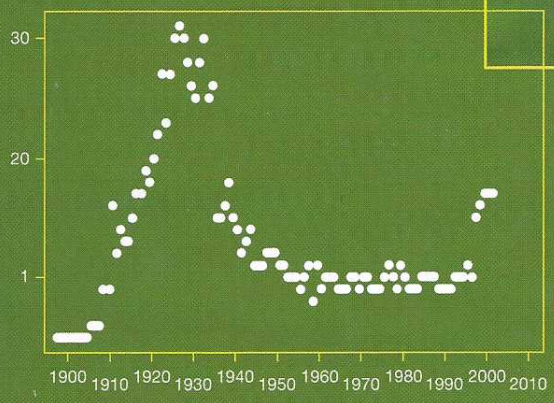


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# Trends and fluctuations and underlying mechanisms in terrestrial orchid populations

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# Flowering and survival of *Dactylorhiza lapponica* and *Gymnadenia conopsea* in the Sølendet Nature Reserve, Central Norway

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**Abstract**
The orchid species *Dactylorhiza lapponica* (LAEST. EX HARTMAN) SOÓ and *Gymnadenia conopsea* (L.) R. BR. have been monitored in permanent plots for more than 20 years. *D. lapponica* is a rich fen species, whereas *G. conopsea* occurs in both rich fens and wet grasslands. The density of flowering individuals showed large fluctuations for both species. The density of *D. lapponica* was positively correlated with summer temperature and early autumn temperature in the year preceding the flowering, possible explanations for this being increased autotrophic activity in summer and increased mycotrophic activity in autumn. No correlation was found between the density of flowering individuals of *G. conopsea* and weather conditions. It is suggested that high mortality after flowering and high tolerance to variations in climatic factors (shown by the species wide regional (zonal) amplitude) are possible explanations. For both species, annual mortality was high the first year after flowering, but then dropped rapidly in the case of *D. lapponica*. Both the high proportion of flowering events preceded and followed by years in vegetative state and the reduced size of individuals after flowering indicate a high cost of flowering in both species. Intensive scything (annually or biennially at the peak of aboveground biomass production) reduced longevity and prolonged the non-flowering periods of both species. Scything had a stronger effect on *G. conopsea* than on *D. lapponica*, possibly because a larger part of the biomass of *G. conopsea* is removed during scything.

**Key words:** cost of flowering, *Dactylorhiza lapponica*, flowering density, *Gymnadenia conopsea*, long-term monitoring, mortality, scything, terrestrial orchids, upper boreal region, weather conditions.

## Introduction

The orchids, *Dactylorhiza lapponica* (LAEST. EX HARTMAN) SOÓ and *Gymnadenia conopsea* (L.) R. BR., occur relatively commonly in some upper boreal rich fen and moist grassland sites in Central Norway, for instance in the Sølendet Nature Reserve where both species occur in millions of individuals. *D. lapponica* has a limited distribution; it is dispersed throughout the central parts of Fennoscandia, north to Alta in Norway and Enonteki in Finland. Outside Fennoscandia, it is reported from the Alps and a few localities in Slovakia, Poland and western Scotland (Fig. 1). The

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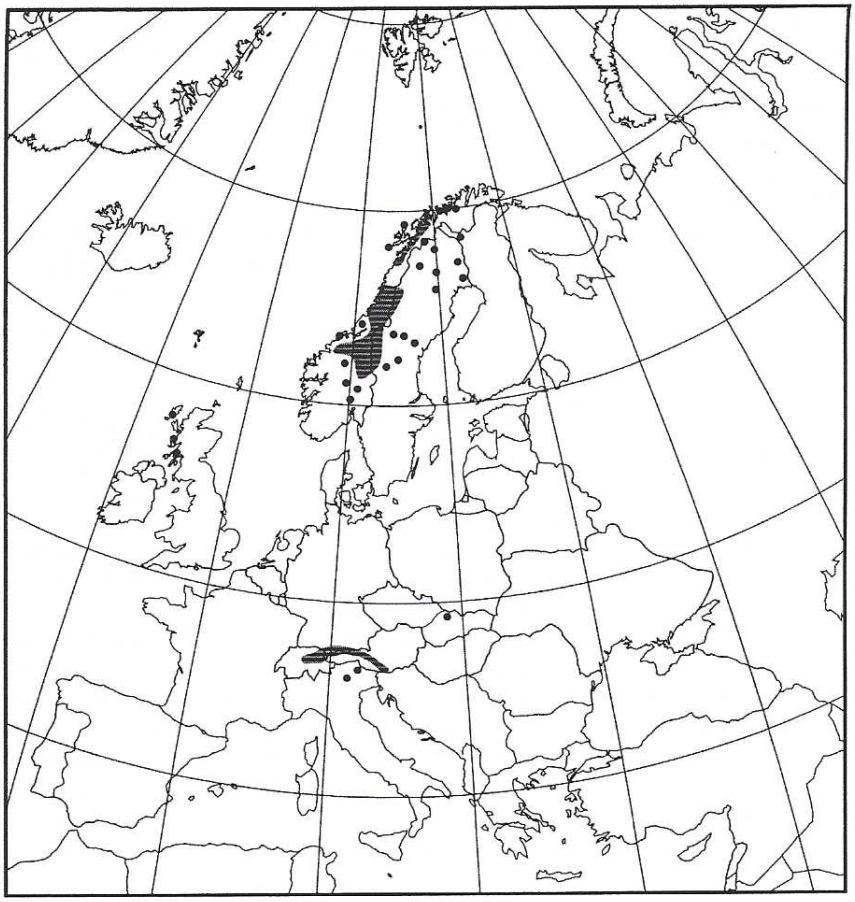

*Figure 1.* World distribution of *Dactylorhiza lapponica*, based on Reinhard (1985, 1987), Kalteisen and Reinhard (1986), Gallerach and Wucherpfennig (1987), Wischmann and Nordal (1987), Kenneth *et al.* (1988), Reinhard *et al.* (1991), Danielsson (1994), Hansson (1994), Vlčko (1995), Lauber and Wagner (1996) and material from the herbarium in Trondheim (TRH).

species is tetraploid and probably formed through hybridisation between *Dactylorhiza fuchsii* (DRUCE) SOÓ and *Dactylorhiza incarnata* (L.) SOÓ (Hedrén 1996). It is morphologically very heterogeneous, showing regional differences, and hybridisation with other *Dactylorhiza* species is common. It is morphologically close to *Dactylorhiza majalis* (RCHB. F.) HUNT ET SUMMERH. and *Dactylorhiza traunsteineri* (SAUTER) SOÓ, and in Central Europe, where all three species occur together, it is difficult to separate *D. lapponica* from the other two. Prior to the work done by Reinhard (1985, 1987) and Kalteisen and Reinhard (1986), most specimens found outside Fennoscandia were determined as either *D. majalis* or *D. traunsteineri*. These works also led to specimens found in Scotland being incorporated as *D. lapponica* (Kenneth *et al.* 1988), and the Scandinavian species *Dactylorhiza pseudocordigera* (NEUMAN) SOÓ being reduced to a synonym of *D. lapponica*. Throughout its distrib-

ution, the species is found in open, low vegetation on wet, calcareous or base-rich soil, such as rich fens, wet grasslands, springs and river banks. In Fennoscandia, it is exclusively found on extremely rich fens and springs in the boreal vegetation zones (after Moen 1999), where it is a characteristic species of *Caricion atrofuscae*, *Schoenion ferruginei* and *Cratoneurion commutati* communities (Moen 1990).

*Gymnadenia conopsea* is a widespread species in Fennoscandia and occurs throughout most of Europe and large parts of nemoral and boreal Asia, east to China. It is also morphologically variable and a number of subspecies or varieties have been described, although their status is very unclear (Hegi 1980, Soliva and Widmer 1999). The populations in Norway are mainly described as var. or ssp. *conopsea*. The species is found in relatively open vegetation on moist to wet or periodically wet ground, such as rich fens (plant community *Caricion atrofuscae*, Moen 1990), fen margins and wet grasslands (plant community *Sphagno-Tomenthypnion*, Dahl 1957), herb-rich woodlands (plant community *Lactucion alpinae*, Nordh. 1943), seashore and mountain grasslands, but also drier grasslands and *Dryas octopetala* L. heaths (plant community *Kobresio-Dryadion*, Nordh. 1943) as well as pastures, although it avoids intensive mowing and grazing (Moen 1990, Nilsen 1995). It grows mainly on base-rich soils, but can also occur on slightly acid soils. In Fennoscandia, it is common in the boreal (including boreonemoral) vegetation zones, but also occurs in both the nemoral and low alpine zones.

In this paper, we present data from ongoing long-term monitoring of the two species. Populations of both species have been followed since 1981 in the Sølendet Nature Reserve in Central Norway (Moen 1985, 1990). The monitoring forms part of a larger programme in the reserve, the main aim of which is to learn more about the composition, production and dynamics of the plant communities, the ecology and population biology of a number of fen and grassland species, and how different management practices affect their populations and communities (Moen 1990, 1995, Aune *et al.* 1996, Arnesen 1999, Moen *et al.* 1999, Øien and Moen 2001). This paper concentrates on aspects of the species population ecology, their flowering pattern and survival, and addresses the following questions:

- Are there any relationships between the variation in the number of flowering individuals and the weather conditions?
- Are age and the cost of flowering important for the probability of flowering and survival?
- How does regular scything affect flowering and survival?

## Material and methods

The nomenclature follows Lid and Lid (1994).

### The study area

The Sølendet Nature Reserve near Røros in Central Norway covers 306 ha and was established in 1974. It is situated 700-800 m above sea level at the transitions between the middle boreal and northern boreal vegetation zones and the oceanic and continental vegetation sections (Moen 1999). The mean temperatures in January and

July are -9.5°C and 10.5°C, respectively (Aune 1993, Øien 1998), and the mean annual precipitation is 600 mm (Førland 1993). The growing season is short, usually from the beginning of June until late August. About half of the area consists of rich fens, mostly extremely rich lawn communities belonging to *Caricion atrofuscae*; the rest is mainly wooded (birch) grassland and heath. The area was used for haymaking until about 1950, after which overgrowing took place for a time before the area was protected and restoration and management started. Today, 160 ha are mown and kept open, and resemble the former cultural landscape. The reserve has a rich flora, including 12 species of orchids, most of which occur abundantly. A large number of hybrid orchids (at least 12 taxa) are also found (Moen 1990). *D. lapponica* and *G. conopsea* are among the most abundant orchids in the reserve, and in some years more than one million individuals of each species are flowering. *D. lapponica* is very common in the extremely rich lawn communities (Table 1). Flowering lasts all July, peaking in the middle of the month. *G. conopsea* is most common in the drier parts of the fens and the wetter parts of the wooded grasslands (Table 1). Flowering lasts from mid July to the beginning of August, with a peak in late July.

## Field methods

Populations of both these species, and a number of other fen and grassland species, were monitored in permanent plots for more than 20 years. The monitoring was carried out in a total of 111 plots, mostly measuring 5 × 2.5 m. The plots were arranged in localities with two or more plots per locality, at least one of which had been scythed every second year since the mid 1970s and at least one left unscythed since traditional haymaking ceased around 1950. Some localities also included annually scythed plots. The material presented in this paper is based on observations made in 1981-2000. Table 2 shows the number of localities, plots and individuals from which the data derive. Two types of registrations were made:

*Counting the number of flowering individuals* – All flowering individuals of both species in the 111 permanent plots (most plots included both species) were counted once a year (mid July).

*Detailed monitoring of individuals* – Stature (withering, grazed, broken, etc.), reproductive status (vegetative or generative), number of flowers per spike (only *D. lapponica*), and size of individuals were recorded once a year in a number of the plots used to count flowering individuals. All individuals that had flowered at least once were included in this monitoring from the time they were first seen flowering. The size of individuals in the vegetative phase was recorded using three classes (small, medium, large) approximately equal to 1-2 leaves with a total leaf area < 2 $cm^2$, 1-3 leaves with a total leaf area of 2-6 $cm^2$ and 2-3 leaves with a total leaf area > 6 $cm^2$ in the rosette, respectively, for both species. The height from the ground to the top of the inflorescence was used as the size of individuals in the generative phase. To enable their identification from year to year, the individuals were marked and their position was recorded. In this way we could also record if any vegetative reproduction took place. A plant was considered to be vegetatively reproduced

*Table 1.* Synopsis of phytosociological analyses made in rich fen and wooded grassland vegetation at Sølendet were *Dactylorhiza lapponica* and *Gymnadenia conopsea* are common. Frequency of occurrence and mean cover. Cover scale: 2: 0-1%; 3: 1-3.125%; 4: 3.125-6.25%; 5: 6.25-12.5%; 6: 12.5-25%; 7: 25-50%; 8: 50-75%; 9: 75-100%. Derived from Moen (1990), Appendix C, Table 3 (rich fen vegetation) and Appendix D, Tables 1 and 2 (wooded damp grassland). Only 40 species listed out of totally about 150. The nomenclature follows Lid and Lid (1994).

| **Vegetation type**<br>Number of plots (25 $m^2$) | **Rich fen expanse**<br>10 | **Rich fen margin**<br>10 | **Wooded damp grassland**<br>5 |
|---|---|---|---|
| ***Dactylorhiza lapponica*** | **100-3** | **100-3** | **missing** |
| ***Gymnadenia conopsea*** | **30-3** | **100-3** | **100-4** |
| *Betula pubescens* (in the tree layer) | missing | missing | 80-5 |
| *Betula pubescens* (in the shrub layer) | missing | missing | 80-4 |
| *Betula nana* | 40-3 | 60-4 | 20-4 |
| *Alchemilla* spp. | missing | 10-3 | 80-5 |
| *Bistorta vivipara* | 80-3 | 100-4 | 100-4 |
| *Crepis paludosa* | 10-2 | 80-4 | 80-5 |
| *Dactylorhiza fuchsii* | missing | missing | 60-4 |
| *Dactylorhiza incarnata* ssp. *cruenta* | 60-3 | 30-3 | missing |
| *Geranium sylvaticum* | missing | 30-3 | 100-6 |
| *Leontodon autumnalis* | missing | 100-3 | 100-4 |
| *Pedicularis oederi* | 80-4 | 100-4 | 80-4 |
| *Potentilla erecta* | 100-5 | 90-5 | 60-6 |
| *Saussurea alpina* | 100-4 | 100-4 | 60-6 |
| *Selaginella selaginoides* | 100-4 | 100-4 | 80-5 |
| *Solidago virgaurea* | missing | 30-3 | 80-4 |
| *Succisa pratensis* | 40-3 | 100-6 | 100-5 |
| *Thalictrum alpinum* | 100-6 | 100-6 | 80-7 |
| *Tofieldia pusilla* | 100-4 | 90-4 | missing |
| *Agrostis capillaris* | missing | missing | 100-4 |
| *Anthoxhantum odoratum* | missing | missing | 100-5 |
| *Carex capillaris* | 60-3 | 100-5 | 60-4 |
| *Carex dioica* | 100-4 | 100-4 | 20-4 |
| *Carex flava* | 100-4 | 70-5 | 20-4 |
| *Carex lasiocarpa* | 50-4 | 60-4 | missing |
| *Carex panicea* | 100-5 | 100-5 | missing |
| *Carex vaginata* | missing | 90-4 | 100-5 |
| *Deschampsia cespitosa* | missing | 100-4 | 100-5 |
| *Eriophorum angustifolium* | 100-3 | 80-3 | missing |
| *Eriophorum latifolium* | 90-5 | 60-4 | missing |
| *Molinia caerulea* | 100-5 | 100-6 | 80-5 |
| *Nardus stricta* | 10-3 | 50-3 | 100-6 |
| *Trichophorum cespitosum* ssp. *cesp.* | 100-7 | 100-5 | 20-4 |
| *Bryum pseudotriquetrum* | 100-4 | 100-4 | 20-4 |
| *Campylium stellatum* | 100-8 | 100-8 | 60-7 |
| *Climacium dendroides* | missing | missing | 60-4 |
| *Fissidens adianthoides* | 100-4 | 100-4 | 60-4 |
| *Hylocomium splendens* | missing | 10-2 | 100-6 |
| *Scorpidium cossonii* | 100-6 | 100-5 | missing |

*Table 2.* Number of localities, plots (mostly 12.5 m²) and individuals sampled during monitoring of *Dactylorhiza lapponica* and *Gymnadenia conopsea* in 1981-2000 at the Sølendet Nature Reserve. Detailed monitoring were carried out in some of the plots used to count individuals. No detailed monitoring were carried out in annually scythed plots.

| | *Dactylorhiza lapponica* | *Gymnadenia conopsea* |
|---|---|---|
| **Counting** | | |
| No. of localities | 13 | 24 |
| No. of unscythed plots | 27 | 45 |
| No. of biennially scythed plots | 28 | 39 |
| No. of annually scythed plots | 9 | 10 |
| **Detailed monitoring** | | |
| ***In unscythed plots*** | | |
| – no. of localities/plot | 5/14 | 7/11 |
| – total no. of individuals followed | 493 | 272 |
| – no. of flowering individuals followed | 432 | 248 |
| ***In biennially scythed plots*** | | |
| – no. of localities/plot | 5/14 | 3/7 |
| – total no. of individuals followed | 340 | 57 |
| – no. of flowering individuals followed | 302 | 56 |

when at a given spot two rosettes appeared of the same size, where in a previous year only one rosette was recorded. We found that this played a minor role for the population size in the two species investigated. The percentage of rosettes originated by vegetative multiplication measured over the total research period was only 1-2% in both species.

## Data analysis

We used multiple linear regression to explore whether there were any relationships between variations in weather conditions and variations in flowering density and the size of individuals. Twenty-four weather parameters (Table 3) were ordinated using PCA in the computer program Canoco for Windows version 4 (ter Braak and Šmilauer 1998) to construct uncorrelated explanatory variables. Four uncorrelated complex variables were constructed, representing the four PCA axes. Fig. 2 shows the relation between these axes and the weather parameters. Regression analyses were performed between this set of variables and the average numbers of flowering individuals per plot each year, the height of flowering individuals and the number of flowers on each spike (only *D. lapponica*). Only data from the unscythed plots were used.

Temperature sums ($T$) were calculated using the following formula (after Laaksonen 1979):

$$T = \sum_{n=a}^{b} T_m - 5$$



*Table 3.* Weather parameter
together for periods longer

| | Yea |
|---|---|
| **Temperature sum** | Prev |
| | Pr |
| | Cu |
| **Precipitation** | Pre |
| | Pre |
| | Cu |

where $T_m$ is the daily
in spring with a (rising
at that time the third d
is the third day in the l
above 5°C, or if there
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at Brekken 3-4 km eas
cal station at Røros, al
ence in altitude (112 m

An individual was
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viduals recorded in the
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results presented in thi

The longevity of ind
combined cohorts of *D.*
two combined cohorts
Curves were fitted by
individuals and the half

*Table 3.* Weather parameters used in the PCA ordination (Table 5). Values for each month are added together for periods longer than one month. For calculation of temperature sums see text.

| | Year | Period | Code |
|---|---|---|---|
| **Temperature sum** | Previous | May | $T\text{-}1_{MAY}$ |
| | | June | $T\text{-}1_{JUN}$ |
| | | July | $T\text{-}1_{JUL}$ |
| | | August | $T\text{-}1_{AUG}$ |
| | | September | $T\text{-}1_{SEP}$ |
| | | May to June | $T\text{-}1_{MAYJUN}$ |
| | | May to July | $T\text{-}1_{MAYJUL}$ |
| | | May to August | $T\text{-}1_{MAYAUG}$ |
| | | June to July | $T\text{-}1_{JUNJUL}$ |
| | | June to August | $T\text{-}1_{JUNAUG}$ |
| | | July to August | $T\text{-}1_{JULAUG}$ |
| | | August to September | $T\text{-}1_{AUGSEP}$ |
| | Previous and current | August to June | $T_{AUGJUN}$ |
| | Current | May | $T_{MAY}$ |
| | | June | $T_{JUN}$ |
| | | May to June | $T_{MAYJUN}$ |
| **Precipitation** | Previous | June to August | $P\text{-}1_{JUNAUG}$ |
| | | August to September | $P\text{-}1_{AUGSEP}$ |
| | | Whole year | $P\text{-}1_{YEAR}$ |
| | Previous and current | August to April | $P_{AUGAPR}$ |
| | | August to June | $P_{AUGJUN}$ |
| | Current | May | $P_{MAY}$ |
| | | June | $P_{JUN}$ |
| | | May to June | $P_{MAYJUN}$ |

where $T_m$ is the daily mean temperature, $a$ is the third day in the first 5-day period in spring with a (rising) mean temperature above 5°C, or if there is still a snow cover at that time the third day in the first 5-day period after the snow has melted, and $b$ is the third day in the last 5-day period in autumn with a (falling) mean temperature above 5°C, or if there is snow at that time the third day in the last 5-day period before the snow returned. Precipitation data derive from the meteorological station at Brekken 3-4 km east of Sølendet. Temperature data come from the meteorological station at Røros, about 25 km to the southwest, and are corrected for the difference in altitude (112 m; Øien 1998).

An individual was included in the monitoring from the first time it was seen flowering, and that year was used as its date of recruitment. Although some individuals recorded in the first years of the monitoring period had probably also flowered prior to the start in 1981, we do not consider this to have consequences for the results presented in this paper.

The longevity of individuals was estimated by drawing depletion curves from three combined cohorts of *D. lapponica* with recruitment years of 1984, 1989 and 1990, and two combined cohorts of *G. conopsea* with recruitment years of 1984 and 1991. Curves were fitted by linear regression of the log-transformed number of surviving individuals and the half-life was found by solving the equation of the regression line.

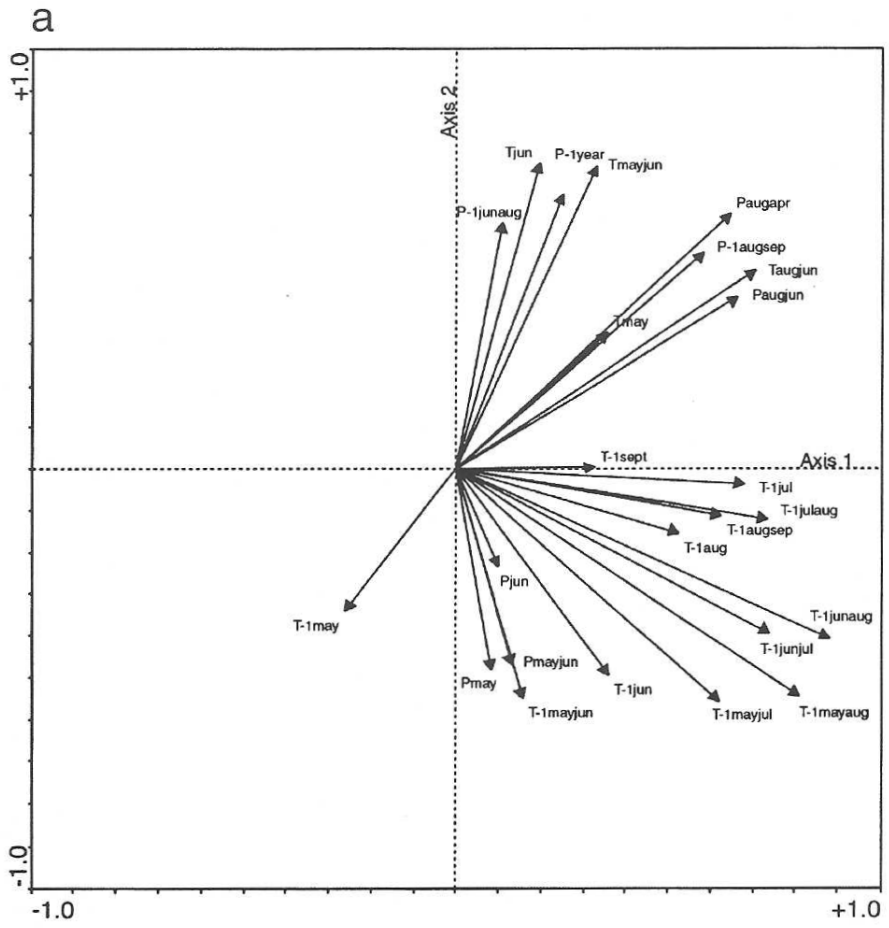


*Figure 2.* PCA ordination diagram of values for the weather parameters during 1981-2000 listed in Table 1. **a**. Axes 1 and 2.

The effect of scything was tested by comparing the slopes of the regression lines in an F-test for the difference between two regression coefficients, elaborated in Sokal and Rohlf (1981: 500-505). We also compared the density in plots with different scything frequency using Tukey's honestly significant difference test in a one-way ANOVA.

To acquire an indication of the cost of flowering, we calculated the proportion of successive flowering events and the difference in the average size class of individuals in the vegetative phase before and after flowering in unscythed plots (for the definition of size classes see above).

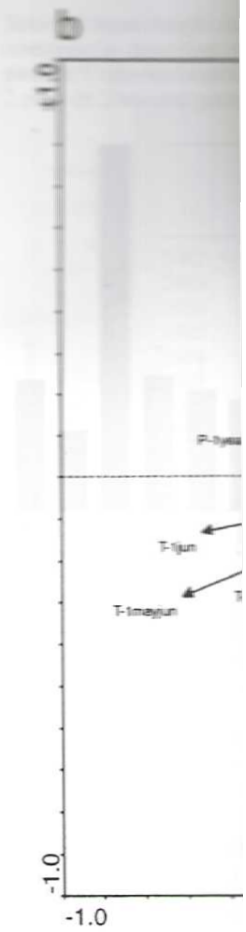


*Figure 2.* **b**. Axes 3 and 4.
ance, since the sum of all
Axis 4 = 0.066.

## Results

### Flowering and weat

The mean density o
variation between ye
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flowering individual
and 1993-97, when th
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from about 0.5 flowe
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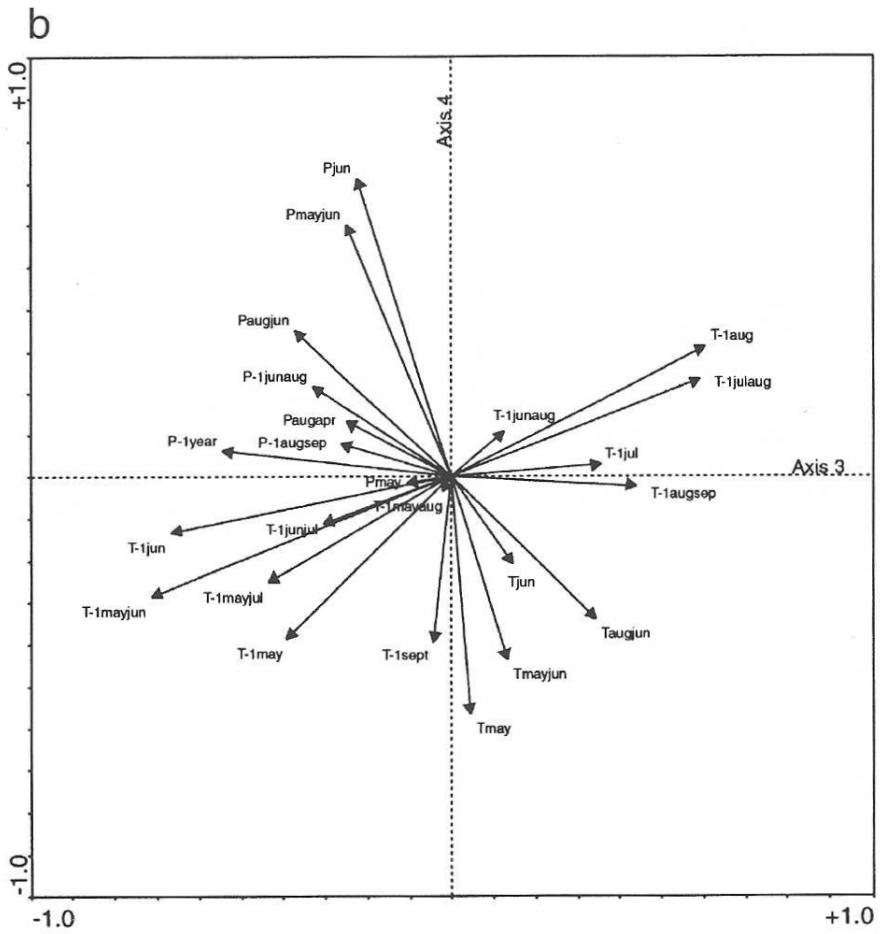


*Figure 2.* **b**. Axes 3 and 4. Eigenvalues (equal the percentage each variable explains of the total variance, since the sum of all eigenvalues is set to 1): Axis 1 = 0.363, Axis 2 = 0.237, Axis 3 = 0.154, Axis 4 = 0.066.

## Results

### Flowering and weather conditions

The mean density of flowering individuals of both species showed considerable variation between years. The erratic curves in Fig. 3 show that this was especially the case for *D. lapponica*, whose mean density fluctuated between fewer than 1 flowering individual per plot (12.5 $m^2$) in 1988 and 9 in 1998. Apart from 1985-88 and 1993-97, when the flowering density was low, a good flowering season was usually followed by a poor one. The variation was less erratic for *G. conopsea*, ranging from about 0.5 flowering individuals per plot in 1993 to about 5 in 1984. The variation in the height of flowering individuals is very similar in both species (Table 4),

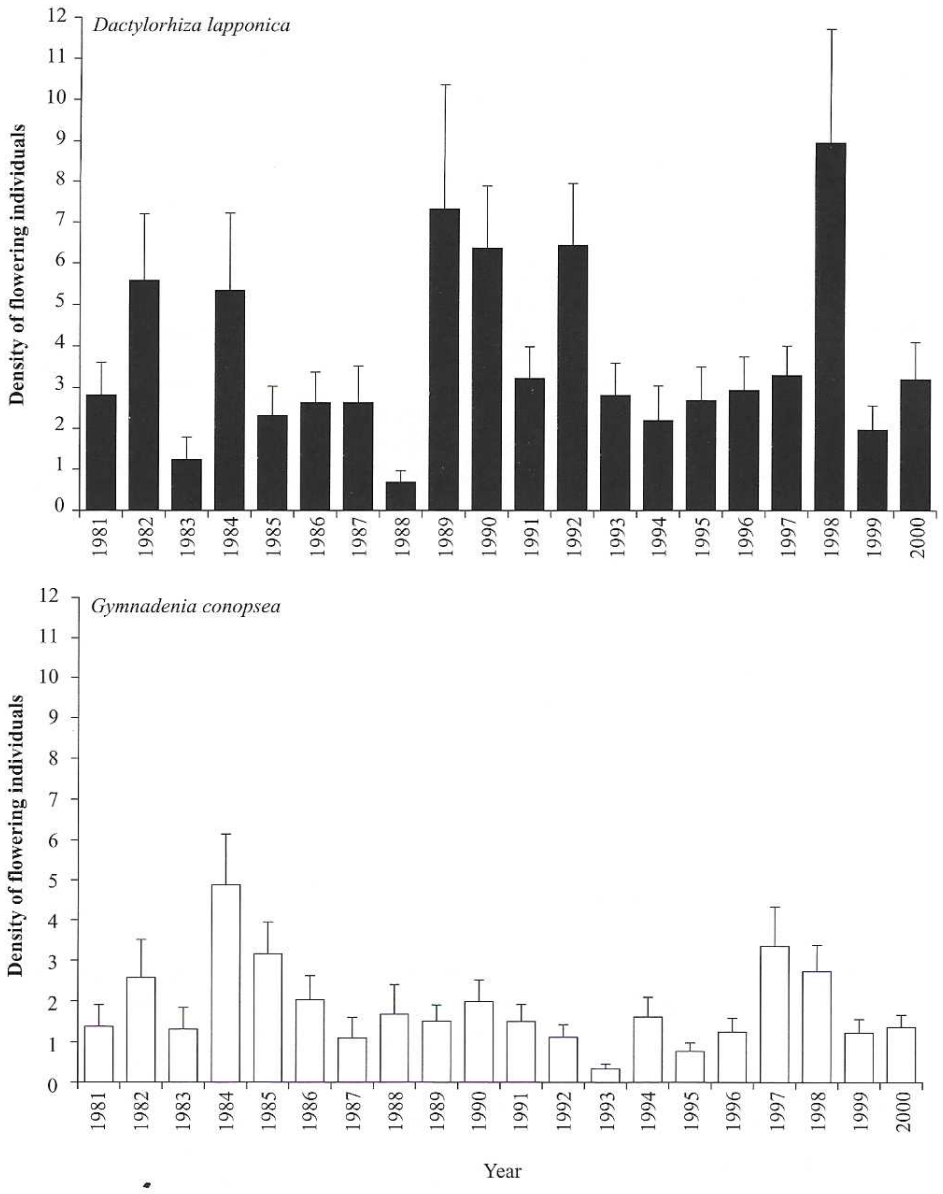


*Figure 3.* Average density of flowering individuals in unscythed 12.5 $m^2$ plots over the period 1981-2000. The averages are based on a total of 27 plots for *Dactylorhiza lapponica* and 45 plots for *Gymnadenia conopsea*.



*Table 4.* Mean height (cr
*conopsea* in unscythed pl
plots in 5 rich-fen localiti
2 plots in 2 wooded grass

| |
|---|
| 1982 |
| 1983 |
| 1984 |
| 1985 |
| 1986 |
| 1987 |
| 1988 |
| 1989 |
| 1990 |
| 1991 |
| 1992 |
| 1993 |
| 1994 |
| 1995 |
| 1996 |
| 1997 |
| 1998 |
| 1999 |
| 2000 |
| All years |

being almost parallel
in *D. lapponica*, and

For *D. lapponica*,
axes and the density
variation (Table 5),
and flowering density
showed a significant
represents increasing
vious to flowering (F
ters also revealed sig
$T\text{-}1_{AUG}$, $T\text{-}1_{MAYAUG}$
between weather con
*ica* was found, nor be
on each spike.

*Table 4.* Mean height (cm) of flowering individuals of *Dactylorhiza lapponica* and *Gymnadenia conopsea* in unscythed plots at Sølendet during 1982-2000. Data for *D. lapponica* come from 14 plots in 5 rich-fen localities. Those for *G. conopsea* derive from 9 plots in 5 rich-fen localities, and 2 plots in 2 wooded grassland localities.

| | *Dactylorhiza lapponica* | | *Gymnadenia conopsea* | |
|---|---|---|---|---|
| | **n** | **mean ± SE** | **n** | **mean ± SE** |
| 1982 | 36 | 13.9 ± 0.5 | 2 | 15.5 ± 3.5 |
| 1983 | 18 | 11.4 ± 1.0 | 5 | 15.2 ± 3.5 |
| 1984 | 71 | 16.9 ± 0.4 | 19 | 19.8 ± 1.1 |
| 1985 | 23 | 16.3 ± 1.0 | 16 | 19.7 ± 0.8 |
| 1986 | 29 | 15.8 ± 0.6 | 10 | 18.7 ± 1.6 |
| 1987 | 21 | 16.1 ± 0.8 | 9 | 17.4 ± 1.5 |
| 1988 | 5 | 20.8 ± 2.9 | 10 | 23.7 ± 0.9 |
| 1989 | 72 | 17.6 ± 0.4 | 16 | 18.1 ± 0.8 |
| 1990 | 74 | 14.9 ± 0.5 | 22 | 17.1 ± 0.5 |
| 1991 | 39 | 19.4 ± 0.5 | 25 | 20.1 ± 0.7 |
| 1992 | 72 | 12.0 ± 0.4 | 25 | 14.2 ± 0.6 |
| 1993 | 35 | 12.5 ± 0.4 | 7 | 15.9 ± 0.9 |
| 1994 | 43 | 16.2 ± 0.7 | 31 | 22.3 ± 0.7 |
| 1995 | 34 | 11.1 ± 0.4 | 18 | 18.1 ± 0.7 |
| 1996 | 45 | 20.5 ± 0.6 | 25 | 21.2 ± 0.8 |
| 1997 | 42 | 17.1 ± 0.6 | 71 | 23.0 ± 0.6 |
| 1998 | 78 | 17.6 ± 0.5 | 51 | 20.0 ± 0.6 |
| 1999 | 30 | 16.0 ± 0.6 | 27 | 19.0 ± 1.1 |
| 2000 | 35 | 18.1 ± 0.5 | 24 | 17.2 ± 1.4 |
| **All years** | **802** | **16.0 ± 0.2** | **413** | **19.7 ± 0.2** |

being almost parallel from 1982-1997. The height ranged from (4) 10-22 (31) cm in *D. lapponica*, and from (5) 15-25 (35) cm in *G. conopsea*.

For *D. lapponica*, the total model of the multiple regression between the PCA axes and the density of flowering individuals explained a significant part of the variation (Table 5), indicating a strong relationship between weather conditions and flowering density. Most of the relationship was related to PCA axis 1, which showed a significant positive correlation with flowering density. This axis mainly represents increasing temperature during summer and early autumn the year previous to flowering (Fig. 2a). Single regression analyses of these weather parameters also revealed significant positive correlations between flowering density and $T\text{-}1_{AUG}$, $T\text{-}1_{MAYAUG}$, $T\text{-}1_{JUNAUG}$, $T\text{-}1_{JULAUG}$, $T\text{-}1_{AUGSEP}$. No significant relation between weather conditions and the height of flowering individuals of *D. lapponica* was found, nor between weather conditions and the average number of flowers on each spike.

*Table 5.* Results of multiple regressions with principal components from a PCA of weather parameter as explanatory variables and flowering density, height of flowering individuals, and number of flowers per spike in *Dactylorhiza lapponica* and *Gymnadenia conopsea* as response variables. Data from the period 1982-2000. Significant relationships ($p < 0.05$) in boldface.

| | *Dactylorhiza lapponica* | | | | | | *Gymnadenia conopsea* | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Density | | Height (cm) | | Flowers/spike | | Density | | Height (cm) | |
| | value | p | value | p | value | p | value | p | value | p |
| **Total model ($R^2_{adj}$)** | **0.350** | **0.031** | -0.077 | 0.618 | 0.008 | 0.422 | -0.087 | 0.656 | 0.260 | 0.083 |
| **Coefficients** | | | | | | | | | | |
| **Constant** | 3.727 | - | 15.924 | - | 7.649 | - | 1.841 | - | 18.549 | - |
| **Axis 1** | **1.436** | **0.002** | -0.598 | 0.393 | 0.128 | 0.652 | 0.049 | 0.843 | -1.075 | 0.069 |
| **Axis 2** | 0.246 | 0.539 | 0.637 | 0.373 | -0.541 | 0.077 | 0.259 | 0.306 | 0.826 | 0.159 |
| **Axis 3** | 0.021 | 0.958 | -0.596 | 0.380 | 0.094 | 0.733 | 0.278 | 0.273 | 0.058 | 0.915 |
| **Axis 4** | 0.256 | 0.523 | 0.500 | 0.481 | -0.204 | 0.483 | 0.032 | 0.897 | **1.332** | **0.030** |

For *G. conopsea*, the multiple regression analysis revealed no relationship between weather conditions and the flowering density, but a positive correlation was found between height of generative individuals and PCA axis 4 (Table 5). This axis mainly represents increasing precipitation during spring and early summer, and decreasing temperature in May and June of the current season (Fig. 2b), but includes very little of the total variation (eigenvalue 0.066). Single regression analyses of these weather parameters did not reveal any significant correlations.

There were more flowering individuals of both species in unscythed plots than in biennially and annually scythed plots, although the difference between unscythed and biennially scythed plots was not statistically significant for *D. lapponica*. The numbers per 12.5 $m^2$ were 3.6, 3.1 and 0.9, respectively, for *D. lapponica*, and 1.8, 0.8 and 0.1, respectively, for *G. conopsea* (Fig. 4).

### Survival and performance of individual plants

In unscythed plots, the annual mortality was lower for *D. lapponica* than for *G. conopsea*, with mean values of 0.10 and 0.14, respectively. For individuals of *D. lapponica*, mortality was highest the first year after recruitment and decreased rapidly before stabilising at a lower level. For individuals of *G. conopsea*, mortality was more variable and stayed high for several years after recruitment, before dropping to zero (Table 6). Depletion curves indicate a half-life of 5.8 years for *D. lapponica* in unscythed plots. More than 30% of the initial cohorts had survived after 10 years (Fig. 5), and several individuals observed in 1981 were still alive in 2000. For *G. conopsea*, the half-life was found to be 3.2 years, and more than 20% of the cohorts were alive after 9 years.

Both species had a higher mortality in biennially scythed plots than in unscythed ones, with mean values of 0.21 and 0.16, respectively (Table 6). The mortality was very variable and did not seem to decrease with age, at least not for *D. lapponica*. For *G. conopsea,* the cohorts in the biennially scythed plots were so small that a clear

*Figure 4.* Average densit
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### Cost of flowering

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## Discussion

### Relationships betwe

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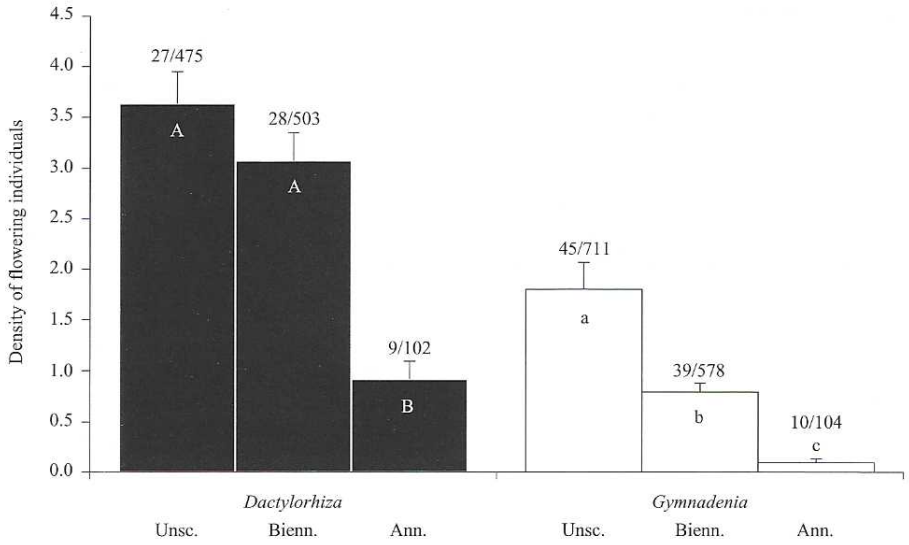


*Figure 4.* Average density of flowering individuals in 12.5 $m^2$ plots over the period 1981-2000 in unscythed (Unsc.), biennially scythed (Bienn.) and annually scythed (Ann.) plots. Narrow bars denote standard error. Letters indicate significant difference ($p < 0.05$) between scything frequencies as a result of Tukey's honestly significant difference test (multiple comparisons) in a one-way ANOVA. Numbers above the bars show the number of plots/number of recordings.

tendency cannot be recognised. The half-life in the biennially scythed plots was reduced for both species, to 2.8 years for *D. lapponica* and 1.3 years for *G. conopsea* (Fig. 5).

### Cost of flowering

87% of all flowering events recorded for *D. lapponica* in unscythed plots were preceded and followed by a year in a non-flowering condition. The corresponding value for *G. conopsea* was 92% (Fig. 6). In both species, the average size of individuals in the vegetative phase before a flowering event was significantly higher than after it, even when individuals missing after flowering were omitted (Fig. 7).

## Discussion

### Relationships between flowering and weather conditions

The flower primordia of *Dactylorhiza* species probably form during the summer previous to flowering (Leeson *et al.* 1991). A relationship between size and subsequent flowering has also been observed in species of this genus and other terrestrial orchids. It has been suggested that the plant has to reach a critical size, or a threshold size (a certain level of carbohydrate reserves), before flowering is induced

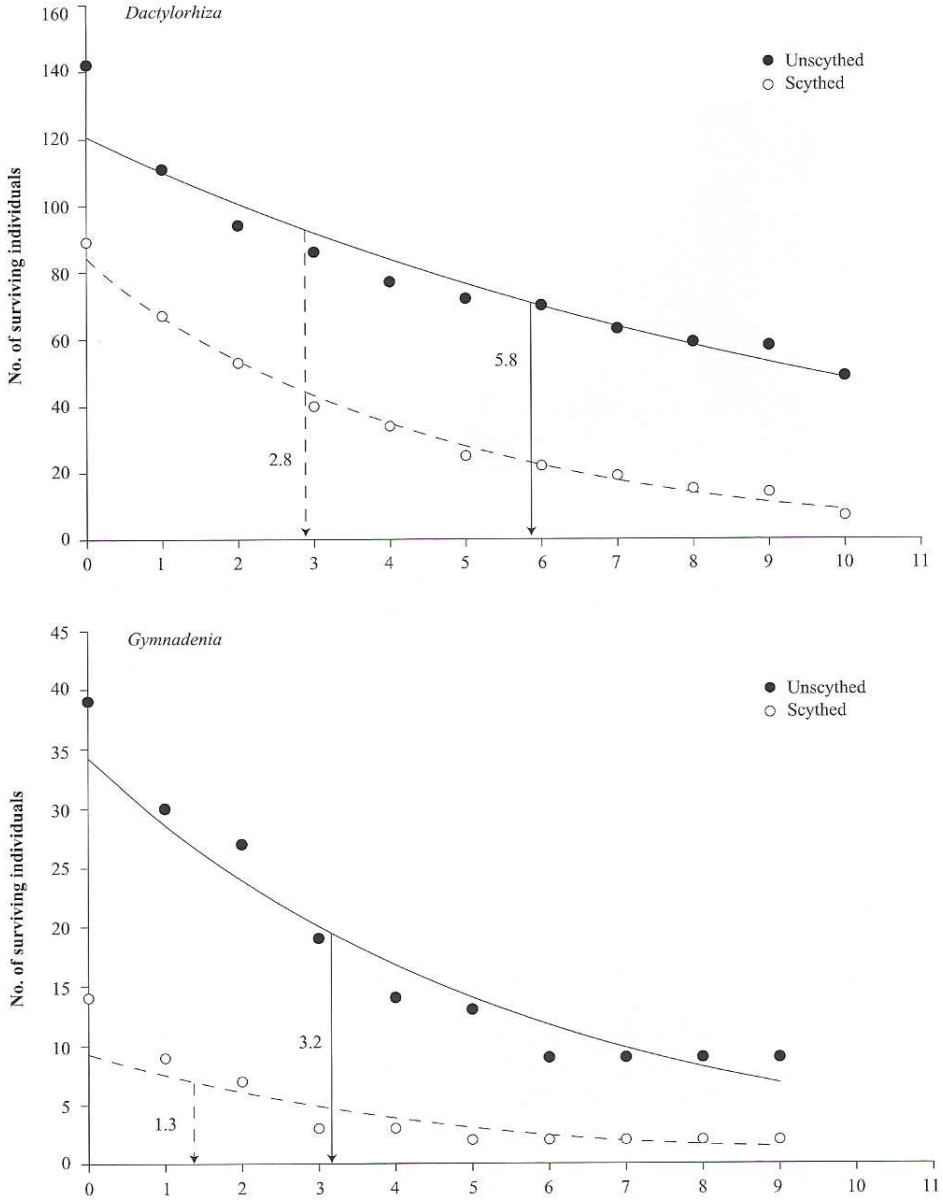


*Figure 5.* Depletion curves of cohorts from unscythed and biennially scythed plots. Surviving individuals in three cohorts of flowering individuals of *Dactylorhiza lapponica* (1984, 1989, 1990) from 10 unscythed plots (n = 142) and 11 biennially scythed plots (n = 89), and two cohorts of flowering individuals of *Gymnadenia conopsea* (1984, 1991) from 6 unscythed plots (n = 39) and 5 biennially scythed plots (n = 14). Arrows with values indicate half-lives. Curves are fitted by linear regression of log-transformed numbers and the half-life was found by solving the equation of the regression. The slope of the curve representing the unscythed plots was significantly different (at p = 0.05) from the slope of the curve representing the scythed plots in *D. lapponica,* but not in *G. conopsea* (F-test for the difference between two regression coefficients).



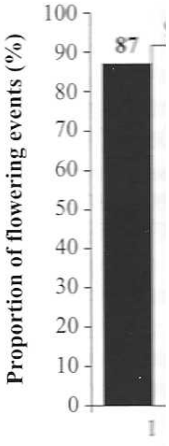


*Figure 6.* Proportion of su
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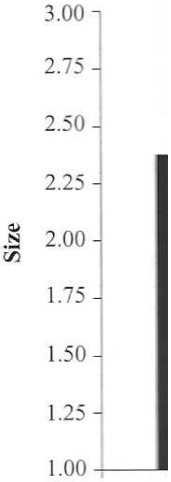


*Figure 7.* Mean size (size
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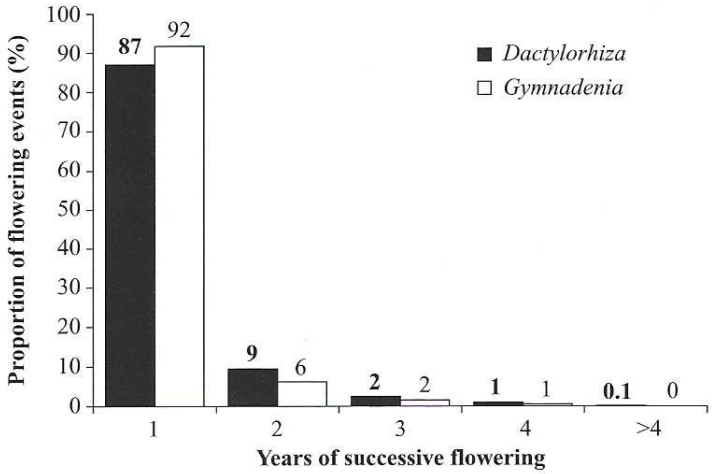


*Figure 6.* Proportion of successive flowering events in unscythed 12.5 $m^2$ plots. Numbers above the bars show the proportion of flowering events in each group. For *Dactylorhiza lapponica,* the diagram is based on data from 417 individuals from 12 plots in 1981-2000; a total of 762 flowering events. For *Gymnadenia conopsea,* the diagram is based on data from 240 individuals from 11 plots in 1982-2000; a total of 387 flowering events.

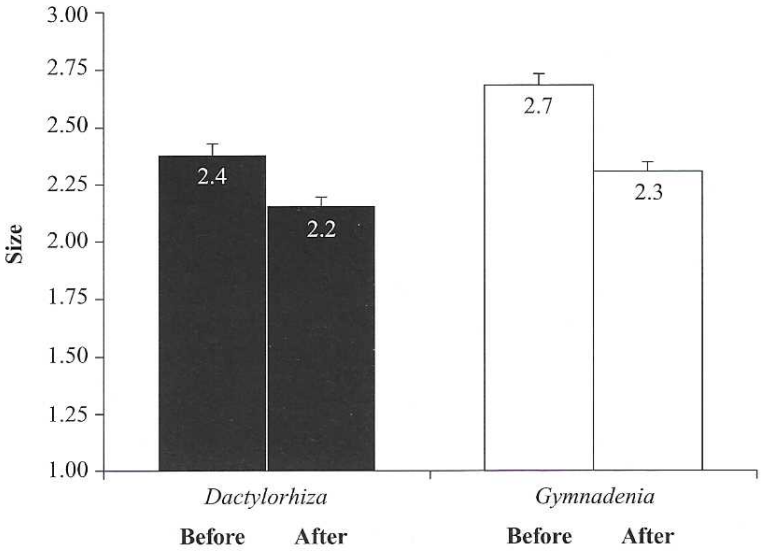


*Figure 7.* Mean size (size classes 1-3, see text for explanation) of vegetative individuals before and after flowering. Narrow bars denote standard error. Individuals not observed above the ground after flowering (missing or dead) are not included in the mean values. Based on the same data as in Fig. 5. The differences in mean size were significantly different for both species ($p < 0.01$ in a t-test).

*Table 6.* Life table of three cohorts of flowering individuals of *Dactylorhiza lapponica* (1984, 1989, 1990) and two cohorts of flowering individuals of *Gymnadenia conopsea* (1984, 1991) in unscythed and biennially scythed plots at the Sølendet Nature Reserve.

| | *Dactylorhiza lapponica* | | | *Gymnadenia conopsea* | | |
|---|---|---|---|---|---|---|
| **Years after first flowering** | **Number observed** | **Proportion surviving** | **Mortality rate** | **Number observed** | **Proportion surviving** | **Mortality rate** |
| **Unscythed plots** | | | | | | |
| $x$ | $a_x$ | $l_x$ | $q_x$ | $a_x$ | $l_x$ | $q_x$ |
| 0 | 142 | 1.00 | 0.22 | 39 | 1.00 | 0.23 |
| 1 | 111 | 0.78 | 0.15 | 30 | 0.77 | 0.10 |
| 2 | 94 | 0.66 | 0.09 | 27 | 0.69 | 0.30 |
| 3 | 86 | 0.61 | 0.10 | 19 | 0.49 | 0.26 |
| 4 | 77 | 0.54 | 0.06 | 14 | 0.36 | 0.07 |
| 5 | 72 | 0.51 | 0.03 | 13 | 0.33 | 0.31 |
| 6 | 70 | 0.49 | 0.10 | 9 | 0.23 | 0.00 |
| 7 | 63 | 0.44 | 0.06 | 9 | 0.23 | 0.00 |
| 8 | 59 | 0.42 | 0.02 | 9 | 0.23 | 0.00 |
| 9 | 58 | 0.41 | 0.16 | 9 | 0.23 | - |
| 10 | 49 | 0.35 | - | - | - | - |
| **Average mortality** | | | **0.10** | | | **0.14** |
| **Biennially scythed plots** | | | | | | |
| $x$ | $a_x$ | $l_x$ | $q_x$ | $a_x$ | $l_x$ | $q_x$ |
| 0 | 89 | 1.00 | 0.25 | 14 | 1.00 | 0.36 |
| 1 | 67 | 0.75 | 0.21 | 9 | 0.64 | 0.22 |
| 2 | 53 | 0.60 | 0.25 | 7 | 0.50 | 0.57 |
| 3 | 40 | 0.45 | 0.15 | 3 | 0.21 | 0.00 |
| 4 | 34 | 0.38 | 0.26 | 3 | 0.21 | 0.33 |
| 5 | 25 | 0.28 | 0.12 | 2 | 0.14 | 0.00 |
| 6 | 22 | 0.25 | 0.14 | 2 | 0.14 | 0.00 |
| 7 | 19 | 0.21 | 0.21 | 2 | 0.14 | 0.00 |
| 8 | 15 | 0.17 | 0.07 | 2 | 0.14 | 0.00 |
| 9 | 14 | 0.16 | 0.50 | 2 | 0.14 | - |
| 10 | 7 | 0.08 | - | - | - | - |
| **Average mortality** | | | **0.21** | | | **0.16** |

(Snow and Whigham 1989, Wells and Cox 1989, Dijk and Olff 1994, Kindlmann and Balounová 1999, Willems and Dorland 2000). The size of the plant, which is highly correlated with the amount of stored nutrients in the tuber, is likely to be affected by the weather conditions. If there is a relationship between plant size and flowering, then this may explain the positive relationship found in *D. lapponica* between summer temperature and flowering density the following year. However, a positive relationship between late summer and early autumn temperature (August+September) and flowering density in the subsequent year was also found. We know from observations that most of the aboveground parts of this species have withered and most of the photosynthetic activity has ceased after the middle of August. High temperature after this time is therefore unlikely to have any effect on the autotrophic production. The explanation of the positive relationship may be found in

the mycotrophic behaviour of the species. It is well known that nutrients are transported from fungi to underground organs of seedlings and juvenile individuals (Hadley and Pegg 1989, Dijk *et al.* 1997, Smith and Read 1997). The degree of mycotrophy in adult individuals is less known, and remains controversial. It has been reported in *Goodyera repens* (L.) R. Br. (Alexander and Hadley 1984, Alexander *et al.* 1984), and there is much indirect evidence that adults of several phototrophic orchid species rely heavily on their fungal partner for organic C (Vermeulen 1947, Smith and Read 1997). According to Vermeulen (1947), the new tuber of *Dactylorhiza* species can be infected already in the autumn, and the organic C acquired from the fungus is likely to be stored in the tuber. This may prolong the growth period of the tuber in years with warm weather in late summer and early autumn, thereby enhancing the probability of the plant surviving the winter and increasing the probability of it developing an inflorescence from its flower primordia.

In *G. conopsea*, we found no statistical relationship between flowering density and weather conditions. The fact that *G. conopsea* has a wide regional (zonal) amplitude (from nemoral to low alpine) indicates that temperature variation is not a problem for this species in the study area. Cool summers may even favour it indirectly by having a negative impact on many of its competitors. High mortality rates independent of weather conditions may also be important in explaining why no relationships were found (see below). The relationships found between the height of generative individuals and precipitation (positive) and temperature (negative) during spring and early summer are probably a result of noise in the data material, as PCA axis 4 represents very little variation. However, it is possible that high temperature and low precipitation during spring can result in conditions sufficiently dry to hamper the growth in some of the grassland localities included in the monitoring. In such situations, lower temperature and higher precipitation will have a positive effect on the height of individuals.

### The effect of age and cost of flowering on subsequent flowering and survival

There is no indication in our material that age has a negative effect on either the probability of flowering or the size of individuals. We have used the first year of flowering as year 0. According to the literature, *G. conopsea* and species from the genus *Dactylorhiza* are able to flower for the first time in the third year after germination, but 4 years or longer are usually required (Vermeulen 1947, Leeson *et al.* 1991, Rasmussen 1995, Dijk *et al.* 1997). Since the growing season in the study area is rather short, the period before first flowering is probably even longer. The individuals of both species may therefore be more than 5 years old at the time of first flowering. After the tuber is fully developed and the plant is able to produce a new tuber, the old tissue is replaced by new tissue every season. In this sense, a plant flowering for the first time eight years ago is no older than a plant flowering for the first time one year ago. Their current performance may only be loosely related to their "age" (Harper 1977, Wells 1981), and is more likely a result of the conditions they have experienced in the last one or two seasons.

The probability of dying after flowering is high in both species, and the risk remains high in *G. conopsea* for several years. The cost of flowering also leads to a low probability of flowering in the surviving individuals. In both species, only about

10% of the individuals surviving the flowering will flower again in the subsequent year (Fig. 6). Both the high mortality and the high cost of flowering are therefore important factors explaining the large fluctuations we observe in the number of flowering individuals in these species. For *D. lapponica*, this indicates that a good flowering season is more likely to be followed by a decline in the flowering density than a continued high flowering density, even if weather conditions are favourable for several years in succession. The results for *G. conopsea* are more dramatic, indicating that a good flowering season is likely to be followed by a lower flowering density for several years, regardless of the weather conditions.

### The effect of regular scything on flowering and survival

Scything reduces the longevity of individuals in both species. A possible explanation is that disturbance in the form of scything reduces the ability of the plant to store nutrients in its tuber, leading to an increased probability of dying during the winter. For the same reason, scything also leads to longer non-flowering periods. Scything also seems to affect *G. conopsea* more than *D. lapponica*. There may be several reasons for this. The main one is probably the difference in phenology between *D. lapponica* and *G. conopsea*. When scything takes place in early August, many individuals of *D. lapponica* have already reallocated large parts of their nutrients to their tuber and started to wither. The amount of nutrients removed by scything is thus smaller in *D. lapponica* than in *G. conopsea*, many individuals of which have not completed their growth and may still be flowering. Their slightly different growth form is also important. In *D. lapponica,* one of the leaves in the rosette is more or less prostrate, and usually remains untouched by the scythe. The leaves of *G. conopsea* are more upraised, and all the leaves are usually cut off during scything. The difference in biotope may also be important. Although this is not a topic for this study, observations have shown us that the impact of scything on *D. lapponica* and *G. conopsea* varies with the vegetation type. In some fertile communities (a majority of the plots were in rather infertile communities), orchids flower and survive almost equally well in plots scythed every second year as in unscythed plots.

## Conclusion

Flowering density in *D. lapponica* seems partly to be governed by weather conditions, whereas that in *G. conopsea* is not. Both species experience a high cost of flowering, expressed as high mortality after flowering, and a low proportion of flowerings in several successive years. Intensive scything (annually or biennially at the peak of production) prolongs the non-flowering periods and reduces the longevity in both species. Intensive scything is thus likely to lead to recruitment failure and rapid decline in the number of individuals. The optimal management in order to maintain large populations of the two orchids will be scything or mowing at intervals sufficiently long to enable them to recover after flowering (more than 2 years), but sufficiently short to restrain the shrubs and trees from invading the rich fens and wooded grasslands in which the orchids live.

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A founder pop
a 30-year strug

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**Abstract**
In this paper the results
Mediterranean orchid spe
southern part of The Neth
to 2001. Application of th
autogamous, (ii) the mini
and, (iii) the juvenile life
four distinct stages are re
ing plant ("founder plant"
number of plants increase
(iv) a rather stable stage
population decline was li
and unfavourable vegeta
absence of plants above g
to year. The age of indivi
many plants present in st
long-lived. Yearly mowing
have access to the inflores
as a protected Nature Re
ment during a long time,

**Key words**: dormancy, fr
lination rate, The Netherl

## Introduction

A fairly large number
ern Europe by local
Orchids from the Me
tion in response to h
prehistoric times, sev
open, semi-natural
(Ellenberg 1988).

*Trends and fluctuations*
*in terrestrial orchid popu*
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