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Populations of Orchids at the Northern Limit of Their Distribution (Murmansk Oblast): Effect of Climate

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Abstract—The effect of climatic conditions on the dynamics of 21 populations of 10 species of the family Orchidaceae at the northern limit of their range in Europe was studied between 1992 and 2004. The abundance of orchid populations proved to depend primarily on air temperature during the previous and current growing seasons.

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Key words: Murmansk oblast, Orchidaceae, northern limit of the range, effect of climate.

The effect of climate on plant populations manifests itself in their distribution over the earth's surface. The demography of orchids is also subject to climatic influences. This has been predicted by many authors, but studies dealing with these influences are scarce (Kull, 2002). Apparently, the effect of temperature on plants varies at different latitudes, at the boundaries of species ranges, and under different ecological conditions (Blinova et al., 2003). Very high temperatures causing summer drought and low temperatures with frosty days in the growing season are equally harmful to orchid populations (Willems, 1989; Tamm, 1991; Blinova, 2002).

The purpose of this study was to estimate the effect of climatic parameters (temperature, air humidity, and snow depth) on the dynamics of orchid populations at the northern limit of their range in Europe. The study was performed with 16 out of 18 orchid species growing in Murmansk oblast (Blinova, 2005).

STUDY REGION

Murmansk oblast (66–70° N) is in the Atlantic–Arctic climatic zone of the temperate belt (Yakovlev, 1961). The greater part of its territory lies north of the Arctic Circle, but the Gulf Stream makes its climate milder than in Far North regions located east of the Kola Peninsula. This accounts for the prevalent development of forest vegetation (Tsinzerling, 1934; Regel, 1935; Mishkin, 1953; Ramenskaya, 1983). Geomorphologically, Murmansk oblast is a part of the Baltic Shield and its topography is generally sloping in a northwest–southeast direction (Strelkov, 1973).

The annual average air temperature varies from 0°C on the coasts of the Barents and White seas to –2°C in the central and mountain regions. Likewise, monthly average temperatures in January and July vary from –8 to –13°C and from 8 to 13°C, respectively. The growing season lasts from June to September. The average amount of precipitation varies from 800 to 1200 mm in mountain regions and from 500 to 800 mm in the greater part of the plain area (Yakovlev, 1961; Yakovlev and Kozlova, 1971).

MATERIAL AND METHODS

Most populations of orchid species selected for analyzing climatic effects grow in the vicinity of the city of Apatity, and some populations grow near the Polar–Alpine Botanical Garden–Institute (PABGI). Meteorological data concerning one of PABGI nursery gardens were analyzed. Semko (1983) showed that air temperature and humidity, the number of frosty days in the growing season, and snow depth (except for in April and May) in that area are very close to those recorded at a weather station in Apatity, with deviations in absolute values (e.g., of snow depth in May) having no effect on the relative ratio and trends of these parameters.

The following long-term data were analyzed: average results of daily measurements of air temperature 2 m above the ground and air temperature 30 cm above the ground during the growing season; air humidity, %; snow depth, mm; and the number of frosty days during the growing season.

The data on temperature were processed statistically to calculate mean values and sums over certain periods. To analyze cause-and-effect relationships, a regression model was used. Samples were compared by Student's

Table 1. Statistical parameters and trends of monthly and annual air temperatures 2 m above the ground (Murmansk oblast, 1991–2004)

Parameter	Temperature by months											
	Jan.	Feb.	March	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
X	–11.2	–11.8	–7.6	–3.4	1.6	8.9	12.3	9.6	5.3	–0.4	–7.5	–9.5
SD	2.7	3.1	2.4	2.8	1.6	1.8	2.3	1.4	2.2	2.5	3.2	2.3
Trend, °C over 10 years	–0.52	–0.5	+0.03	+0.7	+0.43	+0.15	+0.95	+0.21	+0.48	+0.07	+0.23	–0.43
p	0.22	0.40	0.94	0.18	0.09	0.57	**0.01**	0.42	0.18	0.85	0.78	0.32
Annual average	$X = -1.2$°C, $SD = 0.7$°C, trend = +0.18°C over 10 years ($p = 0.23$)											

Note: (X) arithmetic mean, (SD) standard deviation, (p) probability of error.

Table 2. Statistical parameters and trends of some climatic factors during the growing season (Murmansk oblast, 1991–2004)

Parameter	Air temperature, °C				Number of frosty days				Air humidity, %			
	30 cm above the ground, by months											
	June	July	Aug.	Sept.	June	July	Aug.	Sept.	June	July	Aug.	Sept.
X	8.8	12.8	9.5	4.9	2.3	0.2	0.9	9.1	65	69	76	80
SD	2.0	2.1	1.6	2.2	2.2	0.6	1.5	6.6	10.7	8.6	6.7	6.3
Trend over 10 years	+0.28	+1.09	+0.13	+0.49	–0.7	–0.1	–0.4	–1.7	–3.3	–0.6	+1.1	–0.6
p	0.37	**0.01**	0.74	0.17	0.08	0.35	0.13	0.13	0.06	0.67	0.48	0.62
Average from June to September	Temperature: $X = 9.0$°C, $SD = 1.3$°C, trend = +0.45°C over 10 years ($p =$ **0.03**) Frosty days: $X = 12.4$, $SD = 8.3$, trend = –2.7 over 10 years ($p =$ **0.04**) Humidity: $X = 73$%, $SD = 6.9$%, trend = –0.80% over 10 years ($p = 0.51$)											

t-test, considering the differences significant at $p \leq 0.05$. In tables, the values of trends and correlation coefficients significant at $p \leq 0.10$ are shown in boldface.

To study the effect of climatic factors on the size of orchid populations, coefficients of its correlation with the following parameters were calculated: annual average temperature (previous vs. current year), temperature during the growing season (previous vs. current year), monthly average temperature in July (previous vs. current year), the number of frosty days in the previous year, air humidity (previous vs. current year), and snow depth (from October to May).

RESULTS

Dynamics of Weather Conditions between 1991 and 2004

The annual average air temperature over this period was –1.2°C. It tended to increase, but its linear trend was insignificant (+0.18°C over 10 years, $p \geqslant 0.05$) (Table 1). Monthly average temperatures in different seasons changed in opposite directions: winter temperatures (December–February) decreased (–0.4 to –0.5°C over 10 years), whereas spring, summer, and autumn temperatures (March–October) increased (+0.03 to +0.95°C over 10 years). However, a significant trend ($p < 0.05$) was revealed only in July.

In the growing season (April–September), air temperature averaged 9°C and was characterized by a positive (+0.45°C over 10 years) and significant trend ($p < 0.05$) (Table 2), mainly due to a considerable rise of the July temperature (+1.09°C over 10 years, $p < 0.05$). The number of frosty days per growing season' averaging 12.4 days, significantly decreased (–2.7 days over 10 years, $p < 0.05$), as well as the number of such days in September. Air humidity averaged 73% and showed a slight and insignificant tendency to decrease (–0.80 % over 10 years, $p \geqslant 0.05$), especially in June (–3.3% over 10 years, $p = 0.06$). The driest growing seasons were those of 1994, 2001, and 2003 (air humidity 48–54%).

The annual average snow depth was 695 mm (Table 3). This parameter showed an almost significant tendency to decrease (–61 mm over 10 years, $p = 0.06$). This tendency was also negative and significant in the period from October to December (–11 mm over 10 years, $p < 0.05$), although snow depth in October began to

Table 3. Statistical parameters and trends of snow depth (Murmansk oblast, 1991–2004)

Parameter	Snow depth, mm				Temperature, °C			
	months							
	Oct.	Oct.–Dec.	Jan.–May	May	Oct.	Oct.–Dec.	Jan.–May	May
X	8.8	125	570	66.5	–0.4	–5.8	–6.5	1.6
SD	9.5	33	192	45.9	2.5	1.9	1.2	1.6
Trend over 10 years	+2.6	–11	–50	–12.1	+0.07	–0.05	0.01	+0.43
p	0.11	**0.04**	0.09	0.11	0.85	**0.02**	**0.00**	0.09
Annual average	Snow cover: $X = 695$ mm, $SD = 202$ mm, trend = –61 mm over 10 years ($p = 0.06$) Temperature over the snowy period: $X = -6.2$°C, $SD = 1.1$°C, trend = –0.01°C over 10 years ($p =$ **0.00**)							

Table 4. Comparison of air temperatures over two seven-year periods (1991–1997 and 1998–2004, Murmansk oblast)

Parameter	Air temperature, °C			
	annual average		average over growing season	
	1991–1997	1998–2004	1991–1997	1998–2004
X	–1.4	–0.9	**8.3**	**9.7**
SD	0.5	0.8	0.5	0.3
max	–0.8	0.1	10.6	10.6
min	–2.3	–2.1	6.3	8.4
Trend, °C over 10 years	–0.9	+1.1	+0.86	+2.1
p	0.11	0.21	0.63	0.49
Student's *t*-test	$t = 1.81$, $p = 0.22$		$t = 1.81$, $p = 0.05$	

increase slightly (+2.6 mm, $p > 0.05$). Disbalance with respect to temperature (on average, however, both temperature and snow depth increased) apparently reflects unstable weather in October, with snow falling in greater amounts and melting more frequently. Snow depth in May also tended to decrease, but this tendency lacked statistical significance (–12.1 mm, $p > 0.05$).

Comparison of Weather Parameters from 1991 to 1997 and from 1998 to 2004

Some orchid populations were studied between 1992 and 1996, whereas other populations were studied between 1998 and 2004. For this reason, the entire study period (1991–2004) was divided into two seven-year periods. The average annual air temperature was markedly lower between 1991 and 1997 than between 1998 and 2004 (Table 4). It tended to decrease in the first period (–0.9°C) and to increase in the second period (+1.1°C), but both trends were insignificant. The average temperature of the growing season increased from 8.3°C in the first period to 9.7°C in the second period (data statistically significant).

Dynamics of Orchid Populations: Statistical Prognosis for 10 Years

Among 21 populations studied, positive and negative demographic trends were revealed in 10 and 11 populations, respectively (Table 5), but the increase or decrease in the total abundance was statistically significant in only three populations each. A positive trend in the number of generative shoots was characteristic of eight populations, being statistically significant in four populations. A negative trend observed in 13 populations was statistically significant in two cases.

Populations of six out of ten orchid species showed a trend toward an increase in their size (the member of shoots), but it was significant only in *Cypripedium calceolus* and *Platanthera bifolia*; eight species showed a negative trend, which was significant in *Listera ovata*, *Coeloglossum viride*, and *Dactylorhiza incarnata*. Both positive and negative trends were revealed in populations of *Cypripedium calceolus*, *Coeloglossum viride*, *Dactylorhiza maculata,* and *Gymnadenia conopsea*, but they lacked statistical significance. An increase in the number of generative shoots (revealed in six species) was statistically significant only in *Cypripedium calceolus*, *Gymnadenia conopsea*, and *Platanthera*

Table 5. Orchid population size and trends in its dynamics in Murmansk oblast

Species	Population, years	Shoots	*X*	*SD*	Trend over 10 years		*p*
					absolute	relative to current state, %	
Cypripedium calceolus	cc_1 1992–2004	All	243	48	**+26**	11	0.01
		g	31	28	**+11**	35	0.05
	cc_2 1992–2004	All	204	45	+8	4	0.52
		g	6	7	**+4**	67	0.02
	cc_3 1992–2004	All	24	5	–2	–8	0.17
		g	4	3	+1	25	0.69
	cc_4 2000–2004	All	112	12	–4	–4	0.43
		g	35	13	–7	–20	0.16
Listera ovata	lo_1 1998–2004	All	39	15	–1	–3	0.95
		g	10	4	–4	–40	0.46
	lo_2 2001–2004	All	41	13	**–45**	–110	0.06
		g	17	6	–16	–94	0.26
Epipogium aphyllum	eaph_1 1995–2004	g	5	6	–3	–60	0.39
Coeloglossum viride	cv_1 1992–2004	All	61	27	+9	15	0.19
		g	18	10	+1	6	0.64
	cv_2 1992–1996	All	25	10	**–38**	–152	0.06
		g	7	7	**–29**	–414	0.02
Dactylorhiza incarnata	di_1 2001–2004	All	14	1	–4	–29	0.33
		g	3	5	–21	–700	0.24
	di_2 2002–2004	All	10	1	–4	–40	0.33
		g	3	5	–31	–1033	0.27
	di_1a 2001–2004	All	62	8	+42	68	0.45
		g	29	1	–4	–14	0.67
	di_2a 2002–2004	All	50	17	**–116**	–232	0.10
		g	25	12	**–81**	–324	0.05
Dactylorhiza maculata	dm_1 1992–1995	All	30	13	–50	–167	0.31
		g	5	4	–18	–360	0.26
	dm_2 1992–1994	All	46	7	+56	122	0.15
		g	22	3	+24	109	0.12
	dm_3 1992–1996	All	59	10	+6	10	0.82
		g	23	9	–28	–122	0.19
	dm_4 1992–1994	All	20	10	–80	–400	0.14
		g	37	10	–68	–184	0.30
Gymnadenia conopsea	gc_1 1992–1996	All	56	6	–3	–5	0.84
		g	9	6	–18	–200	0.21
	gc_2 1992–1994	All	29	16	+60	207	0.69
		g	11	3	**+20**	182	0.07
	gc_3 1992–1996	All	16	4	+7	44	0.60
		g	7	2	–7	–100	0.16
Platanthera bifolia	pb_1 1992–2004	All	118	41	**+29**	25	0.05
		g	33	13	**+10**	30	0.02
Hammarbya paludosa	hp_1 2001–2004	All	72	32	–137	–190	0.37
		g	48	25	–101	–210	0.39
Malaxis monophyllos	mm_1 1998–2004	All	107	60	+109	102	0.11
		g	25	15	+25	100	0.16

Table 6. Relationships between climatic parameters and the number of shoots in orchid populations

No.	Climatic parameter*	Correlation between climatic parameter and	
		total population abundance	number of generative shoots in populations
1	$t_{(n-1)}$_1–12	cc_1	**cc_2**, cc_3, cc_4, cv_1
2	t_n_1–12	**cc_1**, cc_3, **gc_3**, **dm_1**	
3	$t_{(n-1)}$_6–9	cc_1, **cc_3**, **cv_1**, gc_1(–), dm_3(–)	cc_1, cc_2, lo_2 (–), pb_1, **di_1(–)**
4	t_n_6–9	**lo_1**, lo_2(–), **dm_2**, **di_2**, **hp_1(–)**	cc_2, **lo_2**, pb_1, gc_2, **dm_2**, **dm_4(–)**, hp_1(–)
5	$t_{(n-1)}$_7	cc_1, **cc_3(–)**, **pb_1**, di_1(–)	**pb_1**, di_2(–)
6	t_n_7	**cc_1**, lo_2(–), **dm_3**	**pb_1**
7	$0°_{(n-1)}$_6–9	**cc_1(–)**, **cv_1(–)**	cc_1(–), cc_2(–), cc_4(–)
8	$\%_{(n-1)}$	gc_1, **dm_1**, **dm_4(–)**	cc_3, di_2(–)
9	$\%_n$	lo_2(–), **dm_4**	lo_1(–), cv_2
10	h*_10–5	**cc_1(–)**, **dm_2(–)**	cc_2(–), pb_1(–), **cv_2**, **gc_2(–)**, **dm_2(–)**, **dm_4**

* Climatic parameters: $t_{(n-1)}$_1–12 and t_n_1–12, annual average air temperatures in the previous and current years; $t_{(n-1)}$_6–9 and t_n_6–9, average air temperatures over the growing season in the previous and current years; $t_{(n-1)}$_7 and t_n_7, average air temperature in July in the previous and current years; $0°_{(n-1)}$_6–9, frosty days in the previous year; $\%_{(n-1)}$ and $\%_n$, air humidity during the growing season in the previous and current years; h*_10–5, total snow depth from October to May. Populations characterized by correlation coefficients significant at $p \leq 0.05$ are shown in boldface; in other cases, $p \leq 0.10$.

bifolia. A decrease in this parameter (in eight species) was significant in *Coeloglossum viride* and *Dactylorhiza incarnata*.

Thus, a positive prognosis concerning the probable population growth may be given to approximately half of the species studied, while the other half is characterized by a negative developmental trend. This is especially true of *Listera ovata* and *Dactylorhiza incarnata*. It should be noted that the negative trend in *Coeloglossum viride* populations is apparently explained by a short individual life cycle.

Relationship between Temperature and Size of Orchid Populations

In most populations, their abundance proved to positively correlate with average air temperatures over the year, over the growing season, and in July but negatively correlate with the number of frosty days in the previous growing season (Table 6); however, the proportion of statistically significant correlation coefficients in different samples varied from 19 to 57%. The significance of correlations was higher in populations monitored for longer periods of time (in this study, for all 14 years). Thus, statistically significant relationships between population abundance and different temperature parameters was confirmed for *Cypripedium calceolus, Platanthera bifolia*, and *Coeloglossum viride.* Temperatures of the previous and current growing seasons proved to have the strongest effect on orchid populations. It is noteworthy that such an effect (estimated from the proportion of significant correlation coefficients) was not revealed when only temperatures in the warmest month of the growing season (July) were used in calculations: on the contrary, the proportion of significant coefficients decreased almost by half. This is indirect evidence that temperatures at the beginning and at the end of the growing season are important for orchid populations. A rise in temperature during the growing season leads mainly to an increase in the number of generative shoots. It should be noted that the influence of temperature on different populations of the same species may differ in strength depending on the length of the observation period, the characteristics of individual years, specific features of the population studied (its initial structure and abundance), and anthropogenic factors. For example, in the *Cypripedium calceolus* population studied beginning from 2000 (population cc_4), temperatures of the growing season proved to have no significant effect on plant abundance. Analysis of our data shows that correct data may be obtained in the course of observations on normal, complete populations of at least medium (not minimum) size for at least 10 years.

The populations of *Listera ovata, Dactylorhiza maculata, Gymnadenia conopsea*, and *Epipogium aphyllum* showed a negative correlation between their abundance and temperature. These populations (except for *Epipogium aphyllum*) were monitored for a relatively short period (3–5 years). The above phenomenon appears to be explained by species-specific factors. In a population of *Listera ovata* studied in relatively warm years (2001–2004), these are probably intrinsic factors, as fluctuation of abundance is common in populations of rhizomatous species. Populations of *Dactylorhiza maculata* and *Gymnadenia conopsea* are probably cold-hardy. In populations of *Epipogium aphyllum*, excessive heating and drying of the upper soil layer may impair organogenesis of plant parts.

Relationship between Air Humidity and Abundance of Orchid Populations

The influence of air humidity on population abundance is not unidirectional: the correlation between them is positive in some populations and negative in other populations (Table 6). On the whole, 19–20% of correlation coefficients are statistically significant. A negative correlation between the number of shoots and air humidity in the previous year is characteristic of some populations of *Dactylorhiza maculata* and *D. incarnata*; populations of *Cypripedium calceolus* and *Gymnadenia conopsea* show a positive correlation between these parameters, and both positive and negative correlations are observed in populations of *Dactylorhiza maculata.* This is evidence that the effect of air humidity, unlike the effect of temperature, is connected with other factors, e.g., with moisture content in habitats. As *D. maculata* grows in a wide range of ecotopes, the effect of increase in moisture supply on the abundance of its populations will be positive in relatively dry habitats and negative in moist habitats.

In most cases, high air humidity in the current growing season proved to have an adverse effect on the abundance of orchid populations. For example, a significant negative correlation between these parameters was revealed in *Listera ovata*. A favorable effect of increase in humidity was less frequent. The corresponding positive correlation was significant in some populations of *Coeloglossum viride* and *Dactylorhiza maculata*. The effect of air humidity on the *Hammarbya paludosa* population lacked statistical significance, although its considerable decline was apparently conditioned by droughts at the onset of the growing season in 2001 and 2002.

It appears that correctness in estimating the role of this factor is less dependent on the length of the observation period. The main factors that should be taken into account are conditions in plant habitats, including specific features of the ground vegetation layer and moisture supply.

Relationship between Snow Depth and Abundance of Orchid Populations

The correlation between the number of shoots (especially generative shoots) and snow depth in most populations was negative (Table 6). It was statistically significant in populations of *Cypripedium calceolus, Platanthera bifolia, Gymnadenia conopsea,* and *Dactylorhiza maculata*. It may well be that an excessive depth of snow cover leads to plant rotting in spring. However, two populations (*Coeloglossum viride* and *Dactylorhiza maculata*) showed a significant positive correlation of their abundance with snow depth.

DISCUSSION

The dynamics of orchid populations and variability of their flowering are impossible to explain by the influence of any individual factor such as consumption by insects, temperature, humidity, nutrient supply, or competition with other plants. Light and MacConaill (1998) found that climate has an influence on fruiting in populations of *Cypripedium parviflorum* var. *pubescens* because it determines whether conditions for pollinating insects would be favorable. They also observed that the duration of flowering in this species depends on air temperature (Light and MacConaill, 2002). In central Norway, Oien and Moen (2002) revealed a positive and statistically significant correlation between the density of generative shoots and temperatures of the previous growing season in a *Dactylorhiza lapponica* population, but such a correlation proved to be absent in a *Gymnadenia conopsea* population. The authors attribute this fact to the high tolerance of the latter species to variation in climatic factors. In Sweden, flowering in populations of *Dactylorhiza sambucina* and *Listera ovata* showed a negative correlation with summer drought in the previous growing season (Inghe and Tamm, 1988).

Most studies dealing with the effect of two factors, temperature and precipitation, on orchid populations were performed in countries such as England and the Netherlands, where a stable snow cover is virtually never formed, frosts in the growing season are also absent, but summer droughts occur sometimes. In England, the height of inflorescence in an *Ophrys sphegodes* population proved to correlate with total precipitation between October to May (the period of growth of aboveground plant organs), but other characters (in particular, reproductive) showed no dependence on climatic parameters (Hutchings, 1987a, 1987b). In another species, *Herminium monorchis*, the effect of drought stress on flowering was described (Wells, 1981). In the Netherlands, Willems and Bik (1991) found that the probability of flowering in an *Orchis simia* population strongly depended on weather conditions in the current year.

It is an established fact that some orchid species are sensitive to the amount of precipitation in spring, at the beginning of the growing season. In the Czech Republic, for example, Janeckova and Kindlmann (2002) found that periodicity of flowering in *Dactylorhiza fuchsii* populations strongly correlated with the amount of precipitation in the previous March. In a population of *Ophrys apifera* in England, Wells and Cox (1991) revealed statistically significant correlations of the height of inflorescence and the number of flowers per inflorescence with the amounts of precipitation in certain periods of the current and previous years. As a rule, all these authors studied a monospecific population growing in a certain place. A comparison of populations of the same species growing in different regions shows that their responses also differ. For example, a mild winter and moist spring and early summer are favorable for flowering in populations of *Spiranthes spiralis* in England (Wells, 1981), but the same climatic factors have no such effect in the Netherlands (Willems, 1989).

None of the available publications offers a prognostic analysis of meteorological data in relation to the demography of populations of different species growing in the same region and the population dynamics of the same species in different phytocenoses, as is done in this study. In Murmansk oblast, 10 out of 21 populations showed a positive trend of abundance in response to warming in the growing season. An analysis of correlations between demographic data and meteorological parameters has shown that the effect of the latter on populations of different species is variable. Statistically significant tendencies are not always manifested in the populations studied, which is explained by the influence of additional factors and insufficient sample size.

A comparison of prognoses concerning the climate and the dynamics of orchid populations in Murmansk oblast shows that climate warming will be generally favorable for many of these populations. However, three species—*Epipogium aphyllum, Dactylorhiza incarnata*, and *Hammarbya paludosa*—may come to the brink of extinction, as they are very sensitive to changes in moisture supply. The predicted rise of temperature and consequent aridization of their ecotopes would be fatal for these plants.

CONCLUSIONS

(1) The climate of the study region is generally becoming more continental: the contrast between the cold and warm seasons is increasing; air temperature in the growing season is rising; as a result, the number of frosty days is decreasing (especially at the end of the season) and dry periods occur at the beginning of the season; a stable snow cover is formed earlier and melts also earlier, and snow depth is decreasing.

(2) Among 21 populations studied, positive and negative demographic trends (increasing or decreasing abundance) were revealed in 10 and 11 populations, respectively. However, the trends were statistically significant only in some of these populations.

(3) An analysis of correlations between data on the abundance of orchids and meteorological parameters has shown that the effect of the latter in populations of different species is variable. The abundance of most populations positively correlates with average temperatures over the year, over the growing season, and in July, negatively correlating with the number of frosty days in the previous growing season. The influence of air humidity on population size is multidirectional. In most populations, the number of shoots negatively correlates with snow depth.

(4) A comparison of prognoses concerning the dynamics of climate and the abundance of orchid populations shows that climate warming is generally favorable for the development of populations of many orchid species. However, the populations of species sensitive to changes in moisture supply may be endangered.

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REFERENCES

Blinova, I., A Northernmost Population of *Cypripedium calceolus* L.: Demography, Flowering, Pollination. *Selbyana,* 2002, no. 23 (1), pp. 111–120.

Blinova, I.V., Systematics and Phytogeography of Orchids in the Extreme North of European Subarctic (Murmansk Region, Russia), *Caesiana*, 2005, no. 24, pp. 25–47.

Blinova, I., Willems, J.H., and van Reenen, J., Intraspecific Variation in Orchid Populations in Two Different Climatic Areas in Europe, Murmansk Region and the Netherlands: 1. Phenology, *J. Eur. Orch.,* 2003, vol. 35 (1), pp. 79–99.

Hutchings, M.J., The Population Biology of the Early Spider Orchid, *Ophrys sphegodes* Mill.: 1. A Demographic Study from 1975 to 1984, *J. Ecol.*, 1987a, no. 75, pp. 711–727.

Hutchings, M.J., The Population Biology of the Early Spider Orchid, *Ophrys sphegodes* Mill.: 2. Temporal Pattern in Behavior, *J. Ecol.*, 1987b, no. 75, pp. 729–742.

Inghe, O. and Tamm, C.O., Survival and Flowering of Some Perennial Herbs: 5. Patterns of Flowering, *Oikos*, 1988, no. 51, pp. 203–219.

Janeckova, P. and Kindlmann, P., Key Factors Affecting Shoot Growth and Flowering Performance of *Dactylorhiza fuchsii*, in *Trends and Fluctuations and Underlying Mechanisms in Terrestrial Orchid Populations*, Kindlmann, P., Willems, J. H., and Whigham, D.F., Eds., Leiden: Backhuys, 2002, pp. 99–113.

Kull, T., Population Dynamics of North Temperate Orchids, in *Orchid Biology: Review, and Perspectives*, issue VIII, Kull, T. and Arditti, J., Eds., The Netherlands: Kluwer, 2002, pp. 139–165.

Light, M.H.S. and MacConaill, M., Factors Affecting Germinable Seed Yield in *Cypripedium calceolus* var. *pubescens* (Willd.) Correll and *Epipactis helleborine* (L.) Crantz (Orchidaceae), *Bot. J. Linn. Soc.,* 1998, no. 126, pp. 3–26.

Light, M.H.S. and MacConaill, M., Climatic Influences on Flowering and Fruiting of *Cypripedium calceolus* var. *pubescens*, in *Trends and Fluctuations and Underlying Mechanisms in Terrestrial Orchid Populations*, Kindlmann, P., Willems, J. H., and Whigham, D.F., Eds., Leiden: Backhuys, 2002, pp. 85–97.

Mishkin, B.A., *Flora Khibinskikh gor, ee analiz i istoriya* (The Flora of the Khibiny Mountains: Analysis and History), Moscow: USSR Academy of Sciences, 1953.

Oien, D.-I. and Moen, A., Flowering and Survival of *Dactylorhiza lapponica* and *Gymnadenia conopsea* in the Solendet Nature Reserve, Central Norway, in *Trends and Fluctuations and Underlying Mechanisms in Terrestrial Orchid Populations*, Kindlmann, P., Willems, J. H., and Whigham, D.F., Eds., Leiden: Backhuys, 2002, pp. 3–22.

Ramenskaya, M.L., *Analiz flory Murmanskoi oblasti i Karelii* (Analysis of the Flora of Murmansk Oblast and Karelia), Leningrad: Nauka, 1983.

Regel, C., *Die Vegetationsverhältnisse der Halbinsel Kola: 1. Lieferung*, Berlin-Dahlem: Verlag des Repertoriums, 1935.

Semko, A.P., *Rezhim tepla i vlagi dlya rosta i razvitiya dikorastushchikh i introdutsirovannykh rastenii v Tsentral'noi chasti Kol'skogo poluostrova* (Heat and Moisture Regimes for the Growth and Development of Wild-Growing and Introduced Plants in the Central Kola Peninsula), Apatity: Kola Nauchn Tsentr Ross. Akad. Nauk, 1989.

Strelkov, S.A., Morphostructures of the Northeastern Baltic Shield and Trends in Their Formation, in *Paleogeografiya i morfostruktura Kol'skogo poluostrova* (Paleogeography and Morphostructure of the Kola Peninsula), Leningrad: Nauka, 1973, pp. 5–79.

Tamm, C.O., Behaviour of Some Orchid Populations in a Changing Environment: Observation on Permanent Plots, 1943–1990, in *Population Ecology of Terrestrial Orchids*, Wells, T.C.E. and Willems, J.H., Eds., The Hague: SPB Acad. Publ., 1991, pp. 1–15.

Tsinzerling, Yu.D., *Geografiya rastitel'nogo pokrova Severo-Zapada evropeiskoi chasti SSSR* (Plant Cover Geography of Northeastern European Russia), Leningrad: Nauka, 1934.

Wells, T.C.E., Population Biology of Terrestrial Orchids, in *The Biological Aspects of Rare Plant Conservation*, Synge, H., Ed., Chichester: Wiley, 1981, pp. 281–295.

Wells, T.C.E. and Cox, R., Demographic and Biological Studies on *Ophrys apifera*: Some Results from a 10-Year Study, in *Population Ecology of Terrestrial Orchids*, Wells, T.C.E. and Willems, J.H., Eds., The Hague: SPB Acad. Publ., 1991, pp. 47–63.

Willems, J.H., *Population Dynamics* of *Spiranthes spiralis* in South Limburg, the Netherlands, *Mem. Soc. Roy. Bot. Belg.*, 1989, no. 11, pp. 115–121.

Willems, J.H. and Bik, L., *Population Biology of Orchis simia in the Netherlands, 1972–1990, in Population Ecology of Terrestrial Orchids*, Wells, T.C.E. and Willems, J.H., Eds., The Hague: SPB Acad. Publ., 1991, pp. 33–45.

Yakovlev, B.A., *Klimat Murmanskoi oblasti* (Climate of Murmansk Oblast), Murmansk: Murmansk, Knizhn, Izd., 1961.

Yakovlev, B.A. and Kozlova, L.G., *Klimaticheskie karty. Atlas Murmanskoi oblasti* (Climatic Maps. An Atlas of Murmansk Oblast), Moscow: GUGK, 1971.