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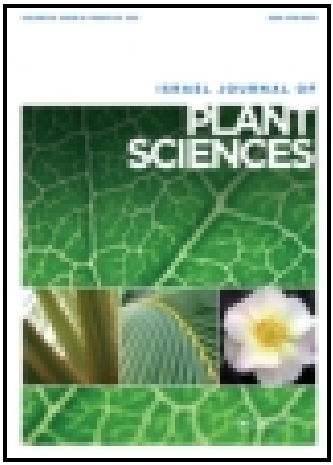

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ASSESSMENT OF LICHEN SENSITIVITY TO CLIMATE CHANGE

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ABSTRACT

Experimental data on net photosynthetic rate change of lichens in response to temperature and water stress were collected and standardized. The method of nonuniform hierarchical structured data interpolation was applied to assess lichen sensitivity to climatic stress for species and territories where sensitivity has not been measured in a laboratory. The alternative method of lichen sensitivity to climatic stress assessment is the analysis of species ranges, abundance, and occurrence. This approach is especially effective for areas with a manifest climatic gradient and where multiple floristic zone boundaries occur. Assessments of sensitivity of the Negev Desert lichens to long-term temperature increase were obtained using the second approach.

INTRODUCTION

In accordance with the Intergovernmental Panel on Climate Change global warming forecast based on the global circulation models, masterfully complex computer programs that seek to simulate atmospheric changes due to the accumulation of greenhouse gases, the global mean temperature will increase by 0.3 °C per decade by the year 2100 (Houghton et al, 1990). A similar trend is expected for the Eastern Mediterranean area (Cohen et al., 1993). An increase in annual precipitation and evaporation will follow these changes in temperature.

Average annual temperature as well as maximal summer and minimal winter temperatures affect the net photosynthetic rate of lichens. Hence, temperature influences both lichen biomass and vitality. Changes in thalli temperature caused by changes in environmental temperature can generate physiological modifications. These modifications can be the reason for the appearance of new ecotypes and for species range shift or reduction (Kershaw, 1985; Holten and Carey, 1992).

Experimental surveys prove the importance of thalli water saturation for a number of metabolic processes: gas exchange, nitrogen fixation, translocation of photosynthates from algae to fungus, and their transformation within fungus (Kershaw, 1985). Water content depends on rains, fog, dew, and vapor pressure (Lange, 1988).

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As the global climate changes, changes in phytocenosis are predicted by many specialists. In particular, Norwegian scientists predict significant changes in phytocenosis of Norway and have appealed for vegetation monitoring using all current approaches and methods (Holten and Carey, 1992). In addition to the vascular plants, the community of spore-bearing plants, in particular lichens, are susceptible to the influence of climatic factors (Halonen et al.,1991; Insarova, 1993; Nash and Olafsen, 1995; etc.). Hence, monitoring is a useful tool for detection and assessment of changes within lichen communities.

Monitoring of lichen communities, influenced by the simultaneous effect of altered climate and background atmospheric conditions, includes (Insarov and Semenov, 1993):

— developing effective sampling procedures for lichen measurement, and field surveying of lichens using this methodology;
— assessment of lichen sensitivity to air pollution and climatic stress in the study areas;
— construction of an Integrated Index of lichen community state having the highest resolution as it relates to detection of global change.

The Index reflects two types of information, the lichen community structure obtained from the field observation, and estimates of lichen species sensitivity to atmospheric pollution and to climatic factors. Monitoring systems of lichens influenced by background atmospheric pollution only have been successfully developed (Monitor, 1985; Insarov et al., 1986; Insarova et al., 1992; Richardson, 1992; Huckaby, 1993). To modify monitoring systems so as to take into consideration the trends induced by simultaneous effects of background air pollution and climate change, estimates of lichen sensitivity to climatic factors are important.

ANALYSIS OF EXPERIMENTAL DATA

DATA

In this section we summarize data on the influence of temperature and humidity on lichen net photosynthesis rate (NPR). There are two reasons why we do not consider the influence of these factors on other processes. Firstly, photosynthesis provides the biomass increase and species vitality. Secondly, the influence of temperature and humidity on the photosynthetic rate has been studied intensively, and a considerable part of the information on the relationship between environmental conditions and physiological processes in lichens is devoted specifically to the influence of temperature and water content on the photosynthetic rate.

Data from literature on the influence of thalli temperature on lichen NPR are collected, unified, and summarized in Table 1. Experiment results placed in this Table were obtained under fixed conditions of photosynthetic active radiation (PAR) and water content in thalli.

The list of species in Table 1 contains 31 lichen species. For some species net photosynthetic rate and sensitivity to temperature changes are given for different localities or for different conditions within the same locality. Most of the species are epilithic

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and epigeal. Two species, *Parmeliopsis ambigua* (Wulf.) Nyl. and *Melanelia olivacea* (L.) Essl., are epiphytic species. Lichen nomenclature follows Galun (1970), Skold and Stengard (1990), Nimis (1993), and Santesson (1993).

The locality column contains names of regions from which lichen specimens were taken for the laboratory studies. The names are cited from the original papers. All localities except one are in the Northern Hemisphere, most are from North America.

The fourth column includes substrate codes. The next three columns, 5th, 6th, and 7th, contain information on experimental conditions, namely on PAR, thalli temperature, and water content in thalli (*WC*) defined as follows:

$$WC = (WW - DW)/DW \cdot 100 \quad (1)$$

where *WW* is wet thallus weight and *DW* is dry thallus weight.

The 8th column contains the results of NPR measurements. Most of the papers provide information on NPR as a function of temperature with various PAR and *WC*. The unimodal curves have an inverted "U" shape. Each paper usually contains a number of such curves. Each curve matches an individual experiment on dependence of NPR on temperature with fixed PAR and *WC*. One of these curves was selected for our further work and included in Table 1. It is the curve in which the highest NPR value is the maximum from the correspondence values among all curves. The highest NPR value (physiological optimum) is given in this column. The corresponding temperature is given in the temperature column. The experimental conditions, i.e., PAR and WC, are given in the appropriate columns.

In descriptions of experiments on *Cladonia caroliniana* Abb., *Cl. evansii* Abb., *Cl. leporina* Fr., *Cl. mitis* (L.) Weber, *Cl. prostrata* Evans., *Cl. rangiferina* (L.) Weber, *Cl. subtenuis* Abb. Evans, and *Cl. uncialis* (L.) Weber, the authors used the relative water content (*RWC*) instead of *WC*. *RWC* is the ratio of the thalli water content to the difference between saturated and dry thallus weight.

$$WWC = (WW - DW)/(SW - DW) \cdot 100 \quad (2)$$

where *WW* is wet thallus weight, *DW* is dry thallus weight, and *SW* is saturated thallus weight. To standardize data we had to convert *RWC* to *WC*. The methodology of this conversion is as follows.

From equations (1) and (2) one can find that

$$WC = RWC \cdot (k - 1) \quad (3)$$

where k is the thallus maximal saturation index, $k = SW/DW > 1$. Index k values for 19 lichen species are given in Table 2.

To find the k value for the lichen species not represented in the Table 2, the method of nonuniform hierarchical structured data interpolation is used (Roitman, 1989). To apply the method, each lichen species receives the six-number identifier in accordance with the Poelt taxonomic system (1973), with further modifications. For instance, *Cladonia squamosa* Hoffm. has identifier 1.1.8.20.2.3. The first number 1 means that this species belongs to perfect lichens (lichenes perfecti). In the case of imperfect lichens (lichenes

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Table 1
Lichen sensitivity to the temperature changes

No.	Species	Locality	Substrate[a]	PAR[b], μE·m^{-2}·s^{-1}	Thalli temperature, °C	Water content in thalli, %	NPR[c], mg CO_2·g^{-1}dry wt·h^{-1}	Sensitivity to ↑ in temp., $S_i(T)$ [d]	Sensitivity to ↓ in temp., $S_d(T)$ [d]	References
1	2	3	4	5	6	7	8	9	10	11
1	*Alectoria ochroleuca*	Alps (Europe)	2	150	–	100	0.81	4	82	Kappen, 1988
2	*Alectoria ochroleuca*	Pen Island, 57°N, NW Ontario (Canada)	2	150	7	100	0.33	6	26	Kappen, 1988
3	*Alectoria ochroleuca*	Melville, 75°N (Canada)	2	150	7	100	0.08	1	1	Kappen, 1988
4	*Cladonia caroliniana*	Juneau County, Wisconsin (USA)	2	1000	27	152	1.19	25	12	Lechowicz et al., 1974
5	*Cladonia ecmocyna*	Loveland Pass, Clear Creek, Colorado (USA)	2	700	12	200	0.23	6	10	Eickmeier and Adams, 1973
6	*Cladonia evansii*	Ocala Natl. Forest, 29°N, 81°W, Florida (USA)	2	1138	25	163	0.97	20	28	Lechowicz and Adams, 1979
7	*Cladonia leporina*	Panacea, 30°N, 84°W, Florida (USA)	2	1138	20	108	0.75	4	90	Lechowicz and Adams, 1979
8	*Cladonia mitis*	Mauston, Wisconsin (USA)	2	1135	22	120	2.40	47	127	Lechowicz and Adams, 1974
9	*Cladonia prostrata*	Ocala Natl. Forest, 29°N, 81°W, Florida (USA)	2	1138	22	130	0.40	7	10	Lechowicz, and Adams, 1979
10	*Cladonia rangiferina*	Mauston, Wisconsin (USA)	2	1135	25	98	2.55	100	30	Lechowicz and Adams, 1974
11	*Cladonia rangiferina*	Wisconsin (USA)	2	800	18	100	0.58	20	48	Adams, 1971
12	*Cladonia rangiferina*	Muskoka Lakes, Southern Ontario (Canada)	2	600	25	150	6.00	350	100	MacFarlane et al., 1983
13	*Cladonia rangiferina*	Muskoka Lakes, Southern Ontario (Canada)	2	400	15	200	5.80	200	400	MacFarlane et al., 1983

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Table 1 *continued*

14	*Cladonia rangiferina*	Muskoka Lakes, Southern Ontario (Canada)	2	600	25	150	9.50	200	120	MacFarlane et al., 1983
15	*Cladonia stellaris*	Hawley Lake, Northern Ontario (Canada)	2	600	25	150	4.50	20	96	Kershaw et al., 1983
16	*Cladonia subtenuis*	Ocala Natl. Forest, 29°N, 81°W, Florida (USA)	2	1138	25	163	0.90	5	40	Lechowicz, Adams, 1979
17	*Cladonia uncialis*	Mauston, Wisconsin (USA)	2	1135	22	163	1.55	40	60	Lechowicz, Adams, 1974
18	*Lasallia hispanica*	Silla de Felipe (Spain)	2	620	20	100	1.50	154	90	Sancho and Kappen, 1989
19	*Lasallia pustulata*	Silla de Felipe (Spain)	2	620	20	100	1.55	84	20	Sancho and Kappen, 1989
20	*Melanelia olivacea*	Abisko, 68°20'N, 18°45'E (Sweden)	1	500	20	150	1.50	160	100	Sonesson, 1989
21	*Parmeliopsis ambigua*	Abisko, 68°20'N, 18°45'E (Sweden)	1	500	15	100	1.00	80	140	Sonesson, 1989
22	*Peltigera polydactyla*	North of Waterdown, Southern Ontario (Canada)	2	300	25	300	6.00	90	200	Kershaw, 1977
23	*Peltigera praetextata*	North of Waterdown, Southern Ontario (Canada)	2	450	15	200	6.70	220	470	Kershaw, 1977
24	*Peltigera rufescens*	Churchill, Manitoba (Canada)	2	1000	35	225	4.40	120	50	Brown and Kershaw, 1984
25	*Peltigera rufescens*	Muskoka Lakes, Southern Ontario (Canada)	3	1000	35	225	10.50	300	450	Brown and Kershaw, 1984
26	*Ramalina maciformis*	Avdat (Israel)	3	700	20	80	2.00	40	30	Lange, 1969
27	*Thamnolia vermicularis*	Europe	2	260	15	200	1.17	34	54	Kappen, 1988
28	*Umbilicaria decussata*	Circo de Grados (Spain)	3	620	10	100	0.99	18	46	Sancho and Kappen, 1989
29	*Umblicaria deusta*	Muskoka District, 44°55'N, 79°48'W, Ontario (Canada)	3	700	14	125	1.85	96	90	Larson, 1980

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Table 1 *continued*

30	*Umbilicaria grisea*	Silla de Felipe (Spain)	3	620	20	100	0.95	60	20	Sancho and Kappen, 1989
31	*Umbilicaria havaasii*	Circo de Grados (Spain)	3	620	15	100	0.37	13	5	Sancho and Kappen, 1989
32	*Umbilicaria mammulata*	Muskoka District, 44°55'N, 79°48'W, Ontario (Canada)	3	700	14	125	0.95	10	40	Larson, 1980
33	*Umbilicaria muhlenbergii*	Muskoka District, 44°55'N, 79°48'W, Ontario (Canada)	3	700	14	125	0.40	21	18	Larson, 1980
34	*Umbilicaria papulosa*	Muskoka District, 44°55'N, 79°48'W, Ontario (Canada)	3	700	14	75	0.85	3	38	Larson, 1980
35	*Umbilicaria spodochroa*	Puerto de Mijares (Spain)	3	620	10	100	0.89	26	40	Sancho and Kappen, 1989
36	*Umbilicaria subglabra*	Circo de Grados (Spain)	3	620	10	100	0.78	6	6	Sancho and Kappen, 1989
37	*Umbilicaria vellea*	Muskoka District, 44°55'N, 79°48'W, Ontario (Canada)	3	700	14	75	0.80	21	7	Larson, 1980
38	*Usnea antarctica*	Antarctic	3	600	13	–	0.30	8	7	Kappen et al., 1995

[a] 1—bark, 2—soil, 3—rocks; [b] Photosynthetically active radiation; [c] Net photosynthetic rate; [d] $10^3 \cdot mg\ CO_2 \cdot g^{-1} dry\ wt \cdot h^{-1} \cdot T^{-1}$.

Table 2
Lichen thalli maximum saturation indexes

No.	Species	$k \cdot 100$	References
1	*Alectoria ochroleuca* (Hoffm.) A. Massal.	200	Kappen, 1988
2	*Caloplaca trachyphylla* (Tuck.) A. Zahlbr.	125	Coxson and Kershaw, 1984
3	*Cetraria cucullata* (Bellardi) Ach.	300	Kappen, 1988
4	*C. ericetorum* Opiz.	300	Kappen, 1988
5	*C. islandica* (L.) Ach.	200	Kershaw, 1975
6	*C. nivalis* (L.) Ach.	300	Kappen, 1988
7	*Cladonia rangiferina* (L.) Weber	400	Tegler and Kershaw, 1980
8	*Lasallia hispanica* (Frey) Llano	225	Sancho and Kappen, 1989
9	*L. pustulata* (L.) Merat	327	Sancho and Kappen, 1989
10	*Nephroma arcticum* (L.) Torss.	300	Kappen, 1988
11	*Ramalina maciformis* (Del.) Bory.	160	Lange, 1980
12	*R. terebrata*	120	Kappen, 1988
13	*Thamnolia vermicularis* (Sw.) Schaer.	200	Kappen, 1988
14	*Umbilicaria cinereorufescens* (Scher.) Frey.	183	Sancho and Kappen, 1989
15	*U. decussata* (Vill.) Zahlbr.	260	Sancho and Kappen, 1989
16	*U. grisea* Hoffm.	180	Sancho and Kappen, 1989
17	*U. havaasii* Llano	230	Sancho and Kappen, 1989
18	*U. spodochroa* (Hoffm.) DC. in Lam. & DC.	450	Sancho and Kappen, 1989
19	*U. subglabra* (Nyl). Harm.	165	Sancho and Kappen, 1989

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imperfecti),"2" would appear at the first position. The second position identifies asco- or basidiomycetes (1 or 2, respectively). The following numbers identify order, family, genera, and species, respectively.

This phylogenetic hierarchical structure may be used for applying data interpolation algorithms (Roitman, 1988, 1989). The algorithm is, in our case, the procedure to calculate the index k estimates and their errors for species, genera, and taxons of higher ranks not represented in the input data. These estimates are based on available k values for a number of species from Table 2. As the output of the algorithm, the estimates of the k values for the above-mentioned species of the genera *Cladonia* were obtained. The *WC* value estimates for these species were then calculated using formula (3) and are presented in Table 1. We will use this method once again for interpolation in floristic space.

Let us consider the unimodal curve $v(T)$ representing dependence of NPR, i.e., v, on temperature T for a lichen species. Tangent of the angle of incidence in the vicinity of the maximum point T_m is selected as the measure of the lichen species sensitivity to the temperature change. Even if the temperature change is small the NPR change is considerable for sensitive species (Fig. 1a). On the other hand, even significant temperature change causes insignificant NPR change for tolerant species (Fig. 1b). Inclination of the curve to the left from the maximum point as a rule differs from the inclination to the right.

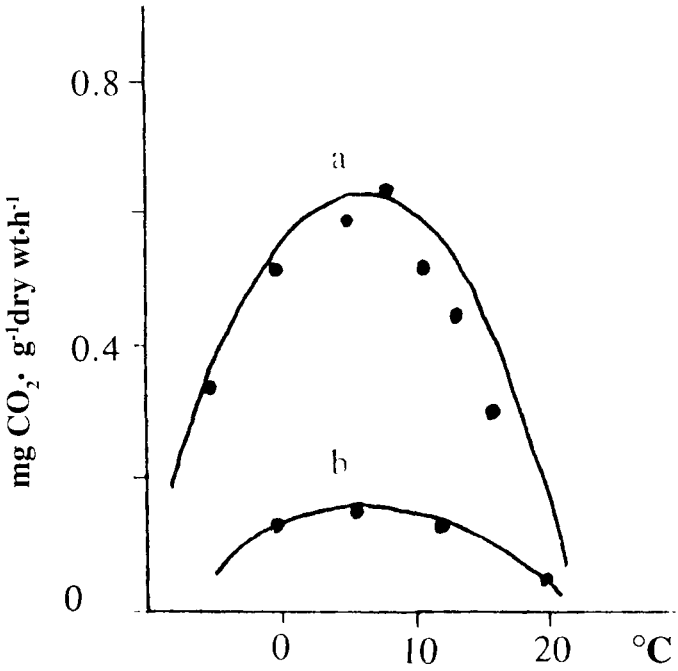

Fig. 1. Temperature-related net photosynthetic rate of *Alectoria ochroleuca* (at 150 μE·m^{-2}·s^{-1} and optimum water content). (a) Alpine population, Alps (Europe), 47°N. (b) Arctic population, Melville (Canada), 75°N (from Larson and Kershaw, 1975; Türk, 1981—in Kappen, 1988, with changes).

Value of lichen species sensitivity $S_i(T)$ to increase in temperature is calculated as follows:

$$S_i(T) = 1000 \cdot (v(T_m) - v(T)) / (T - T_m) \quad (4)$$

where $T = T_m + 5$.

Value $S_i(T)/1000$ has the meaning of NPR decrease caused by a 1 °C temperature increase in the interval $(T_m, T_m + 5)$.

Value of lichen species sensitivity $S_d(T)$ to decrease in temperature is calculated as follows:

$$S_d(T) = 1000 \cdot (v(T_m) - v(T)) / (T_m - T) \quad (5)$$

where $T = T_m - 5$.

Value $S_d(T)/1000$ has the meaning of NPR decrease caused by a 1 °C temperature decrease in the interval $(T_m - 5, T_m)$.

Values $S_i(T)$ and $S_d(T)$ are given in the two next to last columns of Table 1. The shift of 5 °C from the maximum point is selected because exactly this value is used most often as the temperature axis step.

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The data on NPR sensitivity to changes in water content are summarized in Table 3. A list of species in Table 3 contains 26 lichen species. We used the same method to construct this Table as for Table 1. However, photosynthesis here was measured under varying water conditions, rather than temperature. These experiments were carried out under fixed PAR and thalli temperature. We chose one experiment with the NPR maximum value for Table 3 from the series of experiments following the same principle as for Table 1 (see above). Sensitivity to increase and decrease in water content was calculated in an analagous manner to sensitivity to temperature change.

Value of lichen species sensitivity $S_i(WC)$ to increases in water content is calculated as follows:

$$S_i(WC) = 1000 \cdot (v(WC_m) - v(WC)) / (WC - WC_m) \quad (6)$$

where $WC = WC_m + 50$.

Value $S_i(T)/1000$ has the means of NPR decrease caused by a 1% increase in water content in the interval $(WC_m, WC_m + 50)$.

Value of lichen species sensitivity $S_d(WC)$ to decreases in water content is calculated as follows:

$$S_d(WC) = 1000 \cdot (v(WC_m) - v(WC)) / (WC_m - WC) \quad (7)$$

where $WC = WC_m - 50$.

Value $S_d(WC)/1000$ has the means of NPR decrease caused by a 1% decrease in water content in the interval $(WC_m - 50, WC_m)$.

Values $S_i(WC)$ and $S_d(WC)$ are given in the two next to the last columns of Table 3, respectively. The shift of 50% from the maximal point is selected as this value is most often used as the water content axis.

From Table 1 it is apparent that species of genus *Peltigera* are rather sensitive to temperature stress. However, a relationship between $S_i(T)$ and $S_d(T)$ values cannot be predicted a priori because the reaction of species depends on many factors. Such is the case for increase and decrease of the thallus temperature-caused changes in NPR of *Peltigera rufescens* (Weiss) Humb. from Southern Ontario (Brown and Kershaw, 1984). The relation and degree of these changes depends on the season when specimens were collected (Fig. 2). From Fig. 2 one can notice that the temperature optimum of the spring/summer collection differs by 10 °C from the temperature optimum of the winter collection. Moreover, specimens collected in April–December are more sensitive to decreases in temperature, while specimens collected in January are more sensitive to increases in temperature. The reason appears to be seasonal adaptation of the species. In Table 1 the results of experiments with July collection of specimens are included, as NPR values reach the maximum in this season.

Thalli temperatures given in Table 1 are rarely equal to air temperature. Thus, temperature of *Aspicillia calcarea* (L.) Mudd. in July at 10–12 AM is 38 °C, whereas the air temperature is 27 °C. Growing on open stones in arctic Canada, *Parmelia distjuncta* (Erich) Essl. was warmed up to 26 °C towards noon, when the air temperature was 9.2 °C, and that of the stone surface 20 °C (Kershaw, 1985). In Northern Ontario with

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Table 3
Lichen sensitivity to change in water content

No.	Species	Locality	Sub-strate[a]	PAR[b], μE·m^{-2}·s^{-1}	Thalli temperature, °C	Water content in thalli, %	NPR[c], mg CO_2·g^{-1}dry wt·h^{-1}	Sensitivity to ↑ in water content[d]	Sensitivity to ↓ in water content[d]	References
1	*Alectoria ochroleuca*	Southern Alberta, Canada	2	–	14	150	0.35	3	1	Kershaw, 1977
2	*Alectoria ochroleuca*	Pen Island, 57°N, NW Ontario (Canada)	2	250	14	100	0.43	3	3	Larson and Kershaw, 1975
3	*Alectoria ochroleuca*	Pen Island, 57°N, NW Ontario (Canada)	2	250	14	100	0.51	2	2	Larson and Kershaw, 1975
4	*Bryoria nitidula*	Pen Island, 57°N, NW Ontario (Canada)	2	150	12	100	0.20	2	2	Kershaw, 1975
5	*Bryoria nitidula*	NW Ontario (Canada)	2	150	5	100	0.15	1	2	Kershaw, 1975
6	*Bryoria nitidula*	Southern Alberta (Canada)	2	–	7	100	0.15	–	2	Kershaw, 1977
7	*Caloplaca trachyphylia*	Alta, 49°47'N,113°16'W, Southern Alberta (Canada)	3	600	7	75	3.60	68	52	Coxson and Kershaw, 1984
8	*Cetraria nivalis*	Southern Alberta (Canada)	2	–	21	150	0.39	1	2	Kershaw, 1977
9	*Cetraria nivalis*	Subarctic Sweden	2	700	15	218	0.55	2	1	Kappen et al., 1995
10	*Cladonia caroliniana*	Juneau County, Wisconsin (USA)	2	1000	25	152	1.45	45	11	Lechowicz et al., 1974
11	*Cladonia evansii*	Ocala Natl. Forest, 29°N, 81°W, Florida (USA)	2	1138	25	163	1.25	24	7	Lechowicz and Adams, 1979
12	*Cladonia leporina*	Panacea, 30°N, 84°W, Florida (USA)	2	1138	20	108	0.80	2	6	Lechowicz and Adams, 1979
13	*Cladonia mitis*	Mauston, Wisconsin (USA)	2	1135	22	120	2.00	11	64	Lechowicz and Adams, 1974

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Table 3 *continued*

14	*Cladonia rangiferina*	Mauston, Wisconsin (USA)	2	1135	25	98	3.00	8	41	Lechowicz and Adams, 1974
15	*Cladonia rangiferina*	Hawley Lake, Northern Ontario (Canada)	2	600	25	150	3.30	14	22	Tegler and Kershaw, 1980
16	*Cladonia rangiferina*	Muskoka Lakes, Southern Ontario (Canada)	2	600	25	150	6.60	30	40	MacFarlane et al., 1983
17	*Cladonia rangiferina*	Muskoka Lakes, Southern Ontario (Canada)	2	400	25	200	5.80	30	22	MacFarlane et al., 1983
18	*Cladonia rangiferina*	Muskoka Lakes, Southern Ontario (Canada)	2	400	15	200	5.80	32	2	MacFarlane et al., 1983
19	*Cladonia rangiferina*	Muskoka Lakes, Southern Ontario (Canada)	2	600	25	150	9.50	55	40	MacFarlane et al., 1983
20	*Cladonia stellaris*	NW Ontario (Canada)	2	150	5	150	0.30	1	3	Kershaw, 1975
21	*Cladonia stellaris*	Pen Island, 57°N, NW Ontario (Canada)	2	150	5	200	0.31	–	1	Kershaw, 1975
22	*Cladonia stellaris*	Pen Island, 57°N, NW Ontario (Canada)	2	150	20	200	0.23	3	1	Kershaw, 1975
23	*Cladonia stellaris*	Pen Island, 57°N, NW Ontario (Canada)	2	150	20	275	0.30	1	1	Kershaw, 1975
24	*Cladonia stellaris*	Hawley Lake, Northern Ontario (Canada)	2	600	25	150	2.80	8	6	Kershaw et al., 1983
25	*Cladonia stellaris*	Hawley Lake, Northern Ontario (Canada)	2	600	25	150	4.50	8	14	Kershaw et al., 1983
26	*Cladonia subtenuis*	Ocala Nat. Forest, 29°N, 81°W, Florida (USA)	2	1138	25	163	0.97	11	11	Lechowicz and Adams, 1979
27	*Cladonia uncialis*	Mauston, Wisconsin (USA)	2	1135	22	163	1.35	44	7	Lechowicz and Adams, 1974
28	*Parmeliopsis ambigua*	Abisko, 68°20'N, 18°45'E (Sweden)	1	500	15	100	1.60	10	25	Sonesson, 1989

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Table 3 *continued*

29	*Peltigera aphtosa*	Northern Ontario (Canada)	2	350	15	350	2.80	5	6	Kershaw and MacFarlane, 1980
30	*Peltigera aphtosa*	Northern Ontario (Canada)	2	350	15	250	2.30	6	6	Kershaw and MacFarlane, 1980
31	*Peltigera polydactyla*	North of Waterdown, Southern Ontario (Canada)	2	450	35	250	5.30	12	23	Kershaw and MacFarlane, 1977
32	*Peltigera polydactyla*	North of Waterdown, Southern Ontario (Canada)	2	300	25	300	6.00	44	14	Kershaw, 1977
33	*Peltigera praetextata*	Southern Ontario (Canada)	2	300	25	200	5.10	40	50	MacFarlane and Kershaw, 1978
34	*Peltigera praetextata*	Northern Ontario (Canada)	2	450	15	250	8.80	96	22	Kershawand MacFarlane, 1980
35	*Peltigera praetextata*	North of Waterdown, Southern Ontario (Canada)	2	300	35	225	6.50	40	8	Kershaw, 1977
36	*Peltigera praetextata*	North of Waterdown, Southern Ontario (Canada)	2	450	35	175	6.50	4	54	Kershaw, 1977
37	*Peltigera praetextata*	North of Waterdown, Southern Ontario (Canada)	2	450	15	200	6.70	12	64	Kershaw, 1977
38	*Peltigera rufescens*	Central Ontario (Canada)	2	300	25	250	3.20	0	24	MacFarlane and Kershaw, 1978
39	*Peltigera rufescens*	Churchill, Manitoba (Canada)	2	1000	35	250	6.00	10	10	Brown and Kershaw, 1984
40	*Peltigera rufescens*	Muskoka Lakes, Southern Ontario (Canada)	3	1000	35	200	10.50	20	70	Brown and Kershaw, 1984
41	*Ramalina maciformis*	Avdat (Israel)	3	150	10	80	1.40	–	22	Lange, 1969
42	*Rhizocarpon superficiale*	Southern Alberta (Canada)	3	900	0	275	1.60	9	6	Coxson et al., 1983
43	*Stereocaulon pashale*	Abitau-Dunvegan Lake, 60°21'N, 106°54'W, NW Territories (Canada)	2	700	22	140	2.30	5	8	Kershaw and Smith, 1978

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Table 3 *continued*

44	*Thamnolia vermicularis*	Europe	2	260	15	200	1.40	12	6	Kappen, 1988
45	*Umblicaria deusta*	Muskoka District, 44°55'N, 79°48'W, Ontario (Canada)	3	700	14	125	1.85	3	17	Larson, 1980
46	*Umbilicaria mammulata*	Muskoka District, 44°55'N, 79°48'W, Ontario (Canada)	3	700	14	125	0.95	5	6	Larson, 1980
47	*Umbilicaria muhlenbergii*	Muskoka District, 44°55'N, 79°48'W, Ontario (Canada)	3	700	14	125	0.40	3	3	Larson, 1980
48	*Umbilicaria papulosa*	Muskoka District, 44°55'N, 79°48'W, Ontario (Canada)	3	700	14	75	0.85	3	26	Larson, 1980
49	*Umbilicaria vellea*	Muskoka District, 44°55'N, 79°48'W, Ontario (Canada)	3	700	14	75	0.80	6	6	Larson, 1980

[a] 1—bark, 2—soil, 3—rocks; [b] Photosynthetically active radiation; [c] Net photosynthetic rate; [d] $10^3 \cdot$mg $CO_2 \cdot g^{-1}$dry wt$\cdot h^{-1}$.

summer midday conditions of 2,000 $\mu E \cdot m^{-2} \cdot s^{-1}$ PAR and 20 °C air temperature, *Cladonia stellaris* (Opiz.) Pouzar and Vezda thallus temperature on the open wood edges was about 40 °C. At the same time, *Cladonia rangiferina* (L.) Weber thallus temperature under the forest canopy was about 33 °C (Tegler and Kershaw, 1980). However, the temperature of *Verrucaria cazzae* Zahlbr. on shaded rocks in France was close to the air temperature during the daytime. Maximum temperature was about 24 °C (Kershaw, 1985).

Lichen photosynthesis does not occur if the thallus is dried out. Photosynthesis becomes active at a definite level of thallus water saturation. Saturation degree depends on air humidity or on water vapor pressure. The minimal water content necessary for photosynthesis is a species-specific value, and the water content depends on relative air humidity (RH). A good example of this is found in four Californian lichens. In the same location photosynthesis begins at different RH: when RH reaches 73% for *Dendrographa minor Darb.*, 84% for *Ramalina menziezii Tayl.*, 87% for *Evernia prunastri* (L.) Ach, and 97% for *Pseudocyphellaria anthraspis* Magn. (Nash et al., 1990).

In nature the rate of photosynthesis is determined by a combination of factors. Photosynthesis of *Ramalina maciformis* (Del.) Bory in the Negev Desert occurs only in the morning. At night thalli are saturated by dew, and dark respiration also occurs during the night. At 7 in the morning when PAR reaches the level of 300 $\mu E \cdot m^{-2} \cdot s^{-1}$, the CO_2 balance becomes positive and photosynthesis begins to be greater than respiration. At this time RH is about 100%, and water content in thalli (*WC*) is 28%. At 8.30 AM increasing solar radiation leads to RH and *WC* decrease. At this point the photosynthesis rate falls to almost zero (Lange et al., 1970). A similar dependence was shown for *Teloschistes lacunosus* (Rupz.) Sav. from the Negev Desert (Lange et al., 1970), and for fruticose lichens from the Namibian Desert (Lange et al., 1990) and from Atakama (Lange and Redon, 1983).

Identical lichen species from different habitats show different magnitudes of reaction to the same environmental stress. These differences are caused both by global characteristics (average annual precipitation, etc.) and by local habitat peculiarities. Sun and shade ecotypes may be shown as examples of local peculiarities. The season in which lichens are collected as well as the specimens' storage conditions can also change the lichen reaction to environmental stress. However, the characteristics $S_i(T)$, $S_d(T)$, $S_i(WC)$, and $S_d(WC)$ of lichen sensitivity to temperature and water content change permit comparison of the reaction to these changes.

METHOD OF DATA ANALYSIS

Table 3 contains data on species sensitivity to changes in water content from localities within the Boreal Subkingdom of Holarctic. One can see that sensitivity changes from one locality to another. Within each locality, sensitivity varies according to experimental conditions. *Cladonia* species form the largest group, as compared with other genera, so we will show data generalization of this group.

To obtain *Cladonia* species sensitivity estimates for Boreal territories not represented

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in Table 3, we apply the method of nonuniform hierarchical structured data interpolation again. To form structured data we split the Earth into floristic zones after Takhtadzyan (1986). In accordance with this system, the earth surface is divided into six Kingdoms, each Kingdom is split into a number of Subkingdoms. Subkingdoms consist of Regions, and Regions consist of Provinces. We number Provinces with a four-number identifier. For instance, the East-Mediterranean Province receives identifier 1.2.6.8. The first number, 1, means that the Province belongs to the Holarctic Kingdom; the second number, 2, identifies the Boreal Subkingdom within the Holarctic Kingdom; the third number, 6, identifies the Mediterranean Region within the Boreal Subkingdom; and the fourth number identifies the East-Mediterranean Province within the Mediterranean Region. We also numbered localities from Tables 1 and 4 where lichen sensitivity to climatic stress has been estimated. Therefore, the five-number identifier corresponds to each locality. *Cladonia* sensitivity estimates included in Table 3 refer to seven localities. Three localities are in the Canadian Province of the Circumboreal Region, and two localities are in the Appalachian and in the Atlantic and Gulf Coastal Plain Provinces of the North American Atlantic Region (Fig. 3).

We assume that sensitivity of each *Cladonia* species is the realization of a random variable that represents genus *Cladonia* sensitivity. We also assume that *Cladonia* sensitivity x_{ijk} in the locality identified by combination 1.1.i.j.k. within the Boreal Subkingdom, is a random variable that can be composed as follows:

$$x_{ijk} = \mu + r_i + p_{ij} + l_{ijk} \tag{8}$$

where

- μ is *Cladonia* sensitivity in the Boreal Subkingdom,
- r_i is the normal distributed random variable with zero mean value and standard deviation value σ_1, representing *Cladonia* sensitivity in region i of the Boreal Subkingdom,
- p_{ij} is the normal distributed random variable with zero mean value and standard deviation value σ_2, representing *Cladonia* sensitivity in province j of region i of the Boreal Subkingdom, and
- l_{ijk} is the normal distributed random variable with zero mean value and standard deviation value σ_3, representing *Cladonia* sensitivity in locality k belonging to province j of region i of the Boreal Subkingdom.

It is assumed that the three random variables in the right-hand side of the model (8) are mutually uncorrelated. Realizations of l_{ijk} are presented in Table 3. The method of nonuniform hierarchical structured data interpolation (Roitman, 1988,1989) can be applied to data on *Cladonia* sensitivity to change in water content from Table 3, arranged as described above. The algorithm to obtain efficient estimates of *Cladonia* sensitivity to change in water content values $\boldsymbol{x}$ and their standard deviations $\boldsymbol{d}$ (subscripts are omitted) for the Boreal Subkingdom and all floristic zones in it, includes the following steps. Firstly, estimates σ_1, σ_2, and σ_3 of the corresponding standard variation values are obtained by maximization of the likelihood function. This rather complicated

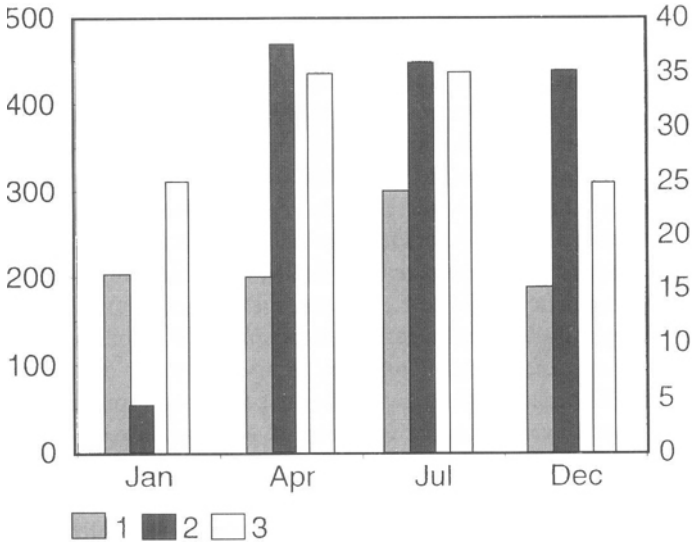

Fig. 2. Seasonal variability of *Peltigera rufescens* net photosynthetic rate (after Brown and Kershaw, 1984). (1) $S_i(T)$, sensitivity to increase in temperature. (2) $S_d(T)$, sensitivity to decrease in temperature. (3) thalli temperature optimum. Sensitivity to change in temperature, $10^3 \cdot$mg $CO_2 \cdot g^{-1}$ dry wt$\cdot h^{-1} \cdot T^{-1}$ is plotted as left ordinate and temperature, °C, as right ordinate.

procedure exploits different numerical methods. Secondly, efficient estimates $\boldsymbol{x}$ of *Cladonia* sensitivity to change in water content for each node of the graph presented in Fig. 3 are calculated as weighted means of known *Cladonia* sensitivity values in all endpoints. Weights are inversely proportional to the sum of standard deviations of transitions from the node to the corresponding endpoint along the graph branches.

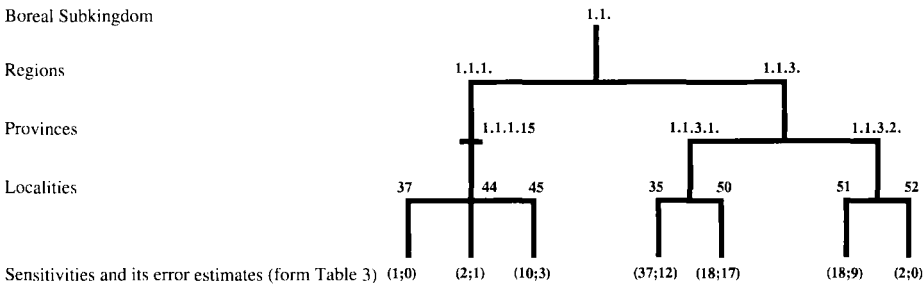

Fig. 3. Structure of input data on *Cladonia* sensitivity to decrease in water content. Sensitivity and its error estimates dimension is $10^3 \cdot$mg $CO_2 \cdot g^{-1}$ dry wt$\cdot h^{-1}$. Floristic zones identification is the same as in Table 4. Numbering of localities: 37—NW Ontario (Canada), 44—Pen Island, 57°N, NW Ontario (Canada), 45—Hawley Lake, Northern Ontario (Canada), 35—Muskoka Lakes, Southern Ontario (Canada), 50—Mauston, Wisconsin (USA), 51—Ocala Nat. Forest, 29°N, 81°W, Florida (USA), 52—Panacea, 30°N, 84°W, Florida (USA).

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Finally, standard deviation ***d*** of the value ***x*** is calculated using estimates σ_1, σ_2, and σ_3.

RESULTS AND DISCUSSION

Calculation results are given in Table 4. Values ***x*** and ***d*** for floristic provinces containing localities where *Cladonia* sensitivity has been measured are presented in Table 4. Estimates for corresponding floristic regions and for the whole Boreal Subkingdom are presented as well. To estimate *Cladonia* sensitivity to changes in water content for other zones (regions and provinces) of the Boreal Subkingdom one takes the estimate for the zone of higher rank containing a given zone and having the lowest rank from all such zones. One uses the corresponding prediction error, ***s***, to estimate error.

For instance, the estimate of *Cladonia* sensitivity to an increase in water content for the Atlantic and Gulf Coastal Province localities, different from the two localities Panacea and Ocala National Forest in Table 3, in accordance with Table 4 is 8.0. Its error estimate is the prediction error estimate ***s*** equal to 4.1. To estimate *Cladonia* sensitivity to a decrease in water content in the Sandnäset Monitoring Area, Western Sweden, one first has to determine its position in Takhtadzyan's floristic system. It is in the Northern

Table 4
Calculated estimates of *Cladonia* species sensitivity to changes in water content ***x***, their errors ***d***, and prediction errors ***s*** for Boreal Subkingdom

Floristic zone			Sensitivity to ↑ in water content[b]			Sensitivity to ↓ in water content[b]		
Code	Name	***n***[a]	***x***	***d***	***s***	***x***	***d***	***s***
1.1.	Boreal Subkingdom	19	11.5	5.3	11.0	11.4	6.1	12.4
1.1.1.	Circumboreal Region	8	9.4	5.0	10.3	8.3	5.5	11.5
1.1.3.	North American Atlantic Region	11	14.7	4.4	10.0	15.7	4.7	11.2
1.1.1.15.	Canadian Province	8	5.6	1.9	3.9	5.1	3.7	7.8
1.1.3.1.	Appalachian Province	8	27.0	2.3	4.1	24.0	4.2	8.1
1.1.3.2.	Atlantic and Gulf Coastal Plain Province	3	8.0	2.3	4.1	11.6	4.3	8.1

[a] Number of measurements; [b] $10^3 \cdot$mg $CO_2 \cdot g^{-1}$dry wt$\cdot h^{-1}$.

European Province of the Circumboreal Region. This Province is not in Table 4, however, the Region is. So the sensitivity estimate is 8.3, and its error is 11.5.[1]

Using Table 4 it is possible to assess *Cladonia* sensitivity to change in water content in any localities of its range in the Boreal Subkingdom. Examples given above are examples of *Cladonia* sensitivity to water content change interpolation within the Circumboreal Region. In the same way it is possible to interpolate sensitivity to water content change for other species from Table 3, and sensitivity to temperature change for species from Table 1.

From Table 4 one can see that the higher the floristic zone rank, the greater the prediction error. This is logical since the greater the distance from one zone to another in

[1]Problems of interpolation accuracy discussed later.

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the floristic hierarchical system, the greater the difference of average sensitivity estimates. Accuracy of inter- or extrapolation depends on species-related locality numbers in the corresponding Table and their positions in the floristic space from, and on their distance to the target zone in floristic space. For instance, it is possible to make extrapolations from North American Provinces to Mediterranean ones for species whose range includes both Boreal and Mediterranean Provinces, such as *Lecanora crenulata* Hook. However, the accuracy of such a procedure is rather low. In any case, the algorithm guarantees the efficient mean value estimates, i.e., estimates with minimal errors.

The model (8) is of the same appearance as random effects models for data from experiments with a multi-stage nested sampling design. Procedures like ANOVA and NESTED ANOVA (Zar, 1984; SAS, 1991) perform analysis of variance for such data, estimating components of the variance corresponding to each factor and testing for their significance. It is assumed that data exist for each combination of factors, i.e., for all cells. As a rule, the numbers of replicates in the cells are equal. Proportional replication within factors is also possible. In the case of unequal or disproportional replication numbers in cells, procedures for data deleting or inserting are applied to arrive at equal or proportional replicate design. These procedures are recommended only in cases where a small number of corrections (no more than 10%) are required. There are some ways (for instance, breaking down the design into complete factorial experiments) to estimate effects from separate factors and interactions for design with missing cells (STATISTICA, 1994). In those cases one should study the pattern of observed and missing cells, formulate specific hypotheses, select one of the ways, and finally apply the standard ANOVA procedures to the modified designs.

Data structures on lichen sensitivity to change in water content (Table 3, Fig. 3) and in temperature (Table 1) are clearly nonuniform. This means that different floristic zones of the same rank contain very different numbers of zones of lower rank where lichen sensitivity has been measured. Thus, there are two provinces in the North American Atlantic region and only one province in the Circumboreal region were *Cladonia* sensitivity to change in water content has been measured. In terms of analysis of variance procedures, this means that the number of cells without data can be relatively large. This is a rather typical structure of arrays of ecological data that originated from different sources.

The algorithm of nonuniform hierarchical structured data interpolation provides efficient estimates of data and their standard deviations in all missing cells for any pattern of observed and missing cells. Use of the efficient estimates (i.e., estimates having minimal standard deviation) is desirable for ecological monitoring (Insarov and Semenov, 1993).

There are two ways of using the interpolation method described above to estimate the sensitivity of lichens from a regional species list to temperature increase. The first way is to estimate each species' sensitivity on the basis of information on the same species sensitivity at localities all over the world. The floristic hierarchical system is used. This way is described above for *Cladonia* species sensitivity to changes in water content.

It may be that if the sensitivity of some species from a regional list is known, then the

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sensitivity of the rest of the species can be estimated. The phylogenetic hierarchical system is used. This kind of interpolation was applied above to estimate the saturation index k for some *Cladonia* species.

ANALYSIS OF SPECIES RANGES

CLIMATE CHANGE AND SPECIES RANGE SHIFT

If we turn to the Negev lichen species list (in Table 5) we will find that only one species from this list, *Ramalina maciformis* (Del.) Bory, is presented in Table 1. Of all the Negev species, sensitivity to temperature stress is known only for this species. For this reason, the two ways to apply the interpolation procedure for hierarchical structured data are unable to estimate the Negev lichen species' sensitivity to temperature stress on the basis of Table 1 data. To obtain sensitivity of the Negev lichens we suggest another approach.

One of the expected consequences of temperature increase is a shift of species distributions and the boundaries of natural zones (Holten and Carey, 1992). Mayr (1970) pointed out that species range changes can be caused by climatic stress. As an example, he gave expansions of some bird and mammal ranges to the north and abandonment by some northern species from the south in response to global climate mildness during the first half of the twentieth century. A shift of the current transition desert/non-desert zones into the present non-desert regions to a depth of some 100–300 km is predicted (Safriel, 1991). This shift will influence lichen communities in the Negev where the Irano-Turanian and Saharo-Arabian floristic zones meet. Lichen species having the northern boundary of their distribution in the Negev (Saharo-Arabian species) will move to the North, and are likely to extend their distribution in the Negev. At the same time, species having their southern distribution boundary in the Negev (Irano-Turanian species) will narrow their presence, or will disappear from the Negev. Such disappearance will take place because the southern peripheral populations cannot adapt to temperature increases. If they could, the southern species range boundary would lie to the south of its present position. This means that southern populations would be more adapted to arid conditions than takes place in reality. The possibility of adaptation to an average temperature increase of 3 °C would correspond to a more than 100 km shift to the south of the species present range.

This shift does not take place, as species boundaries are rather stable (Mayr, 1970). The reason is the fact that peripheral populations hardly maintain their functioning at extreme climatic conditions. For many lichen species growing in the Central Negev on different types of stones and soil as substrates (Insarov and Insarova, 1995), this region is the southern range of the species boundary. While the same substrates can be found to the south, extreme climatic conditions limit expansion of these lichen species to these areas.

Population genetics theory as well as the phenotypic approach support the hypothesis of persistence decreasing along gradient factors from core to periphery. Mayr (1963) notes that the degree of polymorphism usually decreases as distance from the species

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Table 5
Negev lichen species' sensitivity to temperature increase

No.	Lichen species	Point[a]
1	*Buellia epipolia* (Ach.) Mong.	1
2	*B. venusta* (Koerb.) Lett.	1
3	*Collema crispum* (Huds.) G.H.Web.	1
4	*Diploicea canescens* (Dickson) Massal.	1
5	*Tephromela atra* (Huds.) Hafelner in Kalb	1
6	*Aspicilia farinosa* (Floerke) Arnold	2
7	*A. contorta* (Hoffm.) Kremp. ssp. *hoffmanniana* Ekman & Froberg	2
8	*Blastenia rejecta* Th. Tr. var. *bicolor* (Muell. Arg.) Zahlbr.	2
9	*Caloplaca aurantia* (Pers.) Helb. var. *aurantia* Poelt	2
10	*C. ehrenbergii* (Muell. Arg.) Zahlbr.	2
11	*C. erythrina* (Muell. Arg.) Zahlbr. var. *pulvinata* (Muell. Arg.) Zahlbr.	2
12	*C. flageyana* (Flag.) Zahlbr.	2
13	*Collema tenax* (Sw.) Ach. var. *vulgare* (Schaer.) Degel. f. *vulgare* Degel.	2
14	*Ramalina maciformis* (Del.) Bory	2
15	*Psorotichia numidella* Forss.	2
16	*Squamarina cartilaginea* (With.) P. James	2
17	*Teloschistes lacunosus* (Rupr.) Sav.	2
18	*Acarospora reagens* Zahlbr. f.*radicans* (Nyl.) Magn.	3
19	*Buellia subalbula* (Nyl.) Muell. Arg. var. *fuscocapitellata* Lamb.	3
20	*Caloplaca aegyptiaca* (Muell. Arg.) Stein. var. *circinans* Stein.	3
21	*C. interveniens* (Muell. Arg.) Zahlbr.	3
22	*Catapyrenium squamulosum* (Ach.) O. Breuss	3
23	*Diploschistes diacaspis* (Ach.) Lumbsch	3
24	*Lecania subcaesia* (Nyl.) Szat.	3
25	*Lecanora crenulata* Hook.	3
26	*Psora decipiens* (Hedw.) Hoffm.	3
27	*Rinodina bischoffii* (Hepp.) Mass. var. *aegyptiaca* Muell. Arg.	3
28	*Toninia sedifolia* (Scop.) Timdal	3
29	*Xanthoria aureola* (Ach.) Ericks. var. *isidioidea* Beltr.	3
30	*Acarospora areolata* Reichert et Galun	4
31	*Aspicilia desertorum* (Kremplh.) Mereschk.	4
32	*Buellia sorediosa* Reichert et Galun	4
33	*B. zoharyi* Galun	4
34	*Caloplaca arenaria* (Pers.) Muell. Arg.	4
35	*C. luteoalba* (Turn.) Th. Fr.	4
36	*C. negevensis* Reichert et Galun	4
37	*Candelariella minuta* Reichert et Galun	4
38	*Catillaria reichertiana* Galun	4
39	*Dermatocarpon desertorum* Tom.	4
40	*Diploschistes calcareus* Stein.	4
41	*Fulgensia fulgens* (Sw.) Elenk.	4
42	*Squamarina lentigera* (Web.) Poelt	4
43	*Toninia albilabra* (Dufour) H.Oliver	4
44	*T. aromatica* (Turn.) Mass.	4

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45	*Xanthoria steineri* Lamb	4
46	*Arthonia calcicola* Nyl.	5
47	*Acarospora murorum* Mass.	5
49	*Clauzadea immersa* (G.H.Weber) Haf. & Bellemere	5
48	*Dermatocarpon convexum* Reichert et Galun	5
50	*Rinodina mediterranea* Flag.	5

[a]The five-point scale of lichen sensitivity is used. The most tolerant species are assigned 1 point, and the most sensitive species 5 points.

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range boundary decreases, and that the peripheral populations are ordinarily monomorphic. Lewontin (1974) writes that the area of species distribution is a space–time mosaic represented by favorable and unfavorable conditions. Suitable habitat patches density decreases along the geographical gradient. The species range boundary occurs at localities where species cannot maintain a population. Populations close to the boundary are peripheral ones from both geographical and ecological points of view. This thesis is supported by Dobzhansky (1951), Carson (1959), and Timofeeff-Ressovsky et al. (1973). However, the first two authors have different points of view about the appearance of genotypes which are specialized to peripheral environment conditions.

It is worth noting that one may come to the opposite conclusion comparing variability of core population with the group of peripheral ones. Species as a whole may be more variable at the periphery than in the core, as a number of divergent isolates are formed at the periphery. In spite of the fact that each peripheral isolated population has less genetic and phenotypic variability than the core population, a group of peripheral populations may be more variable than the core population (Mayr, 1970). The same conclusion is shown by experiments carried out by Safriel et al. (1994). They studied phenotypic variability in 18 phenological and morphological traits characteristic of wild barley, *Hordeum spontaneum* C. Koch, caused by water stress. Core population variability was compared with the variability of the group of peripheral populations. The group of peripheral populations includes one Turkmenian population at the northern edge of the species range, and five Israeli (Negev and Judean deserts) populations at the southern edge of the species range. It was found that the core population was less variable than the group of peripheral populations from the localities belonging to opposite ends of the precipitation gradient.

The study of lichen photosynthesis rate at Anaktuvuk Pass, Alaska (Nash and Olafsen, 1995) showed that prevailing temperatures during lichen physiological activity in the field were suboptimal. So it is possible to predict that global warming will enhance the photosynthesis and, consequently, the vitality of Arctic lichens. One can predict a similar situation for species having their northern range boundary in the Negev, and for species with a wide range containing the Negev Desert. Such species in the Negev can also benefit from temperature increase. They are rather tolerant to global warming. On the other hand, lichen species having their southern range boundary in the Negev are rather sensitive to temperature increase there. This is a key to constructing the Negev regional scale of lichen sensitivity to temperature increase.

ESTIMATION OF THE NEGEV LICHEN SPECIES SENSITIVITY TO TEMPERATURE INCREASE

We analyzed the list of the Negev lichen species, their distribution all over the world, and their distribution and abundance in the Negev using literature sources (Galun and Reichert, 1960; Galun, 1966, 1970; Poelt, 1969; Kopachewskaja et al., 1971; Dobson, 1992; Nimis, 1993; Santesson, 1993; Insarov and Insarova, 1995) and our own studies. As a result, a five-point scale of the Negev lichens' sensitivity to temperature increase was constructed (Table 5). The most tolerant species are scored 1, the most sensitive ones are scored 5.

Species with very wide distribution are regarded as the most tolerant species. They are scored 1. *Diploicea canescens* (Dickson) Massal. is an example. This species is distributed in Western Siberian, Atlantic-European, Balkan, and Euxine provinces of the Circumboreal Region as well as in Mediterranean, Irano-Turanian, and Saharo-Arabian Regions. It is so widely distributed that the species has to be well adapted to temperature change.

Saharo-Arabian species with the north boundary of distribution in the Negev are regarded as the tolerant species as well. They are given a score of 2. For instance, *Blastenia rejecta* Th. Tr. var. *bicolor* (Muell. Arg.) Zahlbr. is a typical Saharo-Arabian species. Species distributed in Irano-Turanian, Saharo-Arabian, and Mediterranean floristic zones are also scored 2. *Caloplaca aurantia* (Pers.) Helb. *var. aurantia* Poelt and *Ramalina maciformis* (Del.) Bory are examples of such species. They are very abundant and frequent in the Negev. These species are also regarded as species tolerant to temperature increase in the Negev.

Species with distribution in Saharo-Arabian and Irano-Turanian zones are attributed to intermediate ones. They are given a score of 3. The species *Rinodina bischoffii* (Hepp.) Mass. var. *aegyptiaca* Muell. Arg. is an example. Species with distribution in the Irano-Turanian zone, or whose distribution includes the Irano-Turanian zone and some areas to the north, are attributed as sensitive species. These are scored 4. The species *Diploschistes calcareus* Stein. is an example. Endemic species of the Negev, such as *Candelariella minuta* Reichert et Galun, are also scored 4.

Rare species and those not typical for the Negev, with a main range in the Mediterranean floristic zone and in other territories more humid than the Negev, are attributed as very sensitive. These are scored 5. *Arthonia calcicola* Nyl., *Clauzadea immersa* (G.H.Weber) Haf. & Bellemere are examples.

CONCLUSION

Two approaches to estimate sensitivity of lichens to climatic stress are suggested. The first one is the experimental approach. The characteristic of sensitivity is a measure of net photosynthetic rate change in response to the studied climatic factor change. To obtain sensitivity of lichen species not measured in the laboratory or of species measured in other localities, the method of the nonuniform hierarchical structured data interpolation procedure can be applied. Either the phylogenetic lichen system or floristic regionalization of the earth can be used.

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For a region or a taxonomic group with a lack of laboratory data analysis of species ranges, their abundance and frequency can be applied to estimate lichen sensitivity to climatic stress. Peripheral populations under extreme climatic conditions will disappear if these conditions become worse. These populations are very sensitive to the stress. However, peripheral populations at the opposite end of the climatic gradient will benefit from this climatic change. They are rather tolerant to the stress. The second approach is especially effective for areas where manifest climatic gradient exists and which are crossed by floristic zones boundaries. This approach was applied to obtain estimates of the Negev lichens' sensitivity to the temperature increase.

Lichens are ideal organisms to monitor long-term trends in background air pollution. Such monitoring systems as well as long-term ecological research are established in many countries (Monitor, 1985; Insarov and Semenov, 1993; Manual for integrated monitoring, 1993; McCune, 1996). Climatic stress modifies lichen community response to air pollution on a regional and global level. Climate change forecasts may change as new data appear, or existing climatic models are improved, or new ones are created. Anthropogenic modifications of climate can be damped by biota. Nevertheless background monitoring of the simultaneous effect of air pollution and climate change remains actual objective. Lichen sensitivity to climatic stress assessment is an important part of such monitoring systems.

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