Drought is More Stressful for Northern Populations of Scots Pine than Low Summer Temperatures

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Needle fluctuating asymmetry, which is a non-specific stress indicator, was used to evaluate responses of Scots pine (*Pinus sylvestris* L.) to annual climatic variation in the Kola Peninsula, NW Russia, during 1992–1999. Although the 30 trees surveyed for this study demonstrated individualistic responses to the temperature and precipitation of the growth seasons, at the population level we found no effect of temperature and a significant increase in fluctuating asymmetry with a decline in precipitation during the previous August. This finding suggests that the vitality of Scots pine populations at the northern tree limit is controlled by late summer precipitation rather than by temperatures of the growth season.

Keywords *Pinus sylvestris*, fluctuating asymmetry, temperature, precipitation, stress, climate change, Kola peninsula

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1 Introduction

Summer temperatures often limit plant growth in northern areas, and the northern forest distribution limit generally coincides with the +10 °C isoline of the warmest summer month (Brockmann-Jerosch 1919). In Northern Fennoscandia, shoot growth in Scots pine (*Pinus sylvestris* L.) is controlled by the temperature of the previous growth season (Hesselman 1904, Mikola 1962, Hustich 1978, Junttila and Heide 1981); in more southern populations, in comparison, the critical factor is the amount of precipitation during the second half of the previous summer (Tolskij 1913, Shcherbatyk 1988). Similarly, the growth of *Pinus strobus* L. in Canada correlated with previous-year air temperatures (MacHattie and Horton 1963), while the growth of some North American pines is controlled by previous-year water availability (Clements 1970, Wensel and Turnblom 1998). On the other hand, the needle length of Scots pine depends on current summer temperature (Hustich 1948, Mikola 1962, Junttila and Heide 1981). It remains unclear, however, whether cold years or years with low precipitation are in fact stressful for Scots pine, or whether pronounced annual variation in both vertical and radial increments and in needle length is within the norm of phenotypic response to variable environmental conditions.

Developmental instability of different organisms, usually detected by measurements of fluctuating asymmetry (FA), has been widely used in environmental studies to identify the effects of anthropogenic and natural stressors (Freeman et al. 1993, Møller and Swaddle 1997). FA is defined as non-directional variation between the left and right sides of a bilateral character; it may arise as a result of an inability to control development under genetic and environmental stress (Møller 1995, Leamy 1999). Among environmental stressors, the greatest attention has been paid to pollution (Kozlov et al. 1996, 2002a,b, Kryazheva et al. 1996, Møller 1998, Kozlov and Niemelä 1999), while the effects of natural climatic fluctuations on plant developmental stability, to the best of our knowledge, have been documented for mountain birch only (Valkama and Kozlov 2001). In this study we determine which of two climatic factors, temperature and precipitation, best explains variation in stress level in northern populations of Scots pine.

2 Materials and Methods

In June 1999 we sampled needles from ten dominant, randomly selected Scots pines 20 to 30 years old in each of three localities of the Kola peninsula, NW Russia: 10 km E of Kovdor (67°30´N, 30°44´E), 16 km SW of Revda (mouth of the river Azimuth: 67°51´N, 34°23´E), and 26 km S of Revda (mouth of the river Kuftuai: 67°43´N, 34°32´E).

We used the protocol developed in our earlier study (Kozlov and Niemelä 1999). Samples were taken from the branches arising from the trunk; these branches are called by different authors either ‘first-order branches’ or ‘second-order axes’ (tree trunk is the first-order axis). We randomly selected one branch in the mid-crown, cut it and transported to laboratory, where we collected 20 needle pairs (fascicles) from each of the last seven to eight year classes (1991–1998). Current-year (1999) needles did not complete their growth by the time of sampling, and were therefore not collected. Some of our trees had only six needle classes or fewer than 20 needle pairs left in some age classes, which influenced the sample size. The needle pairs were then mounted on paper in such a way, that two needles in the pair were pressed to each other, allowing accurate measurement of the difference in needle length.

Testing for the presence of directional asymmetry makes it necessary to distinguish between the left and right needle in each pair. Since in our earlier study (Kozlov and Niemelä 1999) we demonstrated an absence of directional asymmetry in another data set originating from the same region, here (like in the study of Scots pines from the Karelian Isthmus: Kozlov et al. 2002a) this time-consuming procedure is omitted. We measured only the difference in the length of two needles in the pair; this was done under the stereomicroscope (twice, to the nearest 0.025 mm). The presence of asymmetry in our data set was verified by analysing the distribution of these values (SAS UNIVARIATE procedure). The length of each needle in the pair was measured with a ruler to the nearest 0.5 mm; the FA index was calculated as the ratio between the difference in needle length and the mean length of the needles forming a pair. As a rule, the difference in the length of two needles in a pair is less than 1 mm; however quite exceptionally it may be as high as 15–20 mm, resulting in extremely high FA values. These statistical outliers (amounting to ca. 0.1 %) were excluded from the analysis. The sources of variation in needle FA (year of needle growth, study site, tree nested within the site, and interactions of two latter parameters with year of needle growth) were explored by the General Linear Model procedure (SAS Institute 1990); the original values were square-root transformed to achieve the normality of residuals.

Data on monthly mean temperatures and precipitation for growth seasons of 1991–1998 (Table 1) were obtained from the meteorological station in Monchegorsk; the most distant of the three study sites was located 120 km from this station. In the stepwise regression analysis (SAS

Table 1. Monthly mean temperatures and precipitation at Monchegorsk.

Year	Temperature, °C				Precipitation, mm			
	May	June	July	August	May	June	July	August
1990	3.6	11.2	14.3	12.3	28	65	62	68
1991	2.7	10.6	12.4	12.8	46	59	29	35
1992	6.4	11.3	11.7	9.7	24	57	84	119
1993	4.5	8.1	14.9	11.5	25	81	12	41
1994	2.5	10.1	13.7	12.6	13	41	61	51
1995	3.8	11.9	12.0	11.2	28	51	57	77
1996	1.3	7.9	12.3	13.9	42	34	76	17
1997	2.8	10.9	13.9	14.0	23	19	18	32
1998	3.0	7.5	15.3	10.1	83	116	62	30

Table 2. Sources of variation in needle fluctuating asymmetry of Scots pine.

Variation source	d.f.	Error term	Mean square ($\times 10^3$)	F	Pr > F
Year	7	Year*Tree(Site)	5.68	0.64	0.72
Site	2	Year*Tree(Site)	3.98	0.45	0.64
Year*Site	14	Year*Tree(Site)	4.32	0.48	0.94
Tree(Site)	27	Year*Tree(Site)	25.0	2.81	0.0001
Year*Tree(Site)	148	Error	8.92	2.84	0.0001
Error	3565	-	3.15		

Institute 1990), we first used four variables: averaged temperature and precipitation data for June to August of the previous year (the time when the next-year shoot are preformed) and for May to July of the current year (the time when needle and shoot growth take place in our study area). After the first explanatory variable was selected, the corresponding monthly data were entered into the model.

3 Results

The mean difference in length between the longer and the shorter needle in a pair (0.337 ± 0.007 mm, $n = 3764$) greatly exceeded the accuracy of the measurements (0.025 mm) and was significantly ($P < 0.0001$) greater than zero, confirming the presence of asymmetry in our needle sample. The distribution of the difference values peaked at zero, suggesting an absence of antisymmetry. An absence of directional asymmetry has been demonstrated previously (see Materials and Methods); we therefore classified the detected asymmetry as FA.

There was considerable variation among study trees (nested within sites), and no site-related difference in pine response to climatic changes (Table 2). However, we detected significant interaction between tree and year of needle growth (Table 2). At the population level, pine FA depended only on previous-year precipitation ($R^2 = 0.61$, $P = 0.01$); a test of monthly precipitation values demonstrated that FA increased with a decline in previous-year August rainfall (Fig. 1).

4 Discussion

Plant ecophysiological studies addressing Global Change issues generally employ controlled

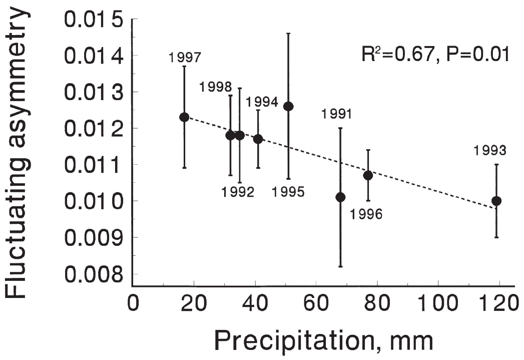

Fig. 1. Relationships between needle fluctuating asymmetry of Scots pine and rainfall during previous August (years refer to needle growth).

manipulative experiments; these, when considered in isolation, are of only limited value if they are to be interpreted in terms of a more realistic combination of environmental factors and over a longer time scale (Kennedy 1995). On the other hand, past annual fluctuations in climatic variables far exceed the expected shift in these parameters (Heal et al. 1998, Lange et al. 1999), and multifactorial analysis of time series can thus be used to evaluate ecosystem vulnerabilities to climate change.

There are at least two potential problems with the analysis of our data set. First, position of the sampled branch in the crown changed during the eight-year period, which may have influenced physiological parameters of the sampled shoots. However, in an earlier study (Kozlov and Niemelä 1999) we demonstrated absence of the differences in needle FA for branches collected in different parts of the crown of Scots pine. Second, analyses of the climatic data, especially search for a pattern in a multi-year data set, are always hampered by the correlation between the climatic variables. Quite luckily, in our data set the correlation between seasonal values of temperature and precipitation of the current and previous year is relatively low (mean $R^2 = 0.17$), allowing to separate between possible effects of different variables by means of stepwise regression analysis. However, we need to emphasise, that our conclusions, based on the detected correlation, should be further verified by carefully designed manipulative study.

Leaves of mountain birch were more asymmetrical in the years with cold spring (Valkama and Kozlov 2001). However, contrary to expectations, cold summer temperatures did not impose stress on northern populations of Scots pine. During 1881–1980, the monthly mean temperatures in our study area for June ranged from 6.1 °C to 15.3 °C (mean 10.2 °C), those for August from 8.6 °C to 16.1 °C (mean 12.0 °C) (Bakkal 1990). Our data covered the larger part of this variation (June 7.5–11.9 °C, August 9.7–14.0 °C), and it is therefore unlikely that the failure to detect a temperature effect on needle FA resulted from the small range of temperatures taken into account. A more plausible explanation is that even extreme temperatures falling within the natural variation range are not perceived as stress by a majority of Scots pine individuals, although tree growth strongly depends on temperatures. This result is also consistent with the conclusion that temperature per se does not explain the upper distribution limit of *P. sylvestris* in the Swiss Central Alps (Hattenschwiller and Körner 1995).

Interestingly, our results indicate that needle FA of Scots pine (which is controlled by precipitation) is independent of tree growth (which is controlled by temperatures: Hesselman 1904, Mikola 1962, Hustich 1978, Junttila and Heide 1981), e. g. in some years Scots pines may exhibit high level of stress but, in spite of that, grow intensively. This result supports our earlier conclusion (Kozlov et al. 2002b) that physiological stress and tree growth or stand productivity are not directly linked to each other, and some increase in productivity can be achieved without alleviation of environmental stress.

The pine needle appeared to be most sensitive to drought at the time of the formation of new terminal buds: developmental instability (assessed by needle FA) increased strongly with the decline in August rainfall below the multi-year mean value of 68 mm (Fig. 1), while current-year water availability did not influence needle FA in either our data set or in a controlled experiment (Otronen and Rosenlund 2001). Since an increase in FA is generally considered to be a sign of fitness decline (Møller 1997), we conclude that the most critical factor for Scots pine is water availability in late summer, and that the vitality of northern pine forests is actually controlled by precipitation.

This finding is in line with the greater sensitivity of northern boreal forests (in terms of both leaf area index and net primary production) to precipitation in comparison with tundra and southern boreal forests (Heal et al. 1998).

Several climatic models agree on a possible increase in precipitation occurring mainly in winter time during the next few decades (Räisänen 1994, Houghton et al. 1995), but it is uncertain whether the concurrent temperature increases will result in an increase or decrease in soil moisture (Maxwell 1992). However, at the regional scales predictions may be more concrete; in particular, model calculations predict a reduction in soil moisture in the forests of Northern Finland, mainly due to enhanced evapotranspiration (Kellomäki and Väisänen 1996). Although acclimation to increased atmospheric CO_2 and temperature could increase the tolerance of Scots pine to water stress (Kellomäki and Wang 1996), our data on the importance of late summer precipitation suggest that the expected increases in both the productivity of extant Scots pine stands (Kellomäki and Väisänen 1997, Kellomäki et al. 1997a) and the success of regeneration (Kellomäki et al. 1997b) close to the timber line may be accompanied by an increase in stress level and therefore appear transient in a long-term perspective.

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