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Suitability of European aspen (*Populus tremula*) for rehabilitation of severely polluted areas

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Abstract

The rehabilitation of polluted sites requires knowledge of the responses of the keystone species to contaminated soils and to co-occurring environmental stressors, such as climate variations and herbivory. To obtain this knowledge, we monitored the performance of young European aspen (*Populus tremula*) trees growing naturally at sites 1.8 to 64.5 km from the Monchegorsk copper-nickel smelter in north-western Russia from 2001–2005. Copper and nickel concentrations near the smelter were 25–30 times higher than the regional background. The radial and vertical increments, leaf size, fluctuating asymmetry and insect herbivory did not change along the pollution gradient. Leaf fluctuating asymmetry positively correlated with the site-specific radial increment. Among-year variations in weather conditions did not interact with spatial patterns in aspen performance. Lack of detrimental effects of extreme pollution on any of the studied traits indicates a high tolerance of European aspen to the harsh environmental conditions of industrial barrens. This tolerance makes aspen a suitable species for rehabilitation of areas with extreme levels of soil contamination by copper, nickel and other metals. The fast-growing aspens established in heavily polluted sites may facilitate natural recovery of plant communities by sheltering dwarf shrubs and tree seedlings and by producing litter that improves soil quality.

Keywords: fluctuating asymmetry; growth; habitat restoration; heavy metals; Murmansk region; pollution tolerance

Introduction

Despite the implementation of strict emission control in developed countries, industrial pollution in some regions still remains unacceptably high and continues to have adverse effects on the ecosystem and human health [1]. In addition, the current generation has inherited large areas that were contaminated in the past and which now require rehabilitation [2, 3] to satisfy demand for ecosystem services and human society sustainability [4]. The legacy effects are especially pronounced around non-ferrous smelters because complete leaching of toxic metals from the contaminated soils may take several hundred years [5]. Within the European Union, 342,000 contaminated sites were identified by the end of 2012, and heavy metals, among all groups of pollutants, contributed the most to the overall soil contamination [6]. Some of these metal-contaminated areas expand over hundreds or even thousands of square kilometres [2], making restoration of healthy ecosystems in these areas a demanding task.

The methods available for the rehabilitation of heavily polluted areas are reasonably well developed [7, 8], but their implementation over large spatial scales requires extensive financial support [9], which is untenable in many countries. The natural recovery of polluted areas sometimes begins as early as 5–15 years after emission decline [10–12]; however, in severely polluted areas, this time lag may last for several decades [13, 14]. This situation calls for the elaboration of low-cost reclamation measures, which can be developed based on studies of local plants that naturally colonize heavily contaminated areas. These plants are able to withstand both the toxicity of pollutants and the climatic stress that results from forest death due to strong winds and deep soil freezing in the winter [2].

One tree species that is able to rapidly colonize disturbed soils and to accumulate metals in stems and foliage is the European aspen, *Populus tremula* L. (henceforth “aspen”). The aspen is a fast-growing deciduous tree, which is often suggested for phytoremediation of metal-contaminated sites [15–17]. However, the effects of air and soil pollution on aspen performance are not sufficiently known. Previous studies showed that aspen trees naturally growing near aluminium smelters in Norway and Siberia had visible leaf injuries [18], smaller leaves and shorter shoots [19]. Similarly, the leaf area of aspens growing near the copper-nickel smelter in Harjavalta, SW Finland, tended to decrease [20], suggesting adverse effects of pollution on aspen performance. However, the responses are inconsistent, as coppiced aspen saplings grown in soil mixed with the filter dust from a non-ferrous metal smelter demonstrated reduced photosynthesis and respiration in most, but not in all, study years [16]. Another experiment showed that heavy metal pollution caused a reduction in the aboveground biomass and leaf area of aspen in only one of two study years [21]. Aspen cuttings showed growth retardation when exposed to cadmium, whereas zinc exposure caused no adverse effects [22].

In 1981, when the first author started to explore changes in forest ecosystems caused by the emissions of the nickel-copper smelter at Monchegorsk, in north-western Russia, young aspen trees were recorded in three of 11 study plots located within 10 km of this smelter but in none of 12 study plots located 11−50 km away from it (M. Kozlov, unpublished data). From 1981 to the mid-1990s, aspens colonized several spots of mechanically disturbed ground between 2 km N and 1 km S of the Monchegorsk smelter and a barren (eroded) site 6.4 km S of the smelter. This spreading of aspens clearly contrasted with the continuous decline in mountain birch (*Betula pubescens* var. *pumila* (L.) Govaerts) in heavily polluted sites around Monchegorsk [13, 23], suggesting a greater tolerance to extreme levels of air and soil pollution in aspen than in birch. Nevertheless, the previous rehabilitation experiments established in barren sites near the Monchegorsk smelter focussed on birch and, to a lesser extent, on different willow species [8, 24, 25]. More keystone plant species need to be involved in rehabilitation process to attempt restoration of healthy ecosystems in heavily contaminated areas.

The absence of quantitative information on aspen growth in severely contaminated and disturbed sites with harsh environmental conditions prompted us to test the hypothesis that aspen is tolerant to extreme pollution loads by recording several performance indices from 2001–2005 in young aspen trees growing naturally at different distances from the nickel-copper smelter at Monchegorsk. Following an approach suggested by Grime [26] for detecting environmental stress effects in plants, we explored plant growth (quantified by vertical and radial increments and by leaf size) along the pollution gradient. All the measured traits were found to decrease significantly in woody plants growing near industrial polluters [27]; thus, the absence of the effect would signal pollution tolerance. The increased densities of insects that feed on birch and willow feeding insects near Monchegorsk [28, 29] urged us to check whether insect herbivory on aspen also increases with pollution because high herbivory can diminish aspen growth and productivity [30]. Finally, we asked whether leaf fluctuating asymmetry (FA), which was previously reported to increase under unfavourable weather conditions [31, 32] and following insect herbivory [29, 33], signals that aspen performance differs between severely polluted and unpolluted localities.

The focus of the present study is the ecological understanding of the outcomes of an unintentional pollution experiment. This approach justifies the publication of our study, despite the data were obtained a long time ago. Furthermore, the ninefold decrease in the amount of atmospheric emission of nickel during the past two decades resulted in only 2.5-fold decrease in the bulk content of nickel in the organic soil horizons, whereas the threefold decrease in the emission of copper was not followed by a significant decreas in its content in the soils [34]. Thus, the optimistic expectations regarding fast unassisted recovery of polluted sites near the Monchegorsk smelter following emission decline were not met, which stresses the importance of rehabilitation measures in restoration of healthy ecosystems in the central part of the Murmansk region.

Materials and Methods

Study area and study sites

A century ago, the area now surrounding the copper-nickel smelter at Monchegorsk (67°56′ N, 32°55′ E) in the Murmansk region of Russia was populated by only a few Saami families and was covered by impenetrable forests of Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) [35]. Since its inception in 1939, the smelter has had strong impacts on the surrounding landscapes. Its emissions into the ambient air peaked in the mid-1980s, reaching 278,000 metric tonnes (t) of sulphur dioxide in 1983 and 13,150 t of non-ferrous metals (primarily nickel and copper) in 1987. The current annual emissions are around 40,000 t of sulphur dioxide and 1000 t of metals [36, 37]. Along with these main pollutants, the smelter emits dozens of other potentially toxic substances [38]. Across study plots located to the north and to the south of the smelter, the concentrations of pollutants in ambient air, plants and soil strongly correlate with the log-transformed distance from the polluter [37, 39].

By the 1990s, the smelter pollution, in combination with cutting and fires, had transformed over 250 km^2 of the previously forested areas centred at the smelter into industrial barrens—bleak open landscapes with small patches of vegetation surrounded by bare land [2]. Both Scots pine and Norway spruce are practically absent in the barren habitats, which are dominated by low-stature (0.2–2 m tall) mature mountain birches growing 5–15 m apart. The barren zone is surrounded by birch and willow-dominated communities, followed by sparse forests in which most of Norway spruce trees have dead upper canopies and demonstrate low needle longevity (3–5 years compared to 15–17 years in pristine forests). Forests that are visibly unaffected by pollution occur only 30–50 km beyond the smelter [36].

For this study, we selected ten sites located 1.8–64.5 km from the smelter (Fig. 1) and containing abundant aspen trees in 2001. The selected sites represent all major classes of pollution-induced habitat deterioration (after [36]) and the entire range of pollution loads existing in the study region (Table 1). The concentrations of the main metal pollutants (copper and nickel) near the smelter were 25–30 times higher than the regional background [37, 39]. The mean air temperatures in our study area are −13.8 °C in January and 14.1 °C in July, and the mean annual precipitation is 561 mm; the frost-free period ranges from 50 to 100 days.

Data collection

We tagged five haphazardly selected young (15–30 years old) aspen trees (median height 196 cm) at each study site. We measured each tree’s height with a ruler to the nearest 1 cm and its basal diameter with callipers to the nearest 1 mm in the late summer of 2001 and of 2005. Leaves from these trees were collected in mid-summer from 2001–2005, after termination of their expansion. We always collected the largest leaf from each of ten shoots, haphazardly selected from different sides of the tree crown at a height of 0.1–2 m, thus yielding 10 leaves per tree. The leaves were transported to the laboratory, where they were mounted on strong paper using adhesive tape and press-dried as ordinary herbarium specimens.

From each collected leaf, we measured the length of the lamina and the width of its left and right sides from the midrib to the leaf margins (at the midpoint between the base and the tip) perpendicular to the midrib. The measurements were conducted with a ruler to the nearest 0.5 mm; the perpendicularity of the measurement line to the midrib was controlled visually. Each leaf was measured twice by different persons who had no knowledge of either the hypotheses being tested or the leaf origin. When the absolute difference between the two measurements exceeded 2 mm, a third measurement was conducted (by a different person with no knowledge of the earlier measurements) to exclude an occasional error.

We adopted the percentage of leaves bearing any signs of damage imposed by defoliating and leafmining insects (marginal damage, holes, skeletonization and mines) as an operational index of herbivory. From mid to late August in each study year (2001–2005), when the majority of insect herbivores had completed their feeding, we counted all leaves bearing insect feeding marks among the first 100 leaves, starting from the tip of a haphazardly selected branch. All censuses were conducted by the same observer.

Data analysis

The values of FA were calculated as follows: $FA=2\times abs(WL-WR)/(WL+WR)$, where WL and WR refer to the width of the left and right halves of leaf lamina. The use of this relative index (named FA2 by Palmer and Strobeck [40]) is justified by the significant correlation between the absolute difference in width of leaf halves and leaf width ($r = 0.15$, $n = 2395$ leaves, $P < 0.0001$).

We used mixed-model ANOVA with the leaf side (right or left) as a fixed factor and the individual leaf as a random factor to explore the repeated measurements of the width of leaf halves for the presence of FA and directional asymmetry (DA) separately for each study year. When mixed-model ANOVA demonstrated the existence of DA, we compared the DA value with the FA4a index ($\mathrm{FA4a} = 0.798\sqrt{\mathrm{var}\ (\mathrm{WR}-\mathrm{WL})}$), as suggested by Palmer and Strobeck [40] to evaluate the potential effect of DA on the FA analysis. We used the index $\mathrm{ME5} = (\mathrm{MSi} - \mathrm{MSm})/(\mathrm{MSi} + \mathrm{MSm})$, where MSi and MSm are the interaction and error mean squares from a side × individual ANOVA for two measurements of each trait in each individual (Palmer and Strobeck 2003) to assess the reproducibility of the measurements.

We explored the variation in tree-specific values of performance indices by mixed-model ANCOVA (SAS GLIMMIX procedure, type 3 tests [41]). Three trees with broken tips were excluded from the analysis of the vertical increment. In all analyses, we used the log-transformed distance from the smelter (a proxy of the pollution load: Kozlov et al. 2009) as a covariate and the site as a random effect. The simultaneous inclusion of both site and distance from the smelter in our analyses accounted for the among-site variation that was not associated with pollution (soil type, plant genotype, etc.). Analyses of leaf length, FA and herbivory included the study year as an additional fixed effect and tree nested within a site as an additional random effect. The proportion of leaves damaged by insects was modelled using a generalized linear mixed model approach with a beta error distribution and a logit link function; other analyses employed Gaussian distribution. We adjusted the standard errors and denominator degrees of freedom following Kenward and Roger [42] and evaluated the significance of a random factor by testing the likelihood ratio against the Chi-squared distribution [43].

Finally, we calculated Pearson product-moment correlation coefficients between all performance indices at two levels. The site-level analysis was based on the values averaged by study site, whereas the tree-level analysis was based on the values standardized (to mean = 0 and standard deviation = 1) by study site to remove the among-site differences in performance.

Results

The vertical increment of aspen trees between 2001 and 2005 ranged from 2 to 217 cm (median value 65 cm), whereas the radial increment ranged from 0 to 18 mm (median value 6 mm; Supplementary data 1). Both vertical and radial increments significantly varied among the study sites ($\chi^2 = 5.12$, df = 1, $P = 0.0118$ and $\chi^2 = 9.60$, df = 1, $P = 0.0010$, respectively); however, this variation was not related to the distance from the smelter (Fig. 2a, b).

Leaf length (Supplementary data 2) did not correlate with either the vertical or the radial increment at both among- and within-site levels ($P > 0.40$). It varied among sites and among individual trees nested within the sites, but it did not change systematically with the distance from the smelter (Fig. 2c; Table 2). No necrotic spots attributable to pollution were observed on any leaves.

The significant side × individual interaction confirmed the existence of FA in leaf width across the samples collected from 2001–2005 (Table 3). The DA was significant in 2005 only, but the DA value (0.16 mm) was much smaller than the FA4a index (2.02 mm), suggesting that the contribution of the DA to the total variation in leaf width is small and can therefore be neglected while analysing FA. None of the explored factors explained the variation in FA among individual trees (Fig. 2d; Table 2). However, at the site level, FA was positively correlated with the radial increment (r = 0.66, n = 10 sites, P = 0.04).

Leaf damage by insects (Supplementary data 3) varied greatly among the sites but not among individual trees nested within the sites. The among-site variation was not associated with the distance from the smelter (Fig. 3; Table 2). The significant annual variation in the proportion of leaves damaged by insects was not modified by the pollution load (Table 2). Herbivory was negatively correlated with leaf length within the study sites (r = -0.43, n = 50 trees, P = 0.0016), whereas the among-site correlation between leaf length and herbivory was only marginally significant (r = -0.59, n = 10 sites, P = 0.07). None of our trees experienced mammalian browsing during the observation period.

Discussion

Aspen performance in polluted areas

We for the first time explored responses of aspen to the combined impacts of soil contaminated by heavy metals and harsh environmental conditions by five-years-long recording of several performance indices in trees naturally growing along the steep pollution gradient. Among 36 species of trees and shrubs, the leaf length and the radial and vertical growth were reduced, on average, to 92, 72 and 64%, respectively, near industrial polluters compared to unpolluted sites, respectively (calculated from the supplementary file appended to [27]). By contrast, none of these performance indices changed in aspen along the Monchegorsk pollution gradient, despite the extreme levels of topsoil contamination near the smelter (2500–4000 mkg g^{-1} of copper and 500–1200 mkg g^{-1} of nickel: M. Kozlov, unpublished data). Thus, aspen does not appear to experience environmental stress as defined by Grime [26], even in extremely polluted sites. This pattern was consistent across study years, suggesting that the annual variation in weather conditions did not interact with the spatial pattern in aspen performance. These results support our hypothesis that aspen is tolerant to extreme pollution loads.

The absence of a pollution effect on leaf FA in aspen is in agreement with the absence of environmental stress (as quantified by tree growth). At the same time, the positive correlation between leaf FA and the rate of radial growth is surprising because fast growth is indicative of plant vigour [26] and should therefore be accompanied by a low FA [44, 45]. At one time, fast leaf growth *per se* was suggested to cause an increase in FA [46, 47], but this hypothesis was not confirmed [48]. This discrepancy between the observed and predicted correlations of FA and plant growth questions the validity of FA as an indicator of environmental stress, at least in aspen.

In 1972, the leaves of young aspen trees growing close to Monchegorsk showed excessive numbers of necrotic spots [49]. The absence of necrotic leaf damage in the 2000s can be explained by both the substantial decrease in the emissions of sulphur dioxide into the ambient air from 117,200 t in 1972 to 43,900 t in 2001 [36] and by the development of pollution tolerance in the exposed populations of aspen through survival selection, as observed in mountain birch [50]. The latter mechanism may also explain why the aspens growing in extremely polluted sites near Monchegorsk performed as well as their counterparts in unpolluted sites, whereas in controlled experiments, the realistic concentrations of pollutants sometimes (although not always) caused detrimental effects on aspens that originated from non-polluted environments [16, 21, 22].

Finally, we found no effect of pollution on insect-inflicted damage of aspen leaves. This result is consistent with the outcomes of multiyear studies of insect herbivory on willows [51] and mountain birch [52] in the same pollution gradient, as well as with the absence of a correlation between aspen leaf infestation by gall mites near the copper-nickel smelter in Harjavalta, SW Finland [20]. Moreover, near the Middle-Ural copper smelter, herbivory on aspen decreased relative to that observed in unpolluted sites [53]. Taken together, these findings confirm a previously expressed opinion [54] that an overall increase in insect herbivory near industrial polluters, discovered by meta-analysis of published studies, may be an artefact caused by research and publication biases. Alternatively, the increase in insect herbivory in polluted areas, which was considered a general regularity several decades ago [55, 56], may have weakened and finally disappeared due either to an overall decline in pollution following strict emission controls or to the adaptation of plants to chronic pollution [57]. Regardless of the mechanisms involved, our data demonstrate that the current levels of environmental contamination are unlikely to enhance insect herbivory and thereby compromise the use of aspen for the reclamation of polluted habitats.

Aspen occurrence in polluted areas

Aspen is a keystone species in boreal forests dominated by conifers [58]. In 1932, aspens were extremely rare in the forested area that became heavily polluted in the 1950s–1960s

[35]. The only group of mature (up to 20 m tall) aspen trees was found in 1932 on a hill near our study plot located 1.8 km N of the smelter. These large trees disappeared well before the 1970s; by 1972, only small bush-like aspens were found in the vicinity of this site [49]. By the 2000s, the aspen population in this area had declined completely, possibly because the topsoil had been almost completely removed by wind erosion (M. Kozlov, personal observation).

No aspen stands currently occur in the central part of the Murmansk region where we conducted our study [59], and we observed only a few small groups of mature aspen trees in spruce and pine forests within 50 km from Monchegorsk. At the same time, the occurrence of aspens in heavily polluted areas around Monchegorsk increased from pre-industrial times, as evident from a comparison of recent observations and data published by Bobrova and Kachurin [35]. This finding parallels the recorded increase in aspen abundance in the Swedish subarctic [60] following the decline of its main competitor, mountain birch. However, the reasons for the decline in birch trees differ between these regions: in our sites, it was driven by extreme pollution [13, 23], whereas in Sweden, it was caused by outbreaks of geometrid moths, primarily *Epirruta autumnata* Bkh. [61]. Aspen is a more thermophilic species than mountain birch [60]; therefore, the expansion of aspen in barren sites near Monchegorsk is further facilitated by the substantial increase in spring and summer temperatures that has occurred over the past decades [62], by the warmer microclimate of the barren sites in summertime [2], and by absence of browsing of young aspens due to the extremely low densities of mammals in the polluted sites [63].

Aspen and recovery of polluted areas

Young aspen trees were once replanted from unpolluted forests to the industrial barren near Monchegorsk [64], but the results of this experiment were never published. This gives particular value to our occasional observation made in the two most polluted plots located 1.8 km N and 6.4 km S of the smelter. In the early summer of 1992, we used sticks (20–30 mm diameter, 30–40 cm length) made of aspen to mark the corners of several study plots. Surprisingly, about half of these sticks rooted and produced shoots. This observation suggests that aspen cuttings can be used for reclamation of heavily polluted sites without any improvement in the soil quality. By contrast, mountain birch and several willow species (*Salix caprea* L., *S. phylicifolia* L., *S. glauca* L.) require liming, fertilisation or addition of fertile soils to assure establishment and vitality when planted in industrial barrens [65].

The establishment of pollution-tolerant, fast-growing aspen in industrial barrens may facilitate the natural recovery of plant communities in two ways. First, groups of aspen trees provide mechanical shelter for low-stature plant individuals, including dwarf shrubs (*Empetrum nigrum* ssp. *hermaphroditum* (Hagerup) Böcher, *Vaccinium myrtillus* L., *V. vitis-idaea* L.) and the seedlings of forest trees. Shelters, both natural and established by the experimenter, increased the survival and performance of dwarf shrubs and birch seedlings in barren sites near Monchegorsk by creating a warmer microclimate, by mitigating wind stress during the growth season, and by protecting plants from snow abrasion and from freezing by trapping snow at the beginning of winter [2, 25]. Second, aspen leaf litter has a high calcium content [66] and thus can make polluted soils less acidic. Third, aspen litter likely enhances mineral nutrient availability in the surface soil horizons [67], and this may be especially important in nutrient-deficient [68] barren sites.

Conclusion

Lack of detrimental effects of extreme pollution on any of the studied traits indicates a high tolerance of aspen to the harsh environmental conditions of industrial barrens. This tolerance makes aspen a suitable species for rehabilitation of areas with extreme levels of soil contamination by copper, nickel and other metals. The fast-growing aspens established in heavily polluted sites may facilitate natural recovery of plant communities by sheltering dwarf shrubs and tree seedlings and by producing litter that improves soil quality, thus promoting improvement of ecosystem health and mitigation of disturbances caused by industrialization of this region.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Table 1. The characteristics of study sites.

Site code[a]	Distance from the smelter, km	Latitude, N	Longitude, E	Foliar Ni[b], mkg g^{-1}	Stand basal area[c], m^2 ha^{-1}	Cover of field layer plants[c]	Habitat type[d]
8N	7.9	67° 59'	32° 54'	90	0.8	5.8	SDF
2N	1.8	67° 56'	32° 49'	340	0.3	0.4	IB
6S	6.4	67°52'	32° 48'	185	0	1.0	IB
12S	12.1	67° 49'	32° 47'	95	19.2	30	SDF
17S	17.3	67° 46'	32° 48'	80	5.0	36	SDF
26S	26.4	67° 41'	32° 49'	45	19.4	42	DF
33S	32.9	67°38'	32° 45’	40	6.3	56	DF
40S	39.8	67°35'	32° 34'	20	11.0	52	UF
49SE	49.0	67°35'	33° 35'	10	1.8	35	UF
64SE	64.5	67°32'	33° 58'	15	18.7	58	UF

[a] The site code indicates approximate distance from the smelter in km and direction to the north, south or south-east of the smelter.

[b] In mountain birch (*Betula pubescens* var. *pumila*); after [39].

[c] After [36].

[d] DF, slightly damaged forest; IB, industrial barren; SDF, severely damaged forest; UF, undamaged forest.

Table 2. Sources of variation in leaf traits and in proportion of leaves of European aspen, *Populus tremula*, damaged by insects (SAS GLIMMIX procedure, type 3 analyses).

Effect type	Explanatory variable	Leaf length		Fluctuating asymmetry		Herbivory	
		Test statistics	*P* value	Test statistics	*P* value	Test statistics	*P* value
Fixed	Distance	$F_{1, 8.0} = 0.15$	0.71	$F_{1, 8.0} = 0.32$	0.58	$F_{1, 8.1} = 0.81$	0.40
	Year	$F_{4, 183.2} = 1.87$	0.12	$F_{4, 184.1} = 1.32$	0.27	$F_{4, 212.8} = 2.86$	0.02
	Distance × year	$F_{4, 183.2} = 0.84$	0.50	$F_{4, 183.6} = 0.79$	0.53	$F_{4, 212.8} = 1.92$	0.11
Random	Site	$\chi^2_1 = 18.58$	<0.0001	$\chi^2_1 = 1.77$	0.09	$\chi^2_1 = 42.45$	<0.0001
	Tree(Site)	$\chi^2_1 = 10.08$	0.0007	$\chi^2_1 = 0.48$	0.24	$\chi^2_1 = 0.09$	0.38

Table 3. Basic statistics on repeated measurements of differences between the width of left and right sides of leaves of European aspen, *Populus tremula* (SAS GLIMMIX procedure, type 3 analyses).

Year	Sample size	DA[1], mm	Mixed model ANOVA				Reproducibility (ME5)
			Side		Side × Leaf		
			Test statistics	*P* value	Test statistics	*P* value	
2001	500	0.08	$F_{1, 498} = 1.29$	0.26	$F_{498, 998} = 8.13$	<0.0001	0.781
2002	500	0.00	$F_{1, 499} = 0.00$	0.97	$F_{499, 999} = 7.11$	<0.0001	0.753
2003	450	0.08	$F_{1, 448} = 1.10$	0.30	$F_{448, 898} = 7.15$	<0.0001	0.752
2004	500	0.02	$F_{1, 497} = 0.05$	0.83	$F_{497, 996} = 4.57$	<0.0001	0.641
2005	450	0.16	$F_{1, 449} = 6.78$	0.01	$F_{449, 900} = 4.22$	<0.0001	0.617

[1] DA, directional asymmetry (signed difference in width of right and left leaf halves).

Figure captions

Figure 1. Location of study sites (dots) in the vicinity of the Monchegorsk nickel–copper smelter (four pointed star) in the Kola Peninsula. Site codes indicate the approximate distance (km) and direction (to the north, south or south-east) from the smelter. Coordinates of the study sites are provided in Table 1. Insert: position of the study area in Northern Europe.

Figure 2. The relationships of performance indices of European aspen, *Populus tremula*, measured from 2001-2005, with the distance from the Monchegorsk nickel–copper smelter: a, annual radial increment; b, annual vertical increment; c, leaf length; d, fluctuating asymmetry. Bars indicate standard errors (*n* = 5 trees at each study site); *F* value refers to covariation with log-transformed distance.

Figure 3. The relationships of the percentage of leaves of European aspen, *Populus tremula*, damaged by insects from 2001–2005, with the distance from the Monchegorsk nickel–copper smelter. Bars indicate standard errors (*n* = 5 trees at each study site); *F* value refers to covariation with log-transformed distance.

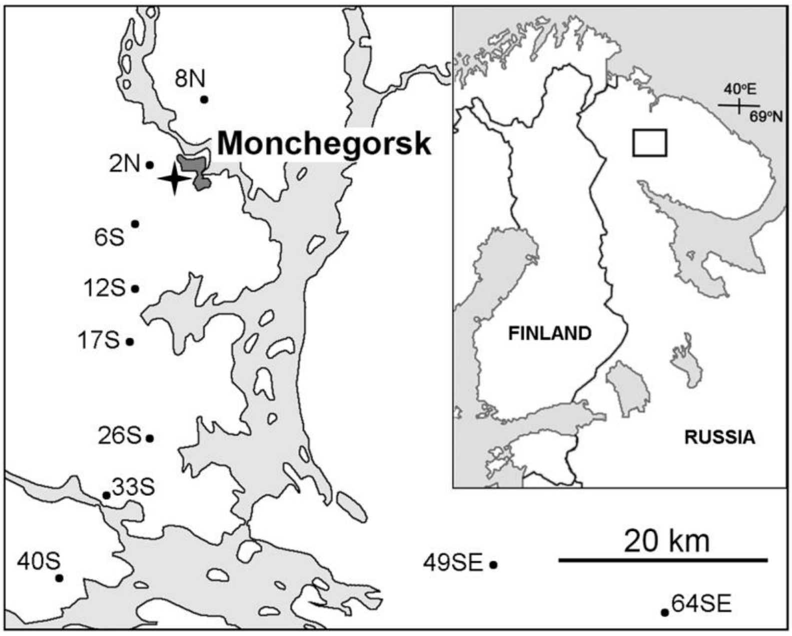
8N
Monchegorsk
2N
6S
12S
17S
26S
33S
40S
49SE
64SE
20 km
40ºE
69ºN
FINLAND
RUSSIA

Fig. 1.

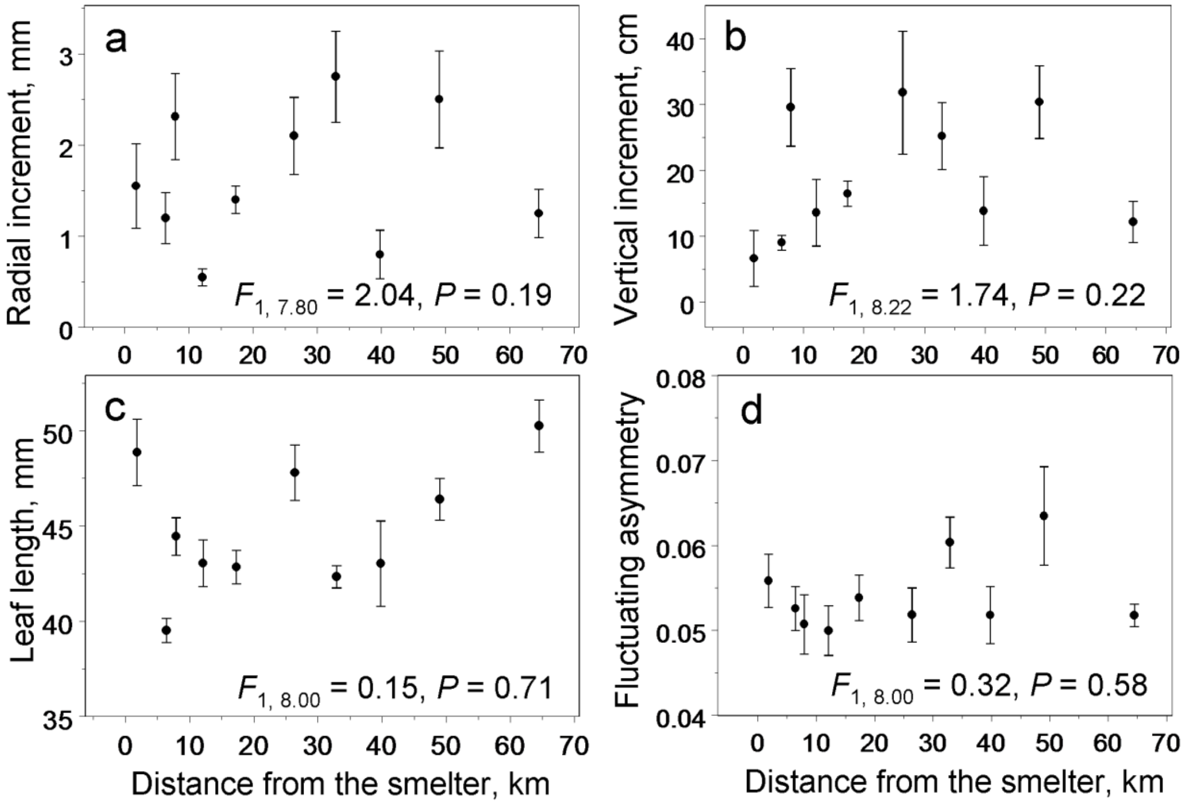
a
Radial increment, mm
0
1
2
3
$F_{1,\ 7.80}$ = 2.04, P = 0.19
b
Vertical increment, cm
0
10
20
30
40
$F_{1,\ 8.22}$ = 1.74, P = 0.22
c
Leaf length, mm
35
40
45
50
$F_{1,\ 8.00}$ = 0.15, P = 0.71
d
Fluctuating asymmetry
0.04
0.05
0.06
0.07
0.08
$F_{1,\ 8.00}$ = 0.32, P = 0.58
0
10
20
30
40
50
60
70
Distance from the smelter, km
Distance from the smelter, km

Fig. 2.

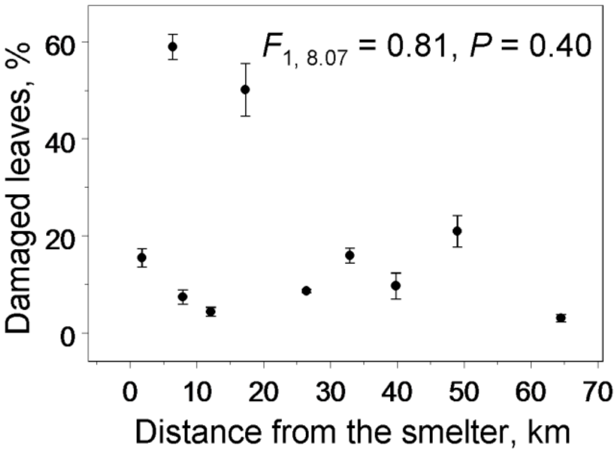
$F_{1,\ 8.07} = 0.81$, $P = 0.40$
Damaged leaves, %
0
20
40
60
0
10
20
30
40
50
60
70
Distance from the smelter, km

Fig. 3.