Changes in urban lichen diversity after a fall in sulphur dioxide levels in the city of Tampere, SW Finland

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As a consequence of air pollution, lichens disappeared from the central part of the city of Tampere. A lichen desert of 5 km² covered the centre in the beginning of the 1970s. Later the mean annual SO₂ concentration decreased from 160 μ g m⁻³ in 1973 to 2 μ g m⁻³ in 1999. The monitoring of lichens on the trunks of *Tilia* x *vulgaris* which began in 1980 showed that recolonisation had started slowly but advanced rapidly after 1985. In 2000, the numbers of species in the monitoring sites were over 10 times and cover values nearly 200 times higher than in 1980. The number of species increased linearly, while cover values rose exponentially. In 2000, the reference sites had twice as many lichen species and over three times higher cover than the city sites. Thus, the recovery of the lichen flora and vegetation will take several decades after the virtual elimination of SO₂.

Key words: environmental monitoring, epiphytic lichens, recolonisation, reduction of emissions, sulphur dioxide

Introduction

The disappearance of lichens from urban and industrial areas due to air pollution is a common phenomenon, and lichens have been widely used in the monitoring of air quality (e.g. Hawksworth & Rose 1976, Seaward 1992). Lichens are suitable for this purpose as they are sensitive to atmospheric sulphur dioxide, which has been a common pollutant in many urban areas. In recent years, several European countries have succeeded in significantly reducing their sulphur dioxide emissions. For instance, the total sulphur dioxide emissions of Finland were 584 000 tonnes in 1980, but less than one fifth of that (96 000 tonnes) in 1995 (Wahlström *et al.* 1996).

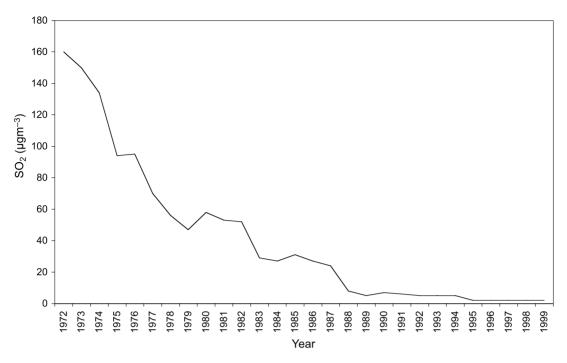


Fig. 1. Mean yearly sulphur dioxide concentration at Tampere Central Square observation station 1973–1999 (μg m⁻³).

In some polluted areas, the consequent improvement of air quality has been rapid and remarkable.

In spite of a significant reduction of domestic sulphur dioxide emissions, Finland still receives considerable amounts of airborne pollutants from other countries. Consequently, large forested areas in southeastern Finland are showing greatly impoverished lichen floras and vegetation (Haapala *et al.* 1996), and in southwestern Finland lichens have not yet recovered from the effects of earlier air pollution (Kuusinen *et al.* 1995).

Recent trends towards lower concentrations of airborne sulphur dioxide have led to changes in lichen distribution and the recolonisation of former lichen deserts (Boreham 1992, Boreham 1993, Cooke *et al.* 1990, Fletcher 1992, Seaward & Henderson 1991, Seaward *et al.* 1994, Seaward 1997, Showman 1981, Wirth 1993). Even pollution-sensitive species have appeared again, in some cases after an absence of several decades (Gilbert 1992). However, recolonisation appears not to be a simple phenomenon where the lichens which have disappeared just return. Recolonisation patterns and speed vary according to species, substrate and dispersal ability (Hawksworth & McManus 1989, van Dobben 1996, van Dobben & de Bakker 1996). Therefore, long-term monitoring is needed to document the arrival of the various species, especially the latecomers.

Tampere is an industrial city (population ca. 195 000), where sulphur dioxide pollution was severe in the 1970s. The most important sources were numerous factories (pulp, cardboard, metallurgical and chemical products), and individual heating of buildings. Industrial emissions started to fall as a consequence of several concomitant actions: the use of low-sulphur fuels, the introduction of sulphur filters, improvements in industrial processes, and the closure of some of the most polluting industrial plants. A centralised heating system with peat as fuel was established in 1982, and it greatly reduced emissions from the heating of buildings. The use of natural gas as a fuel started in 1983. As a consequence of all these actions, the yearly mean SO₂ concentrations started to fall rapidly (Fig. 1). In 1970, the yearly SO_2 emissions in

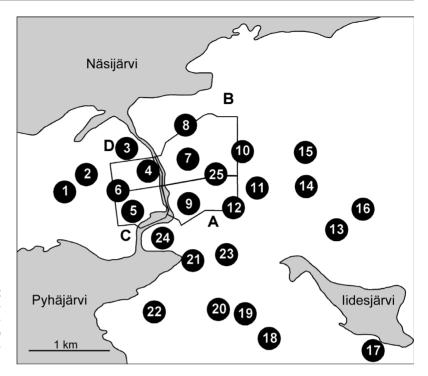


Fig. 2. The 25 permanent study sites and four sectors (A–D) in the city centre for monitoring of the total colonisable tree surface.

Tampere were over 23 000 tonnes, but in 1999 only 972 tonnes (a reduction of 96%) (Salovaara 1999, Tampereen kaupunki 2000). The emissions of other pollutants have also decreased. NO_x emissions (calculated as t NO₂ a^{-1}) decreased from 5182 tonnes in 1987 to 3882 tonnes in 1999.

The annual total deposition of sulphur (S, mg m⁻²) is between 300 and 400 mg m⁻² in the Tampere area (1995). The total deposition of sulphur is now much lower than in the 1980s, but the reduction of the total deposition of nitrogen (NO₃-nitrogen and NH₄-nitrogen combined) is smaller. At its highest the total annual deposition of nitrogen was over 10 kg N ha⁻¹, but nowadays the deposition is about 6 kg N ha⁻¹ (Nordlund 1998). Both sulphur and nitrogen depositon cause acidification, wich may have a negative effect on epiphytic lichens.

In the early 1970s, a lichen desert of about 5 km² with virtually no lichens covered the central parts of Tampere (Sahrakorpi 1973, Ranta 1974). Furthermore, in the surroundings of the lichen desert, lichen vegetation was greatly impoverished. The aim of this study is to present the results of a monitoring scheme established in

1980 to record the changes and recovery of epiphytic macrolichens in relation to falling sulphur dioxide levels. This study is part of a research project on urban ecology in Tampere, with special emphasis on temporal change of urban ecosystems.

Material and methods

In 1980, a permanent system for monitoring lichens was established in Tampere. The sites described below were checked for lichens in 1980, 1985, 1990, 1995 and 2000. The monitoring system consists of (1) 25 study sites mainly in the area of the former lichen desert in the city centre (Fig. 2), (2) six reference sites outside of the lichen desert and further away from the city centre, (3) four sectors in the city centre for monitoring of all the tree trunks (all species included) in the most polluted area (Fig. 2), and (4) all trees (38) along the eastern part of the main street Hämeenkatu.

Each one of the 25 study sites in the city centre consists of five adjacent trees of *Tilia* x *vulgaris*. Only trees with a perimeter of over

Fig. 3. Percentage of trees colonized in four sectors (A–D) in the city centre from 1980 to 2000. One tree in sector A had lichens in 1980. It represents less than 0.1% of total number of trees in sector A. The graphical presentation of that tree is not possible using the actual scale of this figure.

50 cm were selected. In practice the trees are much thicker than the lowest limit: the mean perimeter was 130 cm in 1980. *Tilia* was selected because it is a common ornamental tree in Tampere, and it is present in sufficiently many places along streets and in parks. Two of the 125 studied trees were lost during the monitoring period, and were excluded from the calculations.

The six reference sites are situated further away from the city centre: Härmälä (3.5 km S from central square), Rahola (6 km W), Pyynikki (2 km SW), Linnainmaa (6 km E), Haihara (7 km SE) and Koivistonkylä (3 km SSE). Also these sites include five *Tilia* trees of > 50 cm in perimeter (mean perimeter 158 cm in 1980) monitored in a similar way as the 25 sites in the city centre.

The recolonisation process of lichens in relation to the available surface area of tree trunks was monitored at three levels: (1) the total colonisable surface of all trees, (2) the study site level, and (3) the individual tree level. In the four monitoring sectors (Fig. 2), the presence or absence of lichens on the tree trunks from 0 cm to 200 cm (all tree species included) was noted. In the study sites, cover values of lichen species was measured on each tree in cm² between 0 cm and 200 cm from the ground and converted to % of the total available surface (200 cm × perimeter of the tree). The cover values and trunk surface areas were then summed for the whole study site. On an individual tree level (the 38 trees along the main street), the surface of each tree was divided into four zones: upper sides of branches, upper trunk, rough surfaces and lower trunk. Colonisation of these zones was recorded for every tree. The upper sides of branches were observed from windows and roofs of buildings or with binoculars from the ground. The trees were studied in a similar way in 1980, 1985, 1990, 1995 and 2000.

For each lichen species, its first appearance in the study sites was noted together with subsequent changes of frequency and cover during the monitoring period. The nomenclature of the lichens follows Vitikainen *et al.* (1997).

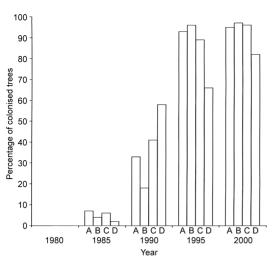
Results

Recolonisation of the total colonisable tree surface area by lichens

The recolonisation process showed the same general pattern in all four sectors: slow in the beginning but rapid advancement after 1985 (Fig. 3). In 1980, only one tree trunk had lichens, but in 2000 the percentage of occupied trees varied between 82% and 97%.

However, the presence-absence data does not reveal the differences in cover values or general condition of lichens. Even in 2000, the lichen vegetation was in a very early stage of succession on some trees. The distribution of lichen-free trees in 2000 was highly irregular and probably not related to air pollution. This may reflect certain randomness associated with the colonisation process. In urban conditions it is doubtful whether a full 100% occupancy will ever be reached, because some trees may grow in locations that are unfavorable for lichens for reasons other than air pollution.

The former lichen desert as a continuous zone disappeared rapidly after 1985. Streetside trees were the last ones to be recolonised probably because of dust, particulates and exhaust fumes from cars, while trees in parks were



recolonised early as in the most central areas of the city.

Recolonisation of the study sites

At the beginning of the monitoring in 1980, only six of the 25 study sites had lichens. In 1985, the number of study sites with lichens was 20 and later 24 (1990) and 25 (1995 and 2000).

The recolonisation did not show a clear geographical pattern. Lichens appeared early also in the centre of the former lichen desert. However, the study sites in the centre of the city still showed lower coverages and species numbers than the reference sites in 2000. The lowest cover and species numbers were observed in study sites along the main streets (Table 1).

Table 1. Number of species (*S*) and total cover (*C*) of lichens on study sites (S1–S25) and reference sites (R1–R6) from 1980 to 2000. Cover in % of the total trunk area (0–200 cm), + means cover values less than 0.01%.

| Site | 1980 | | 1985 | | 1990 | | 1995 | | 2000 | |
|------|------|-------|------|-------|------|-------|-------|-------|-------|-------|
| | S | С | S | С | S | С | S | С | S | С |
| S1 | 1 | + | 3 | 0.03 | 5 | 0.12 | 8 | 5.90 | 8 | 9.22 |
| S2 | 1 | 0.01 | 2 | 0.07 | 5 | 0.27 | 6 | 0.74 | 7 | 1.66 |
| S3 | 0 | 0 | 0 | 0 | 3 | 0.08 | 6 | 0.15 | 6 | 0.49 |
| S4 | 0 | 0 | 3 | 0.14 | 5 | 0.32 | 8 | 1.69 | 9 | 6.18 |
| S5 | 0 | 0 | 2 | 0.09 | 2 | 0.35 | 4 | 1.12 | 4 | 4.77 |
| S6 | 0 | 0 | 0 | 0 | 1 | + | 2 | 0.04 | 4 | 0.52 |
| S7 | 0 | 0 | 0 | 0 | 1 | + | 2 | 0.07 | 3 | 0.39 |
| S8 | 2 | 0.15 | 5 | 0.63 | 7 | 0.12 | 10 | 1.19 | 11 | 2.78 |
| S9 | 0 | 0 | 2 | 0.01 | 4 | 0.18 | 5 | 0.62 | 7 | 1.05 |
| S10 | 0 | 0 | 1 | 0.02 | 3 | 0.14 | 3 | 0.45 | 5 | 0.89 |
| S11 | 0 | 0 | 3 | 0.08 | 5 | 2.32 | 6 | 15.40 | 8 | 31.22 |
| S12 | 0 | 0 | 0 | 0 | 1 | 0.05 | 3 | 0.28 | 5 | 0.44 |
| S13 | 0 | 0 | 3 | 0.17 | 5 | 1.42 | 9 | 4.67 | 8 | 8.91 |
| S14 | 2 | 0.03 | 3 | 0.66 | 3 | 6.33 | 4 | 15.42 | 4 | 32.83 |
| S15 | 0 | 0 | 3 | 0.14 | 5 | 2.73 | 8 | 11.26 | 8 | 18.55 |
| S16 | 0 | 0 | 4 | 0.37 | 6 | 7.78 | 8 | 36.21 | 9 | 67.19 |
| S17 | 7 | 1.35 | 9 | 2.29 | 12 | 3.64 | 14 | 5.78 | 14 | 10.01 |
| S18 | 0 | 0 | 6 | 0.14 | 0 | 0 | 5 | 0.09 | 7 | 0.21 |
| S19 | 0 | 0 | 4 | 0.04 | 4 | 0.39 | 5 | 2.97 | 6 | 9.15 |
| S20 | 0 | 0 | 4 | 0.06 | 4 | 0.39 | 9 | 2.06 | 9 | 7.12 |
| S21 | 0 | 0 | 0 | 0 | 5 | 0.03 | 6 | 0.39 | 8 | 1.59 |
| S22 | 1 | + | 6 | 0.16 | 11 | 4.80 | 11 | 9.47 | 10 | 24.02 |
| S23 | 0 | 0 | 4 | 0.13 | 5 | 1.28 | 9 | 3.86 | 11 | 9.15 |
| S24 | 0 | 0 | 2 | 0.02 | 6 | 1.40 | 8 | 5.45 | 9 | 16.44 |
| S25 | 0 | 0 | 4 | 0.07 | 5 | 0.20 | 7 | 2.74 | 10 | 8.00 |
| Mean | 0.7 | 0.06 | 2.92 | 0.21 | 4.52 | 1.36 | 6.64 | 5.11 | 7.60 | 10.91 |
| SD | 1.55 | 0.27 | 2.20 | 0.47 | 2.76 | 2.11 | 2.91 | 7.92 | 2.61 | 15.01 |
| R1 | 8 | 9.46 | 8 | 11.39 | 10 | 12.36 | 15 | 17.43 | 16 | 18.80 |
| R2 | 7 | 16.30 | 8 | 19.01 | 9 | 21.57 | 14 | 26.43 | 16 | 27.75 |
| R3 | 7 | 5.44 | 7 | 7.92 | 8 | 10.85 | 12 | 11.78 | 14 | 12.48 |
| R4 | 4 | 4.03 | 4 | 5.34 | 5 | 5.97 | 8 | 6.87 | 9 | 10.05 |
| R5 | 6 | 2.50 | 7 | 2.98 | 9 | 3.53 | 14 | 4.26 | 14 | 6.82 |
| R6 | 9 | 9.00 | 11 | 10.90 | 11 | 13.01 | 12 | 15.43 | 14 | 18.66 |
| Mean | 6.83 | 7.79 | 7.50 | 9.59 | 8.67 | 11.22 | 12.50 | 13.70 | 13.83 | 19.60 |
| SD | 1.72 | 4.99 | 2.26 | 5.63 | 2.07 | 6.30 | 2.51 | 7.98 | 2.56 | 7.55 |

Despite the strong recovery, some unsuccesful colonisation attempts by lichens were observed. For example, study site 18 had six lichen species in 1985, but none in 1990. Lichens appeared again in 1995, but the colonising species were different from those recorded ten years earlier. This exceptional colonisation event may be explained by changes of industrial activities in the surroundings. Although the trees within the study sites grow side by side in similar environmental conditions, and are practically of the same size and age, the lichen flora and vegetation may vary greatly among them. For example, the number of species on the five trees that belong to the study site 8, were in 1995 1, 3, 3, 10 and 2. The total cover of lichens on the same trees was 5 cm^2 , 107 cm^2 , 616 cm^2 , 1289 cm^2 and 205 cm^2 .

Table 2. Colonisation of the trees along the main street Hämeenkatu. B = branches, T = trunk, + = lichens observed, - = lichens not observed.

| Trees | 1980 | | 1985 | | 19 | 1990 | | 1995 | | 2000 | |
|----------|------|---|------|---|--------|------|---|--------|---|------|--|
| | В | Т | В | Т | В | Т | В | Т | В | Т | |
| 1 | _ | _ | _ | _ | _ | _ | + | _ | + | | |
| 2 | _ | _ | _ | _ | _ | _ | + | _ | + | + | |
| 3 | _ | _ | _ | _ | _ | _ | + | _ | + | + | |
| 4 | - | - | _ | - | + | _ | + | + | + | + | |
| 5 | - | - | _ | - | + | _ | + | + | + | + | |
| 6 | _ | - | _ | - | + | _ | + | - | + | + | |
| 7 | _ | _ | _ | _ | _ | _ | _ | _ | + | _ | |
| 8 | - | - | _ | - | - | _ | + | - | + | + | |
| 9 | _ | _ | + | _ | + | + | + | + | + | + | |
| 10 | _ | _ | _ | _ | _ | _ | + | _ | + | + | |
| 11 | _ | _ | _ | _ | _ | _ | _ | _ | + | _ | |
| 12 | _ | _ | _ | _ | + | _ | + | + | + | + | |
| 13 | _ | _ | _ | _ | + | _ | + | + | + | + | |
| 14 | _ | _ | _ | _ | + | _ | + | _ | + | + | |
| 15 | _ | _ | + | _ | + | _ | + | + | + | + | |
| 16 | _ | _ | _ | _ | _ | _ | + | + | + | + | |
| 17 | _ | _ | _ | _ | + | _ | + | + | + | + | |
| 18 | _ | _ | _ | _ | _ | _ | + | _ | + | + | |
| 19 | _ | _ | + | _ | + | + | + | + | + | + | |
| 20 | _ | _ | + | _ | + | _ | + | + | + | + | |
| 21 | _ | _ | _ | _ | _ | _ | + | _ | + | + | |
| 22 | _ | _ | _ | _ | + | _ | + | + | + | + | |
| 23 | _ | _ | _ | _ | + | _ | + | + | + | + | |
| 24 | _ | _ | _ | _ | _ | _ | + | _ | + | + | |
| 25 | _ | _ | _ | _ | + | _ | + | + | + | + | |
| 26 | _ | _ | _ | _ | + | _ | + | + | + | + | |
| 27 | _ | _ | + | _ | + | + | + | + | + | + | |
| 28 | _ | _ | _ | _ | _ | _ | _ | + | + | + | |
| 29 | _ | _ | _ | _ | + | _ | + | + | + | + | |
| 30 | _ | _ | _ | _ | + | _ | + | + | + | + | |
| 31 | _ | _ | _ | _ | - - | _ | + | - - | + | + | |
| 32 | _ | _ | _ | _ | _ | _ | + | + | + | + | |
| 33 | _ | _ | _ | _ | _ | _ | + | + | + | + | |
| 34 | _ | _ | _ | _ | + | _ | + | + | + | + | |
| 34 35 | _ | _ | _ | _ | + | _ | + | ++ | + | | |
| 35 36 | _ | _ | _ | _ | _ | _ | | | | + | |
| 36 37 | _ | - | - | _ | + | + | + | + | + | + | |
| 3/ 20 | - | - | - | - | - | - | - | + | + | + | |
| 38 | - | _ | _ | - | - | - | _ | - | + | _ | |

There was no obvious explanation for these differences. The differences of this kind did not level out during the monitoring period.

Recolonisation on individual trees

Monitoring only the tree trunks does not give a complete picture of the recolonisation process of lichens. Even where lichens were absent from tree trunks, rather healthy and species-rich lichen communities could be found on the upper sides of the main branches. The presence or absence of lichens on different parts of the tree was noted during every monitoring cycle.

The appearance of lichens on branches and trunks of the 38 trees along the main street Hämeenkatu followed a pattern in which lichens first appeared on the upper sides of main branches. While the trunks still remained to be colonised, luxurious lichen vegetation, mostly invisible from the ground, already covered the branches. After colonising the branches, the lichens appeared on the rough surfaces and finally on the main trunk (Table 2).

Recolonisation of individual lichen species

The observed lichen species of the study sites and their frequencies are presented in Table 3.

The lichens in the study area can be divided into early colonisers and late colonisers. Early colonisers are those species that appeared during the first five years (1980–1985), whereas late colonisers were observed in 1990 or later (Table 4). Within these groups, practically every species showed a slightly different colonisation pattern. Among the early colonisers, the increase of occupied study sites stabilised after the initial phase. Species like *Tuckermannopsis chlorophylla* and *Hypocenomyce scalaris* are good examples of this colonisation type. *Physcia ad*-

Table 3. Frequency (%) of the lichen species of the study sites from 1980 to 2000.

| Species | Frequency | | | | | | |
|------------------------------|-----------|------|------|------|------|--|--|
| | 1980 | 1985 | 1990 | 1995 | 2000 | | |
| Bryoria sp. | 0 | 0 | 4 | 56 | 60 | | |
| Tuckermannopsis chlorophylla | 4 | 40 | 64 | 60 | 64 | | |
| Cetraria sepincola | 0 | 28 | 60 | 92 | 96 | | |
| Evernia prunastri | 0 | 0 | 0 | 4 | 16 | | |
| Hypocenomyce scalaris | 4 | 20 | 24 | 28 | 32 | | |
| Hypogymnia physodes | 24 | 80 | 96 | 100 | 100 | | |
| Hypogymnia tubulosa | 0 | 4 | 8 | 12 | 12 | | |
| Melanelia exasperatula | 0 | 0 | 4 | 16 | 20 | | |
| Melanelia olivacea | 0 | 0 | 4 | 8 | 16 | | |
| Parmelia sulcata | 4 | 28 | 60 | 76 | 84 | | |
| Parmeliopsis ambigua | 0 | 0 | 8 | 12 | 16 | | |
| Phaeophyscia orbicularis | 4 | 8 | 12 | 20 | 24 | | |
| Physcia adscendens | 4 | 8 | 12 | 20 | 20 | | |
| Physcia aipolia | 0 | 0 | 4 | 12 | 16 | | |
| Physcia tenella | 4 | 4 | 4 | 4 | 4 | | |
| Platismatia glauca | 0 | 8 | 4 | 28 | 32 | | |
| Ramalina farinacea | 0 | 0 | 0 | 0 | 4 | | |
| <i>Usnea</i> sp. | 0 | 0 | 0 | 4 | 12 | | |
| Vulpicida pinastri | 8 | 64 | 64 | 76 | 72 | | |
| Xanthoria candelaria | 0 | 0 | 4 | 8 | 12 | | |
| Xanthoria parietina | 0 | 0 | 4 | 16 | 20 | | |
| Xanthoria polycarpa | 0 | 0 | 8 | 28 | 28 | | |
| Total number of species | 8 | 11 | 19 | 21 | 22 | | |

scendens and Phaeophyscia orbicularis showed a slow increase, but they are not common species on *Tilia*. This applies also to the *Xanthoria* species that occur normally on *Tilia* in areas affected by human activities, like dust from roads. On the other hand, *Parmelia sulcata* and *Vulpicida pinastri* increased constantly and were finally found in most study sites. The very latest colonisers are the sensitive species *Evernia prunastri*, *Usnea* spp. and *Ramalina farinacea*.

Temporal changes in species richness and cover of lichens

The mean number of species on study sites increased from 0.7 (1980) to 7.6 (2000). The increase in the number of species per study site was rapid and continuous. The mean cover remained low from 1980 to 1985, but started to increase rapidly after that. The mean cover increased from 0.06% (1980) to 10.91% (2000). The mean number of species was ten times higher and the total cover nearly 180 times higher in 2000 than in the beginning of monitoring (Fig. 4).

In spite of the rapid recovery, there was still a considerable difference in species richness and total cover of lichens between the 25 study sites in the city centre and the six reference sites. In 2000, the study sites had roughly half of the

Table 4. The reinvading lichen species classified as early and late colonisers in Tampere. The early colonisers appeared in 1980–1985 and the late colonisers in 1990 or later.

| Early colonisers | Late colonisers |
|---------------------------------|------------------------|
| Tuckermannopsis chlorophylla | Bryoria spp. |
| Vulpicida pinastri | Evernia prunastri |
| Cetraria sepincola | Melanelia exasperatula |
| Hypocenomyce scalaris | Melanelia olivacea |
| Hypogymnia physodes | Parmeliopsis ambigua |
| Hypogymnia tubulosa | Physcia aipolia |
| Parmelia sulcata | Ramalina farinacea |
| Phaeophyscia orbicularis | <i>Usnea</i> spp. |
| Physcia adscendens | Xanthoria candelaria |
| Physcia tenella | Xanthoria parietina |
| Platismatia glauca | Xanthoria polycarpa |

species number and the total lichen cover in comparison with the reference sites. The mean number of species in the reference sites increased from 6.83 (1980) to 13.83 (2000). The increase was only two-fold during the monitoring period. The increase of the mean cover was also only over two-fold from 7.79% to 19.60% (Table 1).

The lower increase in the reference sites was due to the higher number of species to begin with, as only the most sensitive species were missing from the reference sites in 1980.

Discussion

The two factors, which could most likely explain the rapid and strong recolonisation of the lichen desert in Tampere, are the very rapid fall of SO₂ levels and the relatively small size of the city. SO₂ concentrations started to fall in the 1970s, and it is estimated that about 2/3 of the decline occurred before 1980 and 1/3 after 1980 when lichen monitoring started. However, the recolonisation of lichens had barely started in 1980, and thus almost the entire recolonisation period has been monitored. Lichen recolonisation started after a lag period of about ten years. The propagules of some lichens reached early to the inner part of the lichen desert, but progress in growth was slow. After 1990, the whole city centre was rapidly colonised by lichens. The observed time lag in the recolonisation may be explained by the fact that the SO₂ concentrations fell more rapidly than the lichens were able to follow. Wide areas suddenly became open for recolonisation but the propagules of lichens needed time to reach the new areas. Once the lichens had started to grow for example on the upper sides of branches there were also local propagules available for further recolonisation.

The recolonisation process of lichens did not show a pattern of an advancing 'wave' or diffusion (Hengeveld 1989). When recolonisation started after 1980, lichens appeared also in the middle of the former lichen desert. At that time the SO_2 levels were fairly low, and practically the whole city area was suddenly open for recolonisation.

Dispersal ability and chance events associated with colonisation probably account for the high variability in species number and cover among individual trees at the same study site during the recolonisation process. Soredia on some species, like *Hypogymnia physodes*, are born in the air and their attachment on a tree may depend on local air currents, i.e. chance. The importance of chance events associated with dispersal is supported by the observation that in 1985 several formerly lichen-free trunks had hundreds of small thalli, whereas adjacent trunks only had a few thalli.

In spite of differences in size and structure of urban areas, the recolonisation of lichens in Tampere shows some similarities to big European cities, such as London (Rose & Hawksworth 1981). Usnea sp. appeared in the centre of Tampere and together with Evernia prunastri and *Platismatia glauca* it may be regarded as a "zone skipper" (Hawksworth & McManus 1989). The sudden appearance of sensitive lichens in the middle of a former lichen desert is attributed also in Tampere to the very rapid decrease of the sulphur dioxide level. However, the increase of some species (like Parmeliopsis ambigua and Hypocenomyce scalaris) has been rather slow in Tampere. Other species appear to be favoured by conditions in the city centre. In Tampere, Cetraria sepincola has the second highest frequency in the city, but it is much less frequent in the reference sites.

Most studies on lichens and air pollution concentrate on the effects of SO₂, which has been clearly identified as the most common pollutant responsible for the disappearance of lichens. Other factors like acidification may also have had some effect on both the disappearance and recolonisation. After the SO₂ nearly disappeared, the nitrogen deposition and to a lesser extent also the sulphur deposition still remain. The acidification of tree bark may be more harmful for typical Xanthorion species that favour less acid bark than Parmelion species. In 2000, 40% of the study sites had at least one Xanthorion species while 100% of the reference sites outside the city centre had species of that group. However, it is clear that Tampere as a city is too small for further analysis.

Although lichens reappeared rapidly in the lichen desert in Tampere, both lichen flora and vegetation are still impoverished in comparison

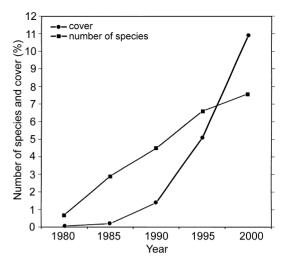


Fig. 4. Increase of the mean number of lichens and the mean total lichen cover (%) at study sites from 1980 to 2000.

to the reference sites and other localities outside the city. In 2000, the reference sites had two times more species and also two times higher average lichen cover than did the city sites. Even in conditions of nearly total absence of SO_2 lichen recovery seems to take several decades. In urban centres there are also other factors, such as particulates, dust, drought and shade that impede the development of luxuriant lichen vegetation on trees. Consequently, there will probably always be a difference in lichen flora and vegetation between urban and rural areas.

Acknowledgements

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