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Leaf morphology in *Arenaria patula* and *Lonicera japonica* along a pollution gradient

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CAIAZZA, NICHOLAS A., JR., and JAMES A. QUINN. (Dept. Bot., Rutgers Univ., Piscataway, N.J. 08854). Leaf morphology in *Arenaria patula* and *Lonicera japonica* along a pollution gradient. Bull. Torrey Bot. Club 107: 9–18. 1980.—Certain plant species have persisted in denuded areas subjected to heavy metals (Zn, Cd, Pb, Cu) and SO_2 air pollution from two zinc smelters in Palmerton, Pennsylvania. The objectives of this research were to determine if correlations existed between the degree of environmental pollution and changes in leaf morphology along a local pollution gradient, and to determine the relative importance of genetic and environmental components responsible for the observed variations in leaf phenotypes. Leaves and epidermal peels from field samples of *Arenaria patula* and *Lonicera japonica* were examined microscopically. Sample sites were chosen to coincide with a previously documented air pollution gradient, and field conditions were monitored. Although stomatal size and leaf volume were not significantly different among populations of a species in the field, those populations of *Arenaria* and *Lonicera* exposed to the highest concentrations of pollutants exhibited the lowest stomatal density and the highest trichome density. Such alterations in leaf morphology should reduce the penetration of gaseous, and especially particulate matter, into the mesophyll and thus reduce susceptibility to pollution damage. Comparisons of results from the field with those of common environments (greenhouse and greenhouse courtyard) indicated phenotypic plasticity as the source of most of the observed field differences in *Arenaria* and *Lonicera;* however, they also provided some evidence for genetic dissimilarity in *Lonicera* populations in stomatal and trichome densities.

Key words: *Arenaria patula;* leaf morphology; *Lonicera japonica;* phenotypic plasticity; pollution gradient.

Adaptive differences in leaf morphology with respect to environmental factors have been reported in several plant species, either as population differentiation in diverse habitats (Briggs and Walters 1969), or as seasonal modifications within individuals (Regehr and Bazzaz 1976; Smith and Nobel 1977). Pollution as a stress has also received recent attention by Sharma and Tyree (1973), Sharma and Butler (1973, 1975), and Sharma (1975). These workers have correlated differences in leaf characteristics in plant populations with environmental changes along implied air pollution gradients. A decrease in stomatal density, along with increasing trichome length and density, in polluted (city) environments was the most common trend exhibited by populations of two clover species (*Trifolium pratense* [2] and *T. repens*) in Tennessee (Sharma and Butler 1973, 1975) and by sugar maple (*Acer saccharum*) in and around Montreal, Canada (Sharma 1975). In addition, populations of sweetgum (*Liquidambar styraciflua*) in Kentucky and Tennessee showed an increased trichome density in the urban sites (Sharma and Tyree 1973).

Sharma (1975) theorized that decreased stomatal density would limit gas exchange, thereby reducing exposure of moist, more susceptible inner leaf surfaces to the damaging effects of pollutants. Increased pubescence may act as a filter, screening out particulate matter and prohibiting it from entering stomata. Sharma and Butler (1973) also suggested that increased pubescence would reduce the amount of solar

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[2] Nomenclature according to Gleason and Cronquist (1963).

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radiation incident upon the leaf surface. Such alteration of the leaf's energy budget might decrease leaf temperature, thus slowing down metabolism. This could be adaptive, considering Treshow's (1970) observation that air pollution damage is decreased in leaves with reduced metabolic rates.

Ideally, a population study concerning alterations in leaf morphology in association with a pollution gradient requires a thoroughly documented, long-persisting gradient. Such a study area exists at Palmerton, Pennsylvania, where zinc ore has been smelted since 1898 with the smelter effluents (SO_2, oxides and particulate matter of Zn, Cd, Pb, and Cu) producing pronounced vegetation damage. Extensive studies (T. H. Nash 1971, 1975; E. H. Nash 1972; Buchauer 1973; and Jordan 1975) have measured and plotted distinct air and soil pollution gradients emanating from the smelter area. The soil pollution (Zn, Cd, Pb, and Cu) is a result of and coincides with the air pollution gradient and can be thought of as a long-term indicator of air pollution levels.

Only a limited number of plant species occur in the polluted areas near the smelters. This paper reports studies on two of the most common, *Arenaria patula* and *Lonicera japonica*. Both species have demonstrated the general ability to colonize disturbed or polluted sites and might therefore exhibit adaptive populational differences in leaf morphology. *Arenaria,* a winter annual of the Caryophyllaceae, is very abundant in the denuded areas in and near Lehigh Gap even though its normal range does not include Pennsylvania (Buchauer 1971). The *Arenaria* at Palmerton has a high zinc tolerance, and its relative abundance may be due to a lack of competition from species that would normally invade such denuded areas (Buchauer 1971). Seedlings of *Arenaria* produce rosettes in the fall, and these rosettes then bolt the following spring to form short (usually under 30 cm in height) bushy plants that flower in early summer. *Lonicera japonica* (Caprifoliaceae), Japanese honeysuckle, is a trailing and climbing woody vine, native to eastern Asia, which has spread rapidly over a wide area of eastern North America since its introduction to the United States in 1806 (Slezak 1976). Japanese honeysuckle has been able to adjust or adapt to a wide variety of habitats and is easily established on poor soils and disturbed sites.

The primary objective of this study was to determine if there is a correlation between the degree of environmental pollution and certain features of adult leaf morphology within these two species along a documented pollution gradient. A second objective was to determine whether observed variability in leaf characters could be attributed to the phenotypic flexibility of individuals, or to genetic differences between them.

Materials and methods. THE STUDY AREA AND THE SAMPLE SITES. The town of Palmerton lies in a valley between Blue Mountain and Stony Ridge (Fig. 1). Blue Mountain (part of the Appalachian Range) consists mainly of Silurian conglomerate, with Martinsburg shale lying to the south and red siltstones and shales to the north. Most soils of the area were formed from colluvium and glacial till (Fisher *et al.* 1962). The mean yearly precipitation at Palmerton is 106.4 cm (climatological standard normal based on the period 1941 to 1970). Winds in the area are variable, but come predominantly from the northwest.

The New Jersey Zinc Company has smelted zinc in Palmerton since 1898 when the west plant was built on the north bank of the Lehigh River (Buchauer 1971). In 1911, the east plant was constructed south of Aquashicola Creek (Fig. 1). Zinc oxide fumes and particulate matter, as well as oxides of Cd, Pb, and Cu, are released from ore roasting processes at both plants. These oxides, along with SO_2 gas, are incompletely recovered by pollution control devices and released into the atmosphere (Jordan 1975). These smelters are the only significant point sources of air pollution within 30 km of Palmerton.

The lower north slope of Blue Mountain at east Lehigh Gap, against which prevailing winds (NW $\rightarrow$ SE) concentrate smelter effluents, shows the most extensive vegetation damage of the area (Buchauer 1971). Rotting stumps are all that is left of the original chestnut-oak forest, and the remaining woody vegetation consists almost exclusively of *Sassafras albidum* root sprouts. The herb layer is almost totally dominated by *Arenaria patula,* although some lichens and mosses remain

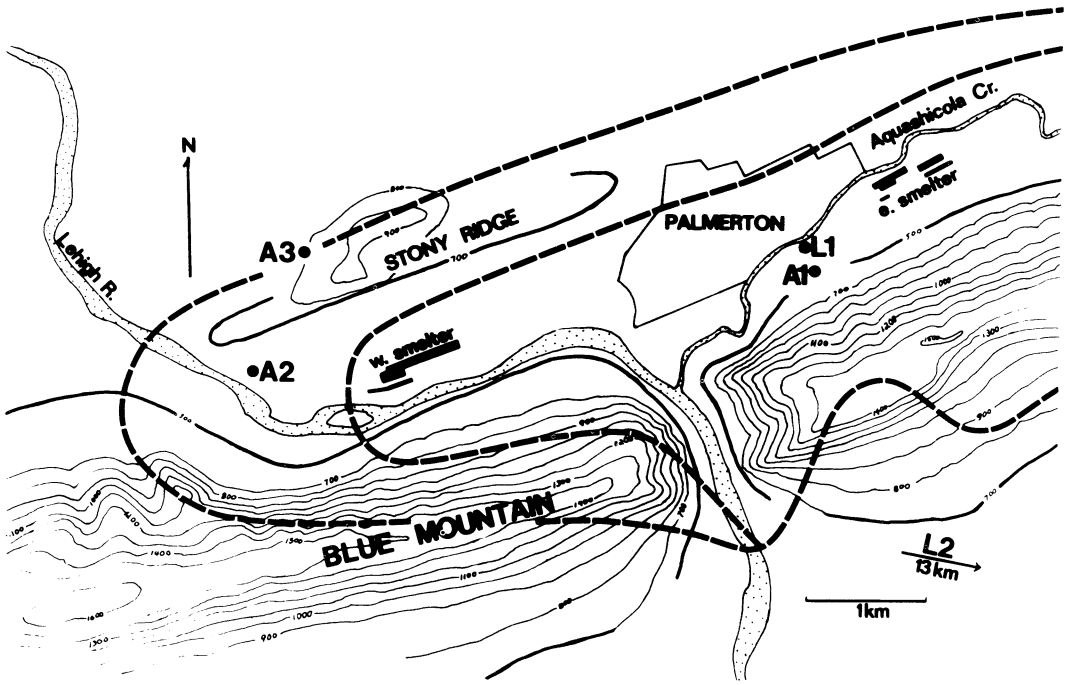

Fig. 1. The Lehigh Water Gap and vicinity. Included are Palmerton, the smelters, contour lines (el. in ft), and the *Arenaria* (A) and *Lonicera* (L) sample sites. The heavy dashed lines show the areas of high (center area including A1 and L1), intermediate (second ring including A2), and low (outside of dashed lines) sulfation values for 1970 (Nash, 1971). According to Nash (1975), the high area had sulfation rates exceeding 9.0 μg $SO_3/cm^2 \cdot$day for at least 2 mo, while in the low area "clean" air values were consistently recorded.

(Nash 1975). Buchauer (1971) estimated the Zn content in the soil at east Lehigh Gap to be as high as 11,000 kg/ha. Cd, Pb, and Cu are also present in elevated concentrations, but at much lower levels than Zn. As one moves away from Palmerton along the north slope or ridge of Blue Mountain, there is a smooth decrease in heavy metal concentrations (Buchauer 1973). SO_2 concentrations drop off more quickly and are above normal levels only in the highly polluted areas adjacent to the smelters (Fig. 1).

The sample sites were chosen to coincide with the above documented air and soil pollution gradients. *Arenaria* was studied at three field sites (A1, A2, A3), and *Lonicera* at two sites (L1, L2) (Fig. 1). The larger site numbers indicate increasing distances or protection from the pollution source. Site A1 is located on the north slope of Blue Mountain at east Lehigh Gap (elevation 490 ft or 149 m) in the region of greatest community damage. Site L1 is situated at the base of this slope (el. 400 ft or 122 m) on the south bank of Aquashicola Creek. Site A2 is 1 km west and upwind of the west smelter at el. 490 ft (149 m), while site A3 is 1 km northwest of this smelter at el. 800 ft (244 m), in a valley protected from smelter fumes by Stony Ridge. Site L2 is approximately 14 km southeast of Lehigh Gap in Beersville, Pennsylvania, just north of Route 248, on a slope at el. 490 ft (149 m).

Environmental data were collected from the field sites at different times during the 1977 and 1978 growing seasons. Soil samples, from 2 to 8 cm below the surface, were collected at all sites in the summer of 1977 for textural and chemical analyses. Textural analysis was by the hydrometer method (Bouyoucos 1953), while soil pH was determined in a 1:1 soil-water suspension using a Fisher's Acumet model 230 pH meter. Zinc and copper concentrations were determined in double acid extracts, using a Perkin-Elmer atomic absorption spectrophotometer. Soil moisture was determined for all sites on three separate

occasions by taking soil samples at 2 to 3 cm below the soil surface and oven-drying them at 104 C for 24 hr. Maximum and minimum temperatures at ground level over a 48-hr period were also taken at all sites on two occasions. Mercury (maximum) and alcohol (minimum) thermometers were placed on the ground and covered with leaf litter to prevent exposure to direct sunlight. Rate of evaporation at approximately 5 cm above ground level was measured with Piche evaporimeters (Livingston 1935) over a 48-hr period on two occasions.

FIELD MATERIALS. Plant cuttings from the three populations of *Arenaria* and the two of *Lonicera* were collected in June, 1977. All materials were taken from plants growing in as close to full sunlight as possible. *Arenaria* leaves were removed at or within one node of the point of branching of the main stem; *Lonicera* leaves were taken at least eight nodes back from the growing end of the vine.

With the exception of *Lonicera* trichomes, which were counted directly using a binocular dissecting microscope, stomatal and trichome densities and stomatal size were determined through the microscopic examination of leaf epidermal peels using Rhoplex, after the method of Horanic and Gardner (1967). Epidermal peels of entire *Arenaria* leaves were made, while peels from *Lonicera* leaves were made adjacent to the mid-vein of the leaf, midway along its length.

Stomatal densities were measured on all leaf surfaces on which stomata occur—upper and lower surfaces of *Arenaria* and the lower surface only of *Lonicera;* 8 plants/population, 2 leaves/plant, and 2 observations/leaf were utilized. Stomatal sizes (length of guard cells) were measured from one leaf surface in all field populations except A2.

Trichome densities were determined for both leaf surfaces of *Arenaria,* while only the upper epidermal hairs of *Lonicera* were counted since lower surface hairs occur discontinuously, being congregated on veins only. All trichome densities in June, 1977, were measured from 10 plants/population, 2 leaves/plant, and 2 observations/leaf.

Data were again collected from the field populations in July, 1978. Stomatal and trichome densities were determined as before, with the exception that all counts at this time were made from 6 newly selected plants/population, 2 leaves/plant, and 3 observations/leaf. In addition, data on leaf thickness and surface area for all populations were collected. Freehand cross-sections of *Arenaria* leaves were made at mid-length, and thickness of each section was determined microscopically using an ocular micrometer. *Lonicera* leaf thickness was measured in a similar manner, with cross-sections being cut adjacent to the mid-vein, midway along the length of the leaf. A Lambda Instrument Corporation electronic planimeter (model #LI-3000) was used to measure leaf area. All thickness and area measurements were taken from 12 plants/population and 2 leaves/plant.

GREENHOUSE AND COURTYARD OBSERVATIONS. *Lonicera* stem cuttings were taken from the field sites in June, 1977, and rooted in a 1:1 mixture of sand and potting soil in the greenhouse at the Nelson Biological Laboratories in Piscataway. In September, 1977, mature *Arenaria* fruiting stalks were collected from the field sites. Seeds and capsules were planted in flats with a 1:1 mixture of sand and potting soil in January, 1978. At this time, the *Lonicera* cuttings were trimmed back, and new foliage was allowed to grow for future sampling. Pots and flats were watered approximately every other day, maintaining a moderate soil moisture level (6 to 17% of dry soil weight). During the study period, the maximum daily temperature in the greenhouse ranged from about 26 to 31 C, while minimum daily temperature ranged from 18 to 22 C. The maximum during a 24-hr period generally exceeded the minimum by at least 8 degrees. Relative humidity ranged from 26 to 46%, and light intensity (measured on clear days between 11 a.m. and 1 p.m. with a Weston Illumination Meter #756) ranged from 4,400 to 5,000 ft-c. After 10 wk, density data were collected for *Arenaria* upper surface stomata and trichomes and for *Lonicera* upper surface trichomes and lower surface stomata. Sampling was similar to the field sampling in 1978. All stomata and trichome counts were taken from 6 plants/population, 2 leaves/plant, and 3 observations/leaf.

After data were taken in the greenhouse, all plants were moved outside to the greenhouse courtyard. *Arenaria* grew there

Table 1. Comparative data for five of the environmental factors monitored at the five study sites.

Sample site	Zinc (ppm)	Copper (ppm)	pH (1:1)	Mean soil moisture[1] (%)	Relative evaporation April 14–16 (ml)	Relative evaporation June 22–24 (ml)
A1	7,500	15	6.3	31.3	10.3	12.6
A2	3,344	10	6.2	22.3	6.7	9.1
A3	975	2.5	5.4	38.7	8.8	10.7
L1	5,875	3	6.8	22.0	—[2]	—[2]
L2	40	1	6.8	21.7	9.2	4.9

[1] Mean of three determinations at 2 to 3 cm below the soil surface.
[2] Data not available.

for approximately 12 wk before sampling, while *Lonicera* was sampled 16 wk after the transfer. Only leaves initiating and developing in the courtyard were used. The sampling and techniques for stomatal and trichome densities and for leaf thickness and area were those used on the July, 1978, field materials with the exception that *Arenaria* leaf surface area was not measured. The range of daily maximum temperature in the courtyard during most of the growth period was 18 to 37 C, while minimum temperatures ranged from 1 to 22 C. Relative humidity at mid-day ranged from 35 to 72%, and mid-day light intensities during clear weather ranged from 5,100 to 7,400 ft-c.

STATISTICAL ANALYSES. An analysis of variance model for hierarchal classifications (Snedecor and Cochran 1967) was utilized for all comparisons of three or more groups. When F was significant, differences between pairs of means were tested for significance using the LSD method. A *t*-test for groups of equal size (Snedecor and Cochran 1967) was utilized for all comparisons involving only two groups.

Results. ENVIRONMENT AT THE SAMPLE SITES. Sites A1, A2, and L1 occur in areas where Nash (1975) reported elevated SO_2 concentrations (Fig. 1). Zinc and copper concentrations in soil at the *Arenaria* and *Lonicera* sample sites were extremely high near the smelters, while dropping off in the distant sample areas (Table 1). These data correspond well with the heavy metal gradients determined by Buchauer (1973) for this area. A general increase in soil pH at *Arenaria* sites close to the smelters was recorded (Table 1), and this agrees with the findings of Buchauer (1971), who attributed the increase to the addition of large quantities of zinc oxide from smelter fumes to nearby soils. This amphoteric compound apparently acts as a base to neutralize the normally acidic soil. Presence of *Lonicera* at a site seemed to result in a higher pH, overriding possible location and texture effects, i.e., samples from similar areas adjacent to *Lonicera* sites had a lower pH.

The soil texture at all sites except L1 is loam, L1 being a loamy sand. The *Arenaria* sites showed differences in soil moisture for two of the three sampling days; site A2 consistently showed the driest soil, while A3 averaged the wettest (Table 1). The two *Lonicera* sites were quite similar in soil moisture.

Maximum and minimum temperature differences, measured twice over a 48-hr period, showed no consistent significant differences between sample sites. Data from Piche evaporimeters (Table 1) indicated that site A1 had the greatest evaporation of all sample sites, although it did not have the lowest soil moisture. This is consistent with the lack of a vegetational windbreak on the open slope at that site.

STOMATAL AND TRICHOME DENSITIES. Those *Arenaria* populations exposed to the lowest pollution levels had the highest stomatal densities in both the 1977 and 1978 field determinations (Table 2). The greater density of A3 was especially evident on the upper surface, where all population means were significantly different at the 0.05 level during 1977. In 1978 a similar range of difference occurred among the populations, although fewer differences were statistically significant because of in-

Table 2. Upper and lower leaf surface stomatal density for the three *Arenaria* populations growing under different conditions. Values are stomata/mm² surface area.

Upper surface				
	Field		Greenhouse	Courtyard
Population	1977	1978	March, '78	June, '78
A1	178.0^{a1,A2}	186.6^{a,B}	72.8^{a,C}	199.2^{a,D}
A2	199.9^{b,A}	211.5^{ab,A}	—[3]	—
A3	210.6^{c,A}	216.9^{b,B}	69.9^{a,C}	212.4^{a,AB}
Lower surface				
	Field		Greenhouse	Courtyard
Population	1977	1978	March, '78	June, '78
A1	129.6^{a1,A2}	135.8^{a,A}	—[3]	161.7^{a,B}
A2	136.1^{a,A}	158.1^{b,A}	—	—
A3	137.2^{a,A}	161.1^{b,B}	—	165.7^{a,B}

[1] Means in a vertical column followed by the same lower-case letter are not significantly different at the 0.05 level.
[2] Means in a horizontal row followed by the same upper-case letter are not significantly different at the 0.05 level.
[3] Data not available.

creased variance within populations. Trichome density showed the opposite trend—as pollution levels decreased, trichome densities decreased in all field comparisons (Table 3). All lower surface trichome density means during 1977 were significantly different, while only population A3, with its virtually glabrous upper leaf surfaces, was significantly different from other populations in upper surface means. The population values were more similar during 1978, while the upper surface densities were approximately double those of 1977.

Table 3. Upper and lower leaf surface trichome density for the three *Arenaria* populations growing under different conditions. Values are trichomes/mm² surface area.

Upper surface				
	Field		Greenhouse	Courtyard
Population	1977	1978	March, '78	June, '78
A1	0.38^{a1,A2}	0.67^{a,B}	0.68^{a,B}	0.59^{a,B}
A2	0.33^{a,A}	0.63^{a,A}	—[3]	—
A3	0.02^{b,A}	0.55^{a,B}	1.14^{a,C}	0.23^{b,D}
Lower surface				
	Field		Greenhouse	Courtyard
Population	1977	1978	March, '78	June, '78
A1	4.92^{a1,A2}	4.11^{a,B}	—[3]	0.08^{a,C}
A2	3.80^{b,A}	3.33^{a,A}	—	—
A3	2.90^{c,A}	3.14^{a,A}	—	0.20^{a,B}

[1] Means in a vertical column followed by the same lower-case letter are not significantly different at the 0.05 level.
[2] Means in a horizontal row followed by the same upper-case letter are not significantly different at the 0.05 level.
[3] Data not available.

Table 4. Lower surface stomatal and upper surface trichome density for leaves of two *Lonicera* populations growing under different conditions.

Lower surface stomata/mm²				
	Field		Greenhouse	Courtyard
Population	1977	1978	March, '78	July, '78
L1	$621.9^{a1,A2}$	$468.8^{a,B}$	$444.1^{a,C}$	$481.6^{a,D}$
L2	$840.5^{b,A}$	$499.8^{a,B}$	$578.2^{b,C}$	$668.6^{b,D}$
Upper surface trichomes/mm²				
	Field		Greenhouse	Courtyard
Population	1977	1978	March, '78	July, '78
L1	$2.55^{a1,A2}$	$0.98^{a,B}$	$2.43^{a,A}$	$1.78^{a,C}$
L2	$0.28^{b,A}$	$0.15^{b,B}$	$1.88^{a,C}$	$0.19^{b,B}$

[1] Means in a vertical column followed by the same lower-case letter are not significantly different at the 0.05 level.
[2] Means in a horizontal row followed by the same upper-case letter are not significantly different at the 0.05 level.

Stomatal density data from greenhouse and courtyard samplings of *Arenaria* (Table 2) showed some abrupt changes from field results. Upper surface stomatal density was much lower for leaves on plants grown in the greenhouse than for those sampled in the field, and when the greenhouse plants were moved outside into the courtyard for several weeks, upper stomatal densities changed again, either to a statistically significant new value (population A1), or back to one similar to that obtained in the field (population A3). Although greenhouse data were not taken, similar changes were evident in lower surface stomatal density. Trichome densities also showed some large changes from field to greenhouse or courtyard, especially for population A3 upper leaf and A1 lower leaf surfaces (Table 3).

The most polluted *Lonicera* site had lower stomatal density and greater pubescence in both 1977 and 1978 (Table 4). Cuttings from both field sites, when grown in the greenhouse or courtyard, showed means significantly different from those of the field plants, and the same individuals showed different values when moved from the greenhouse to the courtyard. Stomatal densities of plants from L1 and L2 in the greenhouse and courtyard remained significantly different, the L2 values always greater. Convergence of values was also lacking in the trichome greenhouse and courtyard data, although the greenhouse means were not significantly different at the 0.05 level.

STOMATAL SIZE. When stomatal size was measured on leaves from the 1977 field samplings, no significant difference was found between population means within a species. This indicates that the degree of leaf porosity when stomata were fully open probably did differ whenever stomatal density differed.

LEAF AREA, THICKNESS, AND VOLUME. The field populations of *Arenaria* showed a somewhat larger leaf area in the less polluted sites (means of A1 and A3 were significantly different); concurrently, leaves were slightly thinner (Table 5). These two opposing trends counteracted one another to provide volume means that did not differ significantly among sites. Courtyard means for leaf thickness differed significantly from the corresponding field values (Table 5), with leaves in the courtyard being 50% thicker. Within the courtyard, population means were equivalent.

No significant differences were detected between leaf area, thickness, or volume for leaves of *Lonicera* populations at the two field sites in 1978 (Table 6). While there were also no significant differences in the courtyard between populations in leaf area, thickness, or volume, there were significant differences between field and courtyard means for area and thickness for both pop-

Table 5. Mean leaf dimensions from *Arenaria* populations in the field (1978) and courtyard locations.

Location	Population	Leaf area (mm^2)	Leaf thickness (mm)	Leaf volume (mm^3)
Field	A1	20^{a1}	0.30^{a}	6.03^{a}
	A2	$21^{a,b}$	0.29^{a}	6.10^{a}
	A3	22^{b}	0.29^{a}	6.55^{a}
Courtyard	A1	—[2]	0.45^{b}	—
	A3	—	0.45^{b}	—

[1] Means in a vertical column followed by the same letter are not significantly different at the 0.05 level.
[2] Data not available.

ulations (Table 6). The changes were opposing, so that volume means were not significantly different from field values.

Discussion. RELATION OF LEAF MORPHOLOGY TO POLLUTANT LEVELS. Greater trichome density and lesser stomatal density in field populations of *Arenaria* and *Lonicera* were correlated with increased concentrations of environmental pollution. It is unlikely that this response was related to site differences in soil moisture, since the *Lonicera* sites showed similar moisture levels and since the trends in stomatal and trichome densities did not correspond to those of soil moisture or evaporation at the *Arenaria* sites (site A3 being wettest and A2 the driest). Stomatal and trichome densities usually increase or decrease simultaneously in response to moisture changes (Sharma and Dunn 1969; Bannister 1976; Ehleringer *et al.* 1976), whereas in our study they changed in opposite directions. In addition, the expectation of greater stomatal densities in open, sunny habitats of low humidity (Meidner and Mansfield 1968; Bannister 1976; Clay and Quinn 1978) was not realized in our polluted, open sites.

Stomatal size and leaf volume were not significantly different among populations of a species in the field. Differences in stomatal densities between the field populations were therefore neither a compensation for differences in size of individual stomata nor a compensatory response to the need for increased diffusion through a more massive leaf.

Although the effects of air and soil pollution were not separated in this study, selection for morphological characters has generally been found to be independent of tolerance to heavy metals in soils (Antonovics and Bradshaw 1970; Antonovics *et al.* 1971). The many differences at the same field site between 1977 and 1978 would also argue against a major effect of soil heavy metal concentrations on leaf morphological characters. The observed alterations in leaf morphology can thus be tentatively viewed as avoidance mechanisms for air pollution stress (Sharma 1975). Increased pubescence combined with decreased stomatal density should reduce the penetration of gaseous and especially particulate matter into the mesophyll of a leaf, a tissue which has been shown to be the most susceptible to several air pollutants (Solberg and Adams 1956; Treshow 1970). *Arenaria,* with its upper surface stomata, would probably benefit from morphological traits that limit penetration of heavy metal oxides and particulate matter and SO_2 into its leaves near the Palmerton smelters. Lower stomatal density in *Lonicera* may also be a response to air

Table 6. Mean leaf dimensions from *Lonicera* populations in the field (1978) and courtyard locations.

Population	Leaf area (mm^2)		Leaf thickness (mm)		Leaf volume (mm^3)	
	Field	Courtyard	Field	Courtyard	Field	Courtyard
L1	1232^{a1}	945^{b}	0.206^{a}	0.242^{b}	254.7^{a}	228.9^{a}
L2	1256^{a}	1014^{b}	0.197^{a}	0.235^{b}	249.2^{a}	238.2^{a}

[1] Means in a vertical column or horizontal row followed by the same letter are not significantly different at the 0.05 level.

pollution, but the increased trichome density measured at site L1 occurs on the upper leaf surface, away from the stomata, ruling out any filtering effect. The greater pubescence is more likely related to leaf energy budget considerations, e.g., greater insolation and the effects of higher leaf temperatures, but may also be significant in lowering metabolic rates in living cells and thus reducing their susceptibility to pollution damage (Sharma and Butler 1973).

VARIABILITY IN LEAF CHARACTERS—PHENOTYPIC FLEXIBILITY OR GENETIC DIFFERENCES? Significant differences within a population grown at different times (1977, 1978) or locations (field, greenhouse, courtyard) illustrate a high degree of phenotypic flexibility in leaf characters for both *Arenaria* and *Lonicera*. Stomatal and trichome densities, as well as leaf thickness and (for *Lonicera* only) leaf surface area, varied significantly within individuals in response to dissimilar environmental conditions. These results support the conclusions of Lewis (1972), who points out that, for several plant species, variations in leaf structure are common between different populations, and that these differences are often the result of the phenotypic plasticity of individuals.

Many of the differences between field populations were apparently environmentally-induced and disappeared, partially or completely, when plants from the field sites were grown under the common environments of the greenhouse and the courtyard. This was especially true for *Arenaria*. Seeds from sites A1 and A3 produced plants with similar (not significantly different) stomatal density in both the greenhouse and the courtyard. There was also some convergence and/or reversal of the field trends in the trichome densities. However, for *Lonicera* populations, comparisons of results from field and common environments provided some evidence for genetic dissimilarity. Stomatal densities of plants from the 2 sites remained significantly different in both the greenhouse and the courtyard. Convergence of trichome densities was also lacking. In this case, the individuals of each population may possess different genetically-fixed ranges of response, within which densities vary as the environment changes.

Literature Cited

ANTONOVICS, J., and A. D. BRADSHAW. 1970. Evolution in closely adjacent populations. VIII. Clinal patterns in *Anthoxanthum odoratum* across a mine boundary. Heredity, Lond. 25: 349–362.

———, ———, and R. G. TURNER. 1971. Heavy metal tolerance in plants, p. 1–85. *In* J. B. Cragg, Advances in Ecological Research, Volume 7. Academic Press, New York.

BANNISTER, P. 1976. Introduction to Physiological Plant Ecology. John Wiley and Sons Inc., New York.

BOUYOUCOS, G. J. 1953. An improved type of soil hydrometer. Soil Sci. 76: 377–378.

BRIGGS, D., and S. M. WALTERS. 1969. Plant Variation and Evolution. McGraw-Hill Book Co., New York.

BUCHAUER, M. J. 1971. Effects of zinc and cadmium pollution on vegetation and soils. Ph.D. diss., Rutgers Univ., New Brunswick, N.J.

———. 1973. Contamination of soil and vegetation near a zinc smelter by zinc, cadmium, copper, and lead. Environ. Sci. Technol. 7: 131–135.

CLAY, K., and J. A. QUINN. 1978. Density of stomata and their responses to a moisture gradient in *Danthonia sericea* populations from dry and wet habitats. Bull. Torrey Bot. Club. 105: 45–49.

EHLERINGER, J., O. BJORKMAN, and H. A. MOONEY. 1976. Leaf pubescence: effects on absorptance and photosynthesis in a desert shrub. Science 192: 376–377.

FISHER, G., R. MATTERN, R. MC COMBS, J. NORGREN, and A. REBERT. 1962. Soil survey of Carbon County, Pennsylvania. U.S. Dept. Agric. Soil Conservation Service, Series 1959, No. 14.

GLEASON, H. A., and A. CRONQUIST. 1963. Manual of Vascular Plants of Northeastern U.S. and Adjacent Canada. D. Van Nostrand Co., Inc., Princeton, N.J.

HORANIC, G. E., and F. E. GARDNER. 1967. An improved method of making epidermal imprints. Bot. Gaz. 128: 144–150.

JORDAN, M. J. 1975. Effects of zinc smelter emissions and fire on a chestnut-oak woodland. Ecology 56: 78–91.

LEWIS, M. 1972. The physiological significance of variation in leaf structure. Sci. Prog. 60: 25–51.

LIVINGSTON, B. E. 1935. Atmometers of porous porcelain and paper, their use in physiological ecology. Ecology 16: 438–472.

MEIDNER, H., and T. A. MANSFIELD. 1968. Physiology of Stomata. McGraw-Hill Book Co., New York.

NASH, E. H. 1972. Effect of effluents from a zinc smelter on mosses. Ph.D. diss. Rutgers Univ., New Brunswick, N.J.

NASH, T. H. 1971. Effect of effluents from a zinc factory on lichens. Ph.D. diss. Rutgers Univ., New Brunswick, N.J.

———. 1975. Influence of effluents from a zinc factory on lichens. Ecol. Monogr. 45: 183–198.

REGEHR, D. L., and F. A. BAZZAZ. 1976. Low tem-

perature photosynthesis in successional winter annuals. Ecology 57: 1297–1303.

SHARMA, G. K. 1975. Leaf surface effects of environmental pollution on sugar maple (*Acer saccharum*) in Montreal. Canad. Jour. Bot. 53: 2312–2314.

————, and J. BUTLER. 1973. Leaf cuticular variations in *Trifolium repens* as indicators of environmental pollution. Environ. Pollut. 5: 287–293.

————, and ————. 1975. Environmental pollution: Leaf cuticular patterns in *Trifolium pratense* L. Ann. Bot. 39: 1087–1090.

————, and D. B. DUNN. 1969. Environmental modifications of leaf surface traits in *Datura stramonium*. Canad. Jour. Bot. 47: 1211–1216.

————, and J. TYREE. 1973. Geographic leaf cuticular and gross morphological variations in *Liquidambar styraciflua* L. and their possible relationship to environmental pollution. Bot. Gaz. 134: 179–184.

SLEZAK, W. F. 1976. *Lonicera japonica* Thunb., an aggressive introduced species in a mature forest ecosystem. M.S. thesis, Rutgers Univ., New Brunswick, N.J.

SMITH, W. K., and P. S. NOBEL. 1977. Influences of seasonal changes in leaf morphology on water-use efficiency for three desert broadleaf shrubs. Ecology 58: 1033–1043.

SNEDECOR, G. W., and W. G. COCHRAN. 1967. Statistical Methods. 6th ed. Iowa State Univ. Press, Ames.

SOLBERG, R. A., and D. F. ADAMS. 1956. Histological responses of some plant leaves to hydrogen fluoride and sulphur dioxide. Amer. Jour. Bot. 43: 755–760.

TRESHOW, M. 1970. Environment and Plant Response. McGraw-Hill Book Co., New York.