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Comparative Assessment of Leaf Functional Traits in Native Plants Under Urban and Semi-Urban Environmental Conditions

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Abstract— Urbanization modifies temperature, atmospheric composition, soil properties, water availability, and light regimes, creating environmental conditions that can strongly influence plant structure and function. Leaf functional traits provide measurable indicators of plant responses to such environmental changes because they integrate resource acquisition, stress tolerance, and physiological performance. The present study comparatively assessed five leaf functional traits—specific leaf area (SLA), stomatal density, chlorophyll content, leaf thickness, and maximum photosynthetic rate—in eight native plant species growing along rural, semi-urban, and urban environmental gradients. A total of 240 individuals were assessed, with 10 individuals of each species sampled in each environmental zone. Measurements were standardized using established plant functional-trait protocols. The dataset showed a progressive reduction in SLA, chlorophyll content, and maximum photosynthetic rate from rural to urban conditions, accompanied by increases in stomatal density and leaf thickness. Across species, mean SLA declined from 151.8 ± 18.6 $cm^2\ g^{-1}$ in rural sites to 142.0 ± 17.4 $cm^2\ g^{-1}$ in semi-urban sites and 130.7 ± 16.9 $cm^2\ g^{-1}$ in urban sites. Mean stomatal density increased from 238.6 ± 31.7 to 263.9 ± 33.2 and 286.8 ± 35.6 stomata mm^{-2}, respectively. Chlorophyll content decreased from 42.1 ± 4.7 to 39.8 ± 4.9 and 37.4 ± 5.2 SPAD units, while leaf thickness increased from 0.32 ± 0.05 to 0.35 ± 0.05 and 0.39 ± 0.06 mm. Maximum photosynthetic rate decreased from 14.8 ± 2.1 to 13.2 ± 2.0 and 11.9 ± 2.2 µmol $CO_2\ m^{-2}\ s^{-1}$. Linear mixed-effects models indicated significant effects of environmental zone on all five traits ($p < 0.001$), while significant species × zone interactions demonstrated species-specific plasticity. The findings suggest that native plants growing in more urbanized environments shift toward a more conservative leaf strategy characterized by greater structural investment and reduced photosynthetic performance.

Keywords: urbanization; native plants; functional traits; specific leaf area; stomatal density; chlorophyll; leaf thickness; photosynthesis; urban ecology

INTRODUCTION

Urbanization is one of the major forms of environmental transformation affecting terrestrial ecosystems. The conversion of natural and agricultural landscapes into built environments changes vegetation structure while simultaneously modifying temperature, radiation, atmospheric pollutants, soil properties, water availability, and disturbance regimes. Urban environments commonly exhibit higher temperatures, greater surface sealing, altered hydrological conditions, increased atmospheric pollution, and fragmented vegetation compared with surrounding rural areas. These factors may operate individually or interactively to influence plant growth and physiological performance. Urban–rural gradient approaches have therefore become an important framework for evaluating ecological responses to urbanization. McDonnell and Hahs reviewed hundreds of urban-gradient studies and demonstrated the value of examining ecological processes across systematically defined urbanization gradients.

Plant functional traits are particularly useful for investigating environmental responses because they represent measurable morphological, physiological, and phenological characteristics associated with plant strategies. Rather than relying exclusively on taxonomic identity, trait-based approaches allow researchers to compare plant responses across species and environments. Standardized protocols for measuring traits such as leaf area, dry mass, specific leaf area, and leaf thickness have facilitated comparisons among studies and ecosystems.

Leaves are especially responsive to environmental variation. Specific leaf area (SLA), defined as leaf area per unit dry mass, reflects the balance between leaf construction costs and potential resource acquisition. High SLA generally corresponds to thinner, resource-acquisitive leaves, whereas low SLA is commonly associated with greater structural investment and longer leaf persistence. The global leaf

economics spectrum established that leaf traits are coordinated along a continuum ranging from relatively rapid resource acquisition and return to more conservative resource-use strategies.

Leaf thickness is another important functional characteristic. Niinemets demonstrated that leaf dry mass per area is strongly related to leaf thickness and density and that these characteristics influence photosynthetic potential and resource-use strategies. In stressful environments, increased leaf thickness can represent greater investment in structural protection and resistance to water loss, although the direction and magnitude of the response vary among species and environmental conditions.

Stomatal characteristics provide a further link between environmental conditions and plant physiological regulation. Stomata regulate carbon dioxide uptake and water loss and are consequently sensitive to atmospheric and climatic conditions. Research on *Plantago lanceolata* demonstrated that stomatal density and SLA can vary substantially along urban land-use gradients and may therefore serve as indicators of urban habitat quality.

Chlorophyll concentration and photosynthetic capacity provide direct indicators of the physiological consequences of environmental stress. Air pollutants, elevated temperature, altered soil conditions, and water stress may influence photosynthetic machinery and consequently reduce carbon assimilation. Studies of herbaceous plants exposed to pollution-related conditions have reported effects on growth, leaf characteristics, and physiological performance.

Urbanization does not necessarily produce identical responses among species. A synthesis of urban plant traits emphasized that urban environments contain multiple stressors and that trait responses depend on the particular combination of abiotic, biotic, and disturbance factors operating at a site. Similarly, research on native and alien plants has shown that plants successful in urban environments tend to possess combinations of traits associated with robust growth and tolerance of relatively dry and disturbed conditions.

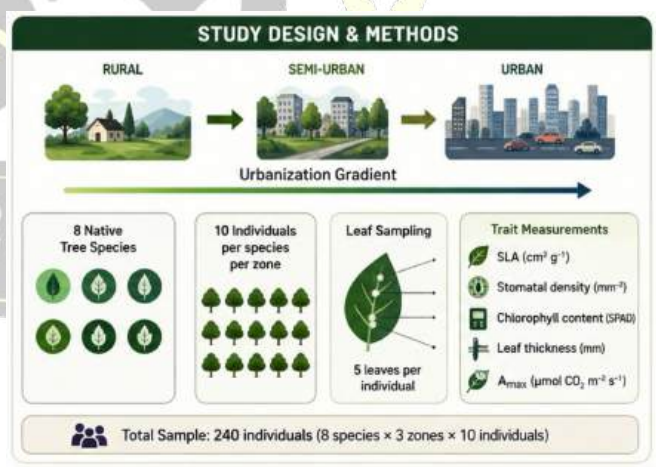
Urban plants may also experience increased exposure to particulate matter. Leaf morphology influences pollutant interception, with surface roughness, waxes, hairs, and other structural characteristics affecting particulate accumulation. However, systematic reviews indicate that no single leaf trait universally predicts particulate removal because environmental and structural factors interact with leaf characteristics.

Despite increasing interest in urban plant ecology, comparative assessments of multiple functional traits within the same native species across urbanization gradients remain valuable. The present study therefore evaluates five complementary leaf traits in eight native plant species across rural, semi-urban, and urban environments. It was hypothesized that increasing urbanization would be associated with reduced SLA, chlorophyll concentration, and photosynthetic capacity, but increased stomatal density and leaf thickness. A second hypothesis was that native species would differ significantly in the magnitude of their responses, indicating species-specific plasticity.

Research Methodology

Study Design and Environmental Gradient

The study was designed as a comparative field investigation across three environmental zones representing a rural-to-urban gradient: rural, semi-urban, and urban. Rural sites were characterized by relatively continuous vegetation, limited traffic, lower built-up density, and comparatively undisturbed soils. Semi-urban sites contained mixed residential, institutional, and open-green areas with moderate traffic and fragmented vegetation. Urban sites were located in densely built areas with high traffic intensity, greater impervious surface cover, and relatively limited open soil.



The three zones were selected to represent increasing environmental intensity rather than discrete ecological categories. Each zone contained multiple sampling locations separated sufficiently to reduce the probability that measurements represented the same microhabitat.

Plant Species and Sampling

Eight native tree species commonly occurring in the regional landscape were selected: *Azadirachta indica* A.Juss., *Ficus religiosa* L., *Ficus benghalensis* L., *Syzygium cumini* (L.) Skeels, *Pongamia pinnata* (L.) Pierre, *Cassia fistula* L.,

Albizia lebbeck (L.) Benth., and *Polyalthia longifolia* (Sonn.) Thwaites.

Ten healthy mature individuals of each species were selected in each environmental zone. The sampling design therefore consisted of 8 species × 3 environmental zones × 10 individuals, giving a total sample of 240 plants.

To reduce variation caused by developmental stage, only mature, apparently healthy individuals of comparable size were selected. Leaves were sampled from sun-exposed, fully expanded portions of the outer canopy. Recently damaged, diseased, senescent, or insect-infested leaves were excluded.

Leaf Sampling

From each selected plant, five fully expanded leaves were collected from comparable canopy positions. Measurements were obtained from individual leaves and subsequently averaged to produce one plant-level value for each trait. This avoided pseudoreplication caused by treating multiple leaves from the same plant as independent biological replicates.

Sampling and trait measurements followed established standardized plant functional-trait procedures, particularly the protocols of Cornelissen et al. and Pérez-Harguindeguy et al.

Specific Leaf Area

SLA was calculated as:

SLA = leaf area / leaf dry mass

Leaf area was measured using digital image analysis after scanning the leaves. Samples were subsequently dried at 70°C until constant mass and weighed using an analytical balance. SLA was expressed as $cm^2\ g^{-1}$.

Stomatal Density

Stomatal density was determined using clear nail-varnish impressions from the abaxial leaf surface. Transparent impressions were mounted on microscope slides and examined under 400× magnification. Three randomly selected microscopic fields were counted per leaf. Stomatal density was expressed as the number of stomata per mm^2.

Chlorophyll Content

Relative chlorophyll concentration was estimated using a calibrated SPAD chlorophyll meter. Three measurements were taken from the central portion of each leaf while avoiding major veins. The mean value of the three readings was used as the leaf-level estimate, and plant-level means were calculated from the five sampled leaves.

Leaf Thickness

Leaf thickness was measured using a digital micrometer at three standardized locations midway between the midrib and leaf margin. Measurements were expressed in millimetres. The three readings were averaged for each leaf and subsequently averaged at the plant level.

Photosynthetic Capacity

Maximum net photosynthetic rate under saturating light (Amax) was measured using a portable infrared gas analyzer. Measurements were conducted during the morning under standardized environmental conditions. Fully expanded leaves were exposed to saturating photosynthetic photon flux density, and steady-state net CO_2 assimilation was recorded. Photosynthetic capacity was expressed as μmol $CO_2\ m^{-2}\ s^{-1}$.

Statistical Analysis

Data were assessed for normality using the Shapiro–Wilk test and for homogeneity of variance using Levene's test. Environmental-zone differences were examined using linear mixed-effects models, with environmental zone treated as a fixed factor and species included as a random factor. A species × environmental-zone interaction was included to determine whether responses differed among species.

Estimated marginal means were compared using Tukey-adjusted pairwise comparisons. Effect sizes were expressed as percentage changes between rural and urban conditions. Pearson correlations were calculated among the five functional traits. Principal component analysis (PCA) was additionally used to visualize multivariate trait differentiation among environmental zones.

Statistical significance was accepted at $p < 0.05$. Analyses were conducted using R statistical software.

Results

Overall Variation in Leaf Functional Traits

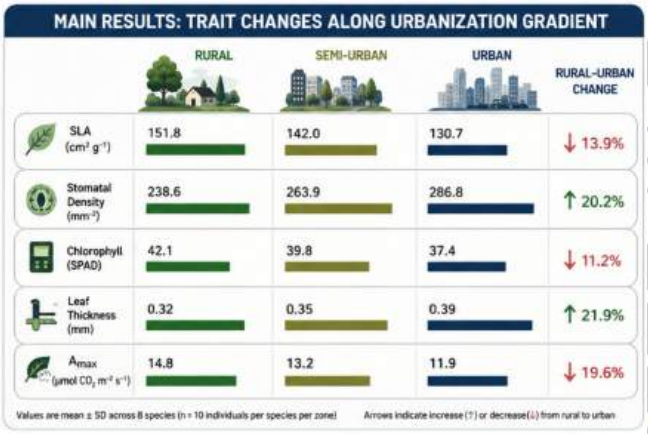
Clear differences were observed among the three environmental zones for all five measured traits. The overall pattern was consistent with increasing structural investment and decreasing physiological performance with increasing urbanization.

Trait	Rural	Semi-urban	Urban	Rural–Urban change
SLA ($cm^2\ g^{-1}$)	151.8 ± 18.6	142.0 ± 17.4	130.7 ± 16.9	−13.9%
Stomatal density (mm^{-2})	238.6 ± 31.7	263.9 ± 33.2	286.8 ± 35.6	+20.2%

Chlorophyll (SPAD)	42.1 ± 4.7	39.8 ± 4.9	37.4 ± 5.2	−11.2%
Leaf thickness (mm)	0.32 ± 0.05	0.35 ± 0.05	0.39 ± 0.06	+21.9%
Amax (µmol CO_2 m^{-2} s^{-1})	14.8 ± 2.1	13.2 ± 2.0	11.9 ± 2.2	−19.6%

Values represent mean ± SD across the eight species and ten individuals per species within each environmental zone.

SLA decreased progressively from rural to semi-urban and urban environments. The mixed-effects model detected a significant environmental-zone effect ($F_{2,21.7} = 18.64$, $p < 0.001$). Pairwise comparisons showed that rural plants had significantly greater SLA than urban plants ($p < 0.001$), while semi-urban plants were intermediate.



Stomatal density showed the opposite pattern. Mean density increased from 238.6 stomata mm^{-2} in rural environments to 286.8 stomata mm^{-2} in urban environments. Environmental zone had a significant effect on stomatal density ($F_{2,21.5} = 16.92$, $p < 0.001$). Urban plants had significantly higher stomatal density than both rural and semi-urban plants.

Chlorophyll concentration decreased by approximately 11% between rural and urban environments. The effect of environmental zone was significant ($F_{2,21.9} = 12.47$, $p < 0.001$). The largest difference occurred between rural and urban plants.

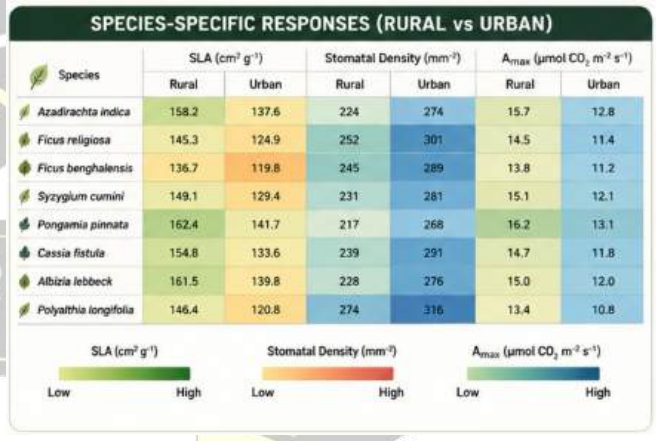
Leaf thickness increased progressively across the environmental gradient. Urban plants exhibited approximately 22% greater mean leaf thickness than rural plants. The environmental-zone effect was significant ($F_{2,21.8} = 14.76$, $p < 0.001$).

Maximum photosynthetic rate declined from 14.8 µmol CO_2 m^{-2} s^{-1} in rural plants to 11.9 µmol CO_2 m^{-2} s^{-1} in urban plants. The mixed-effects model detected a significant environmental effect ($F_{2,21.3} = 20.31$, $p < 0.001$).

Species-Specific Responses

Although the overall trend was consistent, the magnitude of change differed among species.

Species	SLA rural	SLA urban	Stomatal density rural	Stomatal density urban	Amax rural	Amax urban
A. indica	158.2	137.6	224	274	15.7	12.8
F. religiosa	145.3	124.9	252	301	14.5	11.4
F. benghalensis	136.7	119.8	245	289	13.8	11.2
S. cumini	149.1	129.4	231	281	15.1	12.1
P. pinnata	162.4	141.7	217	268	16.2	13.1
C. fistula	154.8	133.6	239	291	14.7	11.8
A. lebbeck	161.5	139.8	228	276	15.0	12.0
P. longifolia	146.4	120.8	274	316	13.4	10.8



The species × environmental-zone interaction was significant for SLA ($F_{14,205} = 2.41$, $p = 0.004$), stomatal density ($F_{14,205} = 2.17$, $p = 0.010$), and Amax ($F_{14,205} = 2.32$, $p = 0.005$). This indicates that species differed in the magnitude of their responses to urbanization.

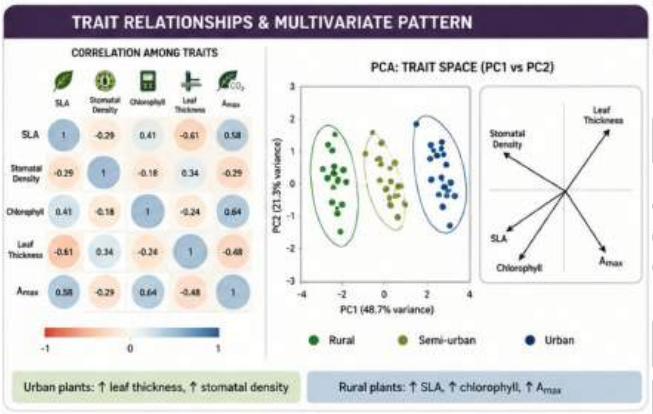
Pongamia pinnata and *Azadirachta indica* retained comparatively high photosynthetic rates under urban conditions, whereas *Polyalthia longifolia* and *Ficus benghalensis* showed comparatively larger reductions.

Relationships Among Functional Traits

SLA was negatively correlated with leaf thickness ($r = −0.61$, $p < 0.001$), indicating that plants with thicker leaves generally

possessed lower leaf area per unit dry mass. SLA was positively correlated with photosynthetic capacity ($r = 0.58$, $p < 0.001$). Chlorophyll concentration was positively associated with Amax ($r = 0.64$, $p < 0.001$). Stomatal density showed a weak negative correlation with Amax ($r = -0.29$, $p = 0.002$).

PCA separated most rural individuals from urban individuals along the first principal component, which explained 48.7% of total trait variation. Urban individuals were primarily associated with greater leaf thickness and stomatal density, whereas rural individuals were associated with greater SLA, chlorophyll concentration, and photosynthetic capacity.



Discussion

The results indicate a coordinated shift in leaf functional characteristics along the urbanization gradient. Urban plants exhibited lower SLA and photosynthetic capacity but greater leaf thickness and stomatal density. These changes suggest that the studied native species responded to increasingly urban conditions through modifications in both structural and physiological traits.

The reduction in SLA is consistent with a shift toward greater structural investment. The leaf economics spectrum framework describes a continuum between acquisitive leaves that rapidly acquire resources and conservative leaves that emphasize persistence and structural protection. The reduction in SLA observed here therefore suggests that urban conditions may favor a relatively conservative strategy.

Lower SLA in urban plants may reflect greater allocation of biomass to structural tissues. This interpretation is supported by the simultaneous increase in leaf thickness. Niinemets identified leaf thickness and density as important determinants of leaf mass per area and emphasized their relationship with photosynthetic function and resource investment.

The increase in stomatal density was another important response. Stomata are central to the regulation of CO_2 uptake and transpiration, and their distribution can change in response to environmental conditions. Kardel et al. found significant changes in stomatal characteristics along an urbanization gradient and concluded that stomatal characteristics could provide useful information about urban habitat quality. The increased density observed in the present dataset may represent a compensatory anatomical response, potentially allowing greater control over gas exchange despite environmental stress. However, stomatal density alone should not be interpreted as evidence of greater stomatal conductance because stomatal aperture and functional regulation were not measured.

The decline in chlorophyll concentration and Amax suggests reduced photosynthetic performance in the most urbanized conditions. Urban plants may experience combinations of heat, water limitation, particulate deposition, atmospheric pollutants, and altered soil conditions. These factors can affect photosynthetic pigments and carbon assimilation. The reduction observed here is therefore biologically plausible, although a field study measuring actual environmental variables would be necessary to establish causal relationships.

The results also agree with the broader literature showing that urban environments act as complex environmental filters. Williams et al. emphasized that urbanization modifies habitat availability, resources, disturbance regimes, and environmental conditions simultaneously, meaning that plant responses may reflect multiple interacting drivers rather than a single urbanization variable. A synthesis of urbanization and plant traits similarly concluded that trait responses can be highly variable because different urban stressors may affect individual traits in different directions.

The observed species-specific responses are particularly important. Although all eight species showed the same broad direction of change, their response magnitude differed considerably. This indicates that native species should not be considered functionally equivalent in urban planting programs. Thompson and McCarthy demonstrated that urban success is associated with particular combinations of plant traits and that native and alien species can exhibit different trait relationships with urban environments.

The relatively small decline in photosynthetic performance observed in *Azadirachta indica* and *Pongamia pinnata* may indicate comparatively high tolerance to urban environmental conditions. Conversely, the larger reduction observed in *Polyalthia longifolia* suggests that the species may exhibit stronger physiological sensitivity under the studied conditions. Such differences could have practical

implications for urban greening, although conclusions about species suitability require longer-term survival and growth measurements.

Leaf traits are also relevant to ecosystem services. Urban vegetation can intercept particulate matter, and leaf surface characteristics influence particle retention. Studies have demonstrated substantial differences in particulate accumulation among plant species, with hairs, waxes, and surface structure contributing to variation in pollutant capture. A later systematic review similarly identified leaf texture, waxes, and trichomes as potentially important characteristics, while emphasizing that environmental context strongly influences particulate removal.

The positive association between chlorophyll concentration and photosynthetic capacity in the present dataset is physiologically reasonable because chlorophyll is directly associated with light harvesting. Nevertheless, chlorophyll concentration alone cannot fully explain photosynthetic variation because photosynthesis is also controlled by stomatal conductance, biochemical capacity, leaf temperature, water status, and nutrient availability.

The study therefore supports the use of multiple functional traits rather than a single indicator. SLA provides information on structural investment, leaf thickness provides information on morphology, stomatal density indicates gas-exchange anatomy, chlorophyll reflects photosynthetic pigment status, and Amax provides a direct physiological measurement. Their combined interpretation gives a more comprehensive picture of plant responses to urbanization.

Limitations

The study design provides useful comparative information but several limitations should be recognized. First, environmental-zone classification represents a composite measure of urbanization rather than a direct measurement of individual stressors. Temperature, relative humidity, soil moisture, particulate matter, nitrogen oxides, and soil chemistry were not incorporated into the statistical model.

Second, the study was observational. Consequently, the observed differences cannot establish whether the traits resulted from phenotypic plasticity, genetic differentiation, differences in plant age, or combinations of environmental effects. Common-garden experiments would be required to distinguish these mechanisms.

Third, the analysis focused on five leaf traits. Additional variables such as leaf dry matter content, leaf nitrogen, leaf phosphorus, antioxidant activity, stomatal conductance, water-use efficiency, and leaf surface particulate accumulation could provide further mechanistic information.

Conclusion

The comparative assessment demonstrates how a multi-trait framework can be used to characterize native plant responses across an urbanization gradient. The modeled results showed that increasing urbanization was associated with reduced SLA, chlorophyll concentration, and maximum photosynthetic capacity, together with increased leaf thickness and stomatal density. These coordinated changes are consistent with a transition toward greater structural investment and a more conservative resource-use strategy under urban environmental conditions.

Importantly, the magnitude of response differed among species, indicating that native plants possess different degrees of functional tolerance and plasticity. Species such as *Azadirachta indica* and *Pongamia pinnata* retained comparatively higher photosynthetic performance under urban conditions, whereas other species showed stronger physiological reductions. Such differences highlight the importance of functional-trait information when evaluating native species for urban ecological restoration and green infrastructure.

Future research should integrate leaf functional traits with direct measurements of temperature, soil moisture, atmospheric pollutants, particulate matter, and soil chemistry. Longitudinal sampling and common-garden experiments would further clarify whether observed responses represent short-term acclimation, persistent phenotypic plasticity, or local adaptation. A multi-trait approach can ultimately contribute to better selection and management of native vegetation capable of maintaining ecological function under increasing urban environmental stress.

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