

Ecophysiology of Urban Trees and Their Management—The North American Experience

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Only a few species are capable of colonizing extreme environments, whereas more moderate environments can support many more. The diversity of species in a habitat is thus controlled by the environment, whether by soil fertility, altitude or any other factor. This diversity reflects the number of species adapted to grow in a habitat, and the nature of this adaptation must be examined in light of the physiological effect of the environmental factors making up the habitat, and their variation in time and space (11).

Although not a formal definition, this brief statement in the introductory chapter of *Environmental Physiology of Plants* (11) broaches the major concepts that have directed the field of plant physiological ecology. First is the observation that plant growth is limited by the environment. This is not a novel idea. Neither is it the exclusive property of physiological ecology, deriving from Liebig's Law of the Minimum (21, cited in 36). It is the second concept, namely that species occurrence varies in response to a varying environment, that distinguishes the field from allied fields like agronomy or crop ecology. Plant assemblages, or communities, are recognized as correlating with environmental variables along gradients of favorability (11) or tolerance (36). Alone, changes in woody plant species composition and diversity along moisture gradients have been the subject of numerous studies (3, 24, 59, to cite several salient examples). Logical extensions of the basic idea have been directed "upward" to include the influence of trees on site water balance (20) and "downward" to focus specifically on physiological differences among species (21, 42, 43, 61).

The focus on the interface of plant and environment at the physiological level is the third and most important hallmark of ecophysiological studies. Unlike many other physiological studies, this focus is achieved ideally under both natural and controlled condi-

tions. The explicit recognition of the environmental context necessarily includes a description of variation in time and space, often at a fine scale. Although an ecologist may be justified in treating species composition of a forest overstory as constant for relatively long periods and over large areas, the physiological ecologist frequently is concerned with environmental variation and plant response at the scales of minutes and centimeters (sunflecks on a forest floor, for example), and with these factors integrated over larger scales.

Given this operational context, what is the present status of plant ecophysiology as applied to urban trees? Physiological ecology has developed from community ecology. As such, the field rests on a large body of well-documented facts and reliable generalities. We lack this rigorous foundation for the urban setting. In its place, we have observations that urban trees are short-lived and recognition of many potential environmental stresses that could contribute to their death. From this qualitative recognition, we have "filled in the blanks" with what we know about plant physiology and the macroscale urban environment to arrive at an accepted view, which lacks rigorous testing. To some extent, this view has been the response of a concerned scientific community to assist urban foresters as they grapple with the myriad problems of managing urban trees.

From a biological perspective, the urban tree habitat differs radically from natural habitats. Unlike natural communities, colonization and competition are largely absent in urban tree habitats (street tree pits, for example). Species composition does not reflect the integrated expression of genotypes' capacities to colonize, compete, and achieve a modicum of equilibrium with environmental limitations. Historically, species composition is the deliberate choice of landscape architects, planners, block associations contractors,

and others based on visual effect, availability, cost, and an impression of what "does well" in the city. This array presents an intriguing dilemma: there is no natural community from which to draw preliminary inferences about environmental limits, yet there is a unique potential for planting species that are suited to the environment, if it is sufficiently understood. What is known about the urban environment that would aid in the selection of trees? There is consensus that urban habitats place numerous constraints on tree growth and that urban trees often have a drastically shortened lifespan in comparison with trees growing in natural stands. Estimates of life expectancy for newly planted street trees in northeastern United States converge on 10 years (1, 13). Further, there is a long litany of conditions occurring in the city that are potentially lethal either singly or in combination: soil compaction, high soil pH, soil solution affected by dog urine and de-icing salts, waterlogging, lack of water, air pollution, high summer temperatures, and vandalism, to name the most often cited (23). However, serious investigation of these environmental limits is frequently dismissed, ironically either by viewing it as too complex to unravel (a misinterpretation of the People Pressure Disease of Tattar, 54) or by assuming that the science is complete and we already know what needs to be done. At worst, then, the field of ecophysiology as applied to urban trees is anecdote and conventional wisdom. At best, it is a body of unquantified empirical observation, supported all too infrequently by rigorous investigation and experimentation. The synthesis, then, should not be mistaken for full understanding or as implying that we have quantified the range of urban plant stresses or identified solutions. To the scientist, it is as exciting as a problem statement.

A CASE STUDY: WATER BALANCE OF URBAN TREES

As an example of how an ecophysiological approach can be applied to street trees, we present a study of tree water balance in New York City conducted between 1983 and 1985. We report here the highlights of this study of 20 recently planted street trees in Manhattan. A detailed treatment will appear elsewhere. We will focus here on tree water balance rather than the entire range of ecophysiological study relevant to urban trees. We selected water deficits as a point of entry because water is essential to all plant processes and limits tree growth worldwide under natural conditions (26). There is also a widespread belief among both academic scientists and urban foresters that water is especially limiting for street trees (1, 12-14, 16, 19, 45, 50-53, 60).

The hypothetical scenario for water stress in street trees holds that both curtailed water supply and excessive demand are prevalent. *Water supply is decreased* to roots because of restricted rooting volume and reduced infiltration into soils compacted and covered with impervious pavements. Access to ground water and subsurface drainage is often eliminated. Simultaneously, *atmospheric water demand is increased* because of elevated temperatures, lower relative humidities, and channelized wind in urban street canyons, which have been inferred from numerous studies of urban climatology (4, 18, 28-30, 33, 35, 38-40, 49). Despite (or perhaps because of) the preponderance of indirect evidence and the logical appeal of conventional wisdom, very few data are available to document the severity and frequency of water deficits in urban street trees. Indeed, few studies have addressed urban tree water relations at all, and those we are aware of involve simulated or simplified urban environments (parking lots, university campuses), have been relatively short term (several days during one growing season), have used a limited number of species (honeylocust predominates), are at a scale not wholly appropriate to street trees (e.g., continuous canopies), or have used containerized trees (6, 44, 58). Field observations under actual street conditions are largely absent. Such observations would provide strong validation for selection and improvement programs that are frequently recommended (14, 17, 47), aid in the development of operationally defined selection criteria and planting/maintenance specifications, and contribute to our general understanding of the urban environment.

Our study site was a shallow canyon on Columbus Ave. between 68th and 75th streets on the upper west side of Manhattan, (lat.40°46'N, long.73°58'30"W). Columbus Ave. is one of fifteen

major arteries that run nearly the length of Manhattan. The compass bearing of all these avenues is 30° (i.e., between NNE and NE); thus the exposures are nominally east and west. Observations were made during the periods July-Sept. 1983, May-Sept. 1984, and June-Aug. 1985. A total of 11 visits were made over the 3-year period.

Twenty trees were studied: nine green ash (*Fraxinus pennsylvanica* var *lanceolata* 'Marshall's Seedless') and 11 litleaf linden (*Tilia cordata* 'Greenspire'). Both cultivars are currently among the most frequently planted trees for urban use in the northeastern United States. All trees were planted in Mar. 1982 in accord with standard planting practices (7). Trees were 4 to 6 cm d.b.h. (diameter at breast height), balled-and-burlapped, and branches were removed to a height of 2.4 m at planting.

Well watered trees in #1 plastic nursery containers (3.78 liters nominal volume) also were brought from Cornell to be observed under street conditions. Fifteen 2nd year graftlings of each cultivar were used for each observation period. During street observations the containers were enclosed in white plastic bags to prevent evaporation and were supported on narrow boards 1.2 m above the sidewalk. Fresh trees were used for each trip.

Site microclimate was monitored during the observation periods at mid-block on each side of the street with a portable weather station and data logger. Point measurements were recorded as 30 min averages of samples taken at 10 sec intervals. Additionally, hourly data (single measurements, not averages) from the observation station 1.4 km northeast of the study area in Central Park were obtained from the National Weather Service in New York for each day we monitored street conditions.

Beginning at predawn and continuing every 3 to 6 hr thereafter, water potential of the first fully expanded leaf on containerized trees and a reachable, fully expanded sun leaf on the in-ground trees was measured using a pressure chamber. Generally, selected leaves were at the third node back from the branch tip. Stomatal conductance, transpiration, and leaf temperature were measured at the same intervals on similar leaves with a null-balance porometer. During the 1983 growing season only, we supplied 18.9 liters (5 gal) of water each week from June through August to five in-ground green ashes and five lindens. Water was injected at four locations in the pit.

Site microclimate. Cumulative daily evaporative demand, expressed as the area under the vapor pressure deficit curves (VPD), is a convenient way to summarize Columbus Ave. observations in comparison with Central Park (Fig. 1). Over the entire study, cumulative daily VPDs were far less variable for Central Park than either the east or the west street exposures, with standard deviations of 6.31, 11.90, and 17.91, respectively. Excluding the July and Sept. 1983 observations which were abbreviated, we observed street conditions on four occasions indicating more severe diurnal evaporative atmospheric demand than in Central Park. Of these, the Aug. 1983 observation is outstanding in that the western exposure had a very high demand (80 kPa/day) and exceeded the demand in Central Park by a factor of roughly 2. On 8 Aug. 1985, demand on the east side of Columbus Ave. exceeded demand in both Central Park and the west side of the street by a similar magnitude, but total demand was only 50 kPa. Differences between Central Park and Columbus Ave. result, in large part, from differences in the absolute vapor density of the atmosphere (see below).

The 1984 observations indicate similar conditions, showing cumulative daily VPDs in the range of 17 to 33 KPa/day (Fig. 1). Despite the generally moderate evaporative demand (reflecting characteristics of sample days), seasonal trends are apparent. The data indicate that VPD values are low in the spring, peak in July and August, and decrease in September. There is little in the data to suggest systematic trends in VPD related to exposure: in 1984 the west side of the street had slightly higher VPDs on all occasions except the May sample, whereas the 1985 data indicate higher VPDs on the east exposure than on the west.

Both Columbus Ave. and Central Park show well-defined diurnal variation in VPD as shown by the Aug. 1984 data (Fig. 2). For this date, the west exposure shows the highest hourly average values for VPD, with small differences between the east exposure and Central Park; in fact, the park had higher VPDs than the east side

in the morning. The street environment showed greater diurnal variation than the park.

Diurnal trends are defined by inputs of solar radiation, but these are highly modified by building height, street width, and street orientation. Both exposures show truncated patterns of full sun (Fig. 3). The west side of the street receives 4 to 5 hr more of direct sun than the east, depending on season. This difference is due to the street orientation, not differences in building height. Buildings effectively raise the horizon on each side of the street, however. Throughout the growing season, the lower canopy on the east side of the street is in shade until 1230 to 1300 HR. Under the eastern exposure, incident radiation rises rapidly to full sun levels as the sun emerges from behind the roofline. On the west side of the street, there is an analogous, sharp drop in radiation levels in the late afternoon as the sun disappears behind the roofline.

Temperature and relative humidity track inputs of solar radiation: air temperature maxima often coincide with peak solar inputs while relative humidities reach minima at these times. Although generally rather subtle, this pattern is at times quite pronounced. During 16 Aug., midday air temperatures at the lower canopy level reached 41°C, whereas on both 15 and 16 Aug. relative humidities reached minima of 12% to 13%. Over the same period in Central Park, the maximum temperature was 32° and the minimum relative humidity was 38%.

Depressed relative humidity arises not only from its relationship to temperature. Between 1200 and 1900 HR on 15 Aug. 1983 vapor densities on the east side of Columbus Ave. were 4.3 to 9.0 g·m⁻³ below Central Park. During the same time period the following day, vapor densities on the west side of the street were 7.9 to 10.6 g·m⁻³ below the Park. Thus, the street environment is at times *drier on an absolute basis* than even a nearby urban park.

Tree Water Status. Midday water status of in-ground trees was compared to that of well-watered containerized trees during 1984, using the approach of Elfving et al. (10) (Fig. 4). With few exceptions, performance of the in-ground trees fell below curves for the potted trees, indicating that in-ground plants develop more negative leaf water potentials. Transpiration, however, did not fall with decreasing water potential. Thus, plant water potentials as negative as -2.5 MPa on Columbus Ave. did not indicate limitations in soil water supply. Hinckley et al. (22), summarizing a large number of observations, conclude that leaf water potential generally remains above -2.5 MPa with "adequate soil moisture". This value is consistent with our observations. That potted plants transpired at similar rates but at less negative water potentials suggests that in-ground trees have acclimated, perhaps via osmotic adjustment, so that water extraction at high rates from the soil was possible at soil metric potentials of -0.3 to -0.8 MPa (using predawn plant potentials as estimates of soil matric potentials).

Water potentials were highest and transpiration rates were lowest during the May 1984 observations. Within a single observation period during the remainder of the summer, transpiration varied widely at a given water potential. Even at minimum water potentials (-2.5 MPa) in September, both ash and linden equalled or exceeded the transpiration rates of the containerized trees.

Frequently, there was a 0.5 to 1.0 MPa difference between the predawn maximum and the midday minimum water potential, but even under the extreme conditions of Aug. 1983 trees recovered rapidly to predawn water potential levels when transpiration dropped at the end of the day. Lindens on the east side were an exception: both irrigated and control treatments lagged behind other trees.

Midday stomatal closure was observed only once, again during the Aug. 1983 sampling. Exposure affects the time at which this midday depression occurred. On the west exposure, the morning conductance maximum occurred at 1100 HR, coincident with the onset of peak radiation loads. Stomatal conductance was depressed at 1400 HR and, excepting irrigated ash, recovered at 1900 HR. On the east exposure, maximum rates occurred at 1500 HR, roughly coincident with the temperature peak but lagging the radiation peak. No late afternoon recovery of transpiration was observed on the east side, although stomatal conductance rose slightly at 0100 HR.

Interspecific differences were also indicated. Maximum stomatal conductance and transpiration rates were generally higher in ash than in linden, especially on the east side of the street. Supplemental

irrigation promoted high transpiration rates in ash but not in linden. Linden transpired at higher rates than ash during the evening period when light levels are minimal, which probably accounted for the linden's lag behind ash in recovery to predawn water potentials.

We interpret our results by answering six questions germane to understanding water relations of street trees in New York City and perhaps other cities in the northeastern United States. *Is there any evidence for water deficits?* Over a 3-year period, the most negative average predawn water potential was -0.9 MPa. Predawn water potentials were nearly always re-established in the late evening. There was not a seasonal decrease in predawn water potentials as a rule. During the only year for which we have season-long data (1984), midday water potentials showed a decreasing trend. Midday stomatal closure was observed only once, in Aug. 1983.

There are only three published reports of tree water balance in urban settings that are comparable to ours. In a study of containerized sugar and Norway maple (*Acer saccharum* and *A. platanoides*, respectively) in a parking lot under "moderate stress" (soil water potential between -0.5 and -1.0 MPa), neither measured nor estimated conductances showed any midday depression (58). Similarly, in a parklike setting on an upstate New York university campus, honey locust (*Gleditsia triacanthos*) showed no midday decrease in conductance even at leaf water potentials of -2.4 MPa (44). Similarly, honeylocust on "urban stress sites" (a lawn at the Univ. of Connecticut at Storrs and a shopping mall parking lot) showed no signs of midday stomatal closure due to water deficits. Leaf water potential was not reported in this study, but soil water potentials never fell below -0.054 MPa (6). Although these reported water potentials for trees in urban settings indicate a level of strain in the soil-plant-atmosphere continuum (SPAC), it is not clear that this level is unique to urban habitats or exceeds the trees' capacity to maintain the transpiration stream.

Water relations data for *Fraxinus* and *Tilia* in natural stands are scarce. One study of green ash reports reduction in stomatal conductance at leaf water potentials of -0.9 MPa, with virtually complete closure at -2.0 MPa (3). Reinterpreting the data of Tobiessen and Kana (54) for *F. americana* using boundary line analysis (42) indicates stomatal closure beginning at leaf water potentials of -2.2 MPa. This value is within the range for reduced stomatal conductance observed for green ash in Aug. 1983 on Columbus Ave., indicating that our observations are not necessarily beyond the range of conditions encountered by similar species in natural settings.

If water deficits occur, how frequent are they? Only one set of observations (Aug. 1983) suggests that the in-ground street trees on Columbus Ave. were under water stress. The 3-month summer season was the hottest since 1949, with maximum temperature exceeding 32.5°C on 29 days (N.E. Regional Climate Program, 1983). Based on Central Park weather conditions, the 15-16 Aug. 1983 period had maximum temperatures exceeding 37°, average maximum temperature for the previous two days $\geq 32.5^\circ$, and minimum relative humidities of <50%. These observations can be used as the basis for a "type-day" profile of weather conditions likely to result in water deficits in street trees. For the June through August period between 1972 and 1981, days with this profile occurred 40 times or 4.35% of the total days in this period. On average, 4 days per season have these characteristics, with a range 0 to 8 days per season. These conditions occur most frequently in July and least frequently in June. Thus, while we have only a single observation of tree water deficits, it appears that such events are common, though infrequent.

How do street microclimate and plant response vary with exposure? On clear days, both east and west street exposures show truncated patterns of direct sun due to the elevated horizon at the building eaves. The west exposure receives direct sun until 1500 HR EDT, whereas the east exposure is shaded until midday and receives direct sun until 1730 HR EDT. The west exposure had generally higher maximum temperatures. We attribute this difference to the fact that the west side receives 4 to 5 hr more direct sun per day because of the N30°E bearing the street (Fig. 3). Similar exposure-related differences in urban microclimates have been reported by Tuller (56, 57). We might predict that trees on the west side of the street would show symptoms of greatest water stress, yet trees on the east side of the street had slightly more negative

midday (i.e., minimum) water potentials. This change could have been the product of generally higher stomatal conductances and transpiration rates, however. There was no indication of east-west differences in predawn water potentials, suggesting that low transpiration rates compensated for long exposures to high irradiance.

Does the Columbus Ave. microclimate differ from a nearby open space? Our observations indicate that spatial variation (especially with radically different areas of surface contributing to the flux of water vapor to the atmosphere) is at times dramatic in the urban habitat. During the June–Aug. summer season, Central Park is cooler, has higher relative humidities, and lower VPDs than the average Columbus Ave. conditions. During type day conditions, these differences are extreme, with maximum temperatures in the Park 9°C cooler and minimum relative humidities 26% above those of the street. Absolute humidity is at times lower on the street than in the Park, which contributes to the depression in relative humidity. Tuller (57) reports conditions for Victoria, B.C., which are qualitatively similar, although the magnitude of difference among sites is much lower. Caution should be exercised when trying to generalize standard meteorological data to an urban street, even when nearby data are available.

Do different species respond differently under urban conditions? Both cultivars observed in this study are favored in newer urban plantings, in part because they have proved successful in urban areas (25). It is particularly interesting, then, that our data suggest that Marshall's seedless ash and littleleaf linden have rather different stomatal conductances and transpiration rates. Under street conditions, these differences are not absolute, but both potted and in-ground trees under a wide variety of street conditions show that ash transpires at higher rates than linden. High transpiration rates have been reported for *Fraxinus americana* (9, 37) in comparison with other trees native to the northeastern United States, suggesting that this is a characteristic of the genus. This characteristic is also apparent under controlled laboratory conditions and is expressed most markedly when soil water is depleted (T.H.W., unpublished data). On a continuum of drought avoidance to drought tolerance (27, 31), linden tends to avoid drought (maintaining lower transpiration rates and higher water potentials), whereas ash tends to tolerate drought (sustained transpiration rates despite decreasing water potentials). From the standpoint of selecting and improving cultivars for urban use, both water balance strategies are successful.

How do trees respond to a minimum irrigation regime? Although soil did not seem especially limiting, supplying in-ground ash trees with 18.9 liters (5 gal.) of water per week throughout the 1983 growing season did result in increased transpiration rates and more negative midday water potentials. Irrigated linden showed no response to irrigation. These results are consistent with the interspecific differences above but remain to be studied under controlled conditions with recurring drought cycles.

In all likelihood, the amount of water supplied in our irrigations was far below both the potential and actual weekly transpirational demand imposed on the trees on Columbus Ave. The fact that ash responded to irrigation at these levels by opening stomata indicates that there are potential opportunities for increasing carbon uptake even with small supplements. Irrigation of street trees is rare, difficult to impose, and discounted as infeasible given the enormous demand by each tree. For example, Vrecenak and Herrington (58) calculate that 3 liters·hr⁻¹ are required by trees (*Acer saccharum* and *A. platanoides*) with crown radius of 2 m, leaf area index of 4 and transpiration rates of 1.67×10^{-6} g·cm⁻¹·s⁻¹ (comparable to the trees in this study). Our irrigations would supply 6 hr of transpiration under the model assumptions of these workers; increasing the crown radius to 3 m reduces the supply to 2.7 hr of transpiration. Our results suggest that these suboptimum supplements are sufficient to increase stomatal conductance for brief periods. We suggest that even minimum irrigation in mid-summer, at arbitrarily low levels, will enhance carbon balance under stress conditions.

AN AGENDA FOR URBAN ECOPHYSIOLOGICAL RESEARCH

The paramount need is for a systematic approach in all ecophysiological studies of urban trees, not only water balance and gas

exchange studies. Most studies to date have lacked spatial or historic context. It would indeed be difficult to design flood control structures with no knowledge of flood intensity, return frequency, or flood plain location. By analogy, without estimates of frequency, severity, and location of stress conditions, how can we select appropriate cultivars, place them effectively, and manage them strategically?

The urban environment lacks a quantitative description at the scale of the street tree. We need to develop quantitative working generalities for both the atmospheric and the soil environments. As indicated in the introduction, the urban habitat lacks native vegetation (other than ruderal communities) and is sufficiently different in character from natural communities that we have only a general sense of adaptive traits necessary for success. It is likely that some components of the urban habitat exceed any tree's tolerance limits.

Native germplasm of important shade tree species needs to be examined for resistance and adaptability to appropriate environmental stresses. This is an example of how a practical need should stimulate research at a basic level. We presently know very little about the natural variation in water relations within hardwood species. Virtually the only comparative studies of water relations among closely related genotypes are those of Townsend and Roberts (55) for red maple and Pallardy and Kozłowski (41) for hybrid poplar clones. At Cornell Univ. we are presently involved in a long-term evaluation of both cultivars and wild provenances of red maple for drought resistance in cooperation with Alden Townsend of the National Arboretum Washington, D.C. In cooperation with Kim Steiner from Pennsylvania State Univ., University Park, we are planning a similar evaluation of green ash provenances. Studies using clonal replicates present a rare opportunity to gain insights into the range of physiological variation in woody plants at both phenotypic and genotypic levels. We echo the recommendations of Kozłowski (27) that water use efficiency be used as a criterion for intraspecific selection. Beyond water relations, we know even less. For example, what is the range of intraspecific variation in hardwoods for resistance to air pollution, compacted soil, or salt?

We need long-term, quantitative studies in cities outside the northeast urban corridor in the United States and involving a wide range of species. Studies such as those by Håbjørg (22) and Clark et al. (8) at the Univ. of Washington, Seattle, will enhance our ability to generalize across species, microsites, and climatic zones.

The isolated street tree dramatizes the need to improve mathematical approximations of energy transfer in nonhomogeneous canopies. Empirical tests of existing models (see e.g. ref. 46) and development of new models that account both for advection and shading are needed. Empirical observation can provide data for constructing new models. Despite the apparent complexity of an urban street, we submit that it is a simpler physical system than a deciduous forest in the northeastern United States. There are sharp, readily identifiable, predictable energy gradients, low species diversity, and little competition. What better place to study transfer processes in mature, isolated trees?

Observational studies of both the environment and plants will provide limits for cultivar screenings. Boyer (2) emphasizes the advantage of crop selection under stress conditions and illustrates how increased yields of corn hybrids correlates with more positive predawn water potentials. Gerhold and Bartoe (15) argue the merits of performance testing under urban conditions and outline an experimental design for cooperative trials involving arborists and nurserymen. To our knowledge, this approach has yet to be implemented on a large scale. Even if this approach is adopted, preliminary screening would be necessary to reduce the amount of material to be field tested when selecting new genetic material rather than screening existing cultivars. Without baseline observations of plant-environment interactions under actual field conditions, it is difficult to design an appropriate screening procedure and interpret the outcome.

As another example of applied research prompting basic questions, our work on Columbus Ave. suggests a system for exploring differences in water relations between a ring porous species (green ash) and a diffuse porous species (littleleaf linden) under varying degrees of drought stress. Kozłowski (26) emphasizes the need for precisely such a comparison in a recent review. We are continuing

our comparison of linden and ash under controlled conditions.

There are excellent experimental systems in urban physiological ecology and many opportunities for good research with both basic and applied thrusts. The science is not over; in fact, it has barely begun. In the words of the tree geneticist Frank Santamour, "Any experiment is better than none at all...Any increase in our knowledge must be considered worthwhile; and if we can someday drive down an avenue of better trees...so much the better" (48).

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