

DROUGHT RESISTANCE ADAPTATIONS IN URBAN HONEYLOCUST

by Donald F. Potts and Lee P. Herrington

Abstract. Honeylocust is being widely planted in urban environments. The species is reputed to be well adapted for survival in these locations, but nevertheless exhibits premature senescence, tissue damage and early mortality on urban sites. Despite ample rainfall or irrigation, the problem seems to be drought induced. Morphologic and physiologic drought stress resistance adaptations of honeylocust were evaluated. Small boundary layer resistances, leaf folding, wilting, small stomata, low stomatal densities, and even premature senescence itself provide the species with more xeric ecological amplitude. However, the species exhibits extremely poor stomatal control over excess water use. Advected sensible heat drives excess evapotranspiration, resulting in long periods of low plant water potentials. This in turn, probably results in metabolic imbalance, loss of carbohydrate reserves, reduced vigor and early mortality.

Key Words: Honeylocust (*Gleditsia triacanthos* L. f. *inermis*), urban forestry, drought stress resistance

The seedless, thornless honeylocust (*Gleditsia triacanthos* f. *inermis*) is a mesic intolerant species native to the lower Mississippi River Valley bottomlands. Honeylocust is increasingly being planted in American cities. While the species is enthusiastically endorsed as being well suited to urban environments, it nevertheless exhibits premature senescence, tissue damage and early mortality on urban sites (Richards and Stevens 1979).

Honeylocust seems physiologically tolerant to much of the urban chemical and physical environment. Hanes *et al.* (1970), Ivanov (1972) and Dirr (1974) found extreme resistance to salinity. Drummond (1971) observed only average susceptibility to the pollutant peroxyacetyl nitrate (PAN). Treshow (1970) found it somewhat resistant to ozone. Dimitrov (1968) found good adaptation to soil moisture shortage, noting relatively constant CO₂ assimilation, which he interpreted as indicating minimal stomatal closure regardless of soil moisture availability. However, none of these observations discounts the possibility that premature senescence, tissue damage and early mortality seen in urban honeylocust are drought induced.

Therefore the purpose of this study was to evaluate honeylocust's morphological and physiological drought stress resistance (Levitt 1972) adaptations and identify those which may help the species survive in harsh physical environment and those which may contribute to premature senescence, tissue damage and short life.

Methods

Two three-meter tall honeylocust were planted in 1m³ weighing lysimeters in the spring of 1976. The lysimeters approximated the confined root environments encountered by most trees planted in typically high bulk density "man-made" urban soils. The lysimeters were located on the S.U.N.Y. College of Env. Sci. & Forestry campus on an open grassy knoll surrounded by large buildings, parking lots and park-like vegetation. The site was similar to many urban amenity spaces but less severe than typical street-side planting locations.

The study trees were grown throughout the summer of 1976 so the root systems could become established and fully occupy the soil volumes. After successful over-wintering and the termination of leaf elongation, morphologic and physiologic evaluations began in early summer 1977.

Estimates of average leaflet area and characteristic dimensions, average compound leaf area, and total tree leaf area were obtained. Crown dimensions and leaf angle distribution were measured. Stomatal densities and dimensions were determined from scanning electron photomicrographs of leaf abaxial surfaces.

Relationships among and between photosynthetically active radiation (P.A.R.), leaf water potential, soil water potential, and stomatal resistance were determined. P.A.R. was measured with a LI-COR Quantum Sensor held in

the plane of the leaves of which stomatal resistance was simultaneously determined. Leaf water potential was estimated in a large sample of detached compound leaves taken from random crown locations using a portable pressure chamber. Diurnal leaf water potential curves were developed for clear and overcast conditions at varying soil water potentials.

Soil water potentials were measured with Wescor dew-point hygrometers and microvoltmeter. The values used were the average readings of six sensors spaced uniformly in the soil volume. The lysimeters allowed control over soil moisture availability. Through the study, watering was scheduled so that soil water potential fluctuated between 0 and -0.8 MPa. every two weeks.

Stomatal conductances were determined using a LI-COR diffusive resistance sensor and meter (Kanemasu *et al.* 1969). Because of the small honeylocust leaflets, the instrument's standard sensor aperture of 200 mm^2 ($10 \times 20\text{mm}$) was reduced to 40 mm^2 ($4 \times 10\text{mm}$). The instrument was then carefully calibrated per manufacturer's instructions. Recalibration carried out halfway through the data acquisition found no change in the instrument output.

Stomatal resistances were obtained in the early morning at varying light intensities when leaf water potentials were higher than -1.0 MPa., and at midday when light intensity variations were due to shading in the crown and leaf water potential was generally lower than -1.0 MPa.

Results and Discussion

Leaf and crown morphology. There were an average of 2300 compound leaves on the nearly identical lysimeter trees. The photometrically determined average compound leaf area (one side) was 13.3 cm^2 . The leaf area index was estimated at 3 to 4. Clumping of leaves and angular branching habit raise some doubt as to the utility of those estimates (see Figure 1.).

Honeylocust pinnately or bi-pinnately compound leaves are "radiator-like". That is, they have a characteristic dimension providing low resistance to heat and mass transport. Each compound leaf of the study trees averaged 24

leaflets. Each leaflet was about 0.55 cm^2 (one side) resulting in a characteristic dimension, assuming random orientation of 0.74 cm . By contrast the characteristic dimension of a green ash (*Fraxinus pennsylvanica*) leaf is about 3 cm . The efficiency of heat and mass transfer through its boundary layer (at a given wind velocity) is roughly half that for honeylocust. Under similar ambient conditions, the larger characteristic dimension might result in a 5° to 10° C . higher leaf temperature (Gates and Papian 1971; Grace 1977; Gates 1980).

Radiant energy loads on leaf surfaces are most likely to be dissipated by convection, thus reducing a demand for transpirational cooling. However, under strongly advective situations, sensible heat is just as easily transported to the leaf surfaces, driving the evapotranspiration process. Local



Figure 1A). Street-side honeylocust in Syracuse, N.Y. in mid-summer. Note dead branches and missing foliage.



Figure 1(B). Crown of study tree.

advection, common in urban environments (Oke 1978; Halverson and Potts 1981), is likely to be a contributor to extended periods of drought stress in any urban vegetation. Nevertheless, Campbell (1977) observed that small leaves have the highest water use efficiency (WUE) regardless of the severity of evaporation demand.

Honeylocust has a horizontal pre-stress leaf angle distribution which theoretically offers less direct sunlit leaf area than other distributions (Campbell 1977). This is somewhat misleading however, as it assumes that the leaf area of the top canopy layer is effectively intercepting beam radiation and preventing it from irradiating lower levels of the canopy. As already discussed, angular branching habit and clumping of leaves probably allow greater penetration of beam radiation into lower levels of the honeylocust crown.

On days of intense solar radiation and/or periods of high transpirational demand, the compound leaves fold along the petiole — nearly 60° from pre-stress orientation. Radiation geometry dictates that beam irradiance on the folded leaf surfaces would be half that of unfolded leaves (see Figure 2). Such response has been reported in other leguminous species (Begg 1980). The folding due to turgor loss results in an effectively vertical leaf distribution. Seen often in xeric vegetation, this adaptation allows optimal photosynthesis with a minimal heat load (Campbell 1977). Leaf wilt was also observed after long periods of high transpirational demand. This passive response is also suspected as being an

adaptation to minimize heat load (Begg 1980).

Stomatal function. No obvious ecological significance can be attached to honeylocust stomatal-light response, midday levels of stomatal resistance (Figure 3), or diurnal patterns of leaf water potential (Figure 4), as they agree favorably with those of other hardwood species (Hinckley *et al.* 1978). The study trees remained in deep shadows until the sun was about 20° over the horizon. Within moments, PAR flux density changed rapidly from less than $200\mu\text{Em}^{-2}\text{s}^{-1}$ to more than $1000\mu\text{Em}^{-2}\text{s}^{-1}$. The changes in stomatal resistance kept pace with the changes in radiant flux density allowing very rapid diffusion of water vapor from saturated substomatal cavities. At the other extreme, artificial shading to produce sudden low light intensities revealed extremely slow stomatal closing. Rapid stomatal opening has been associated with shade tolerance (Woods and Turner 1971) and was not expected in an intolerant species. Woods and Turner (1971) associated slow stomatal closing with intolerance. This would seem to be a disadvantage when water is limited, and indicates poor stomatal control over water loss.

A "bagged leaf" experiment, run to quantify resistance to water movement across the leaf trace, found an average potential difference of



Figure 2. Mid-afternoon leaf folding.

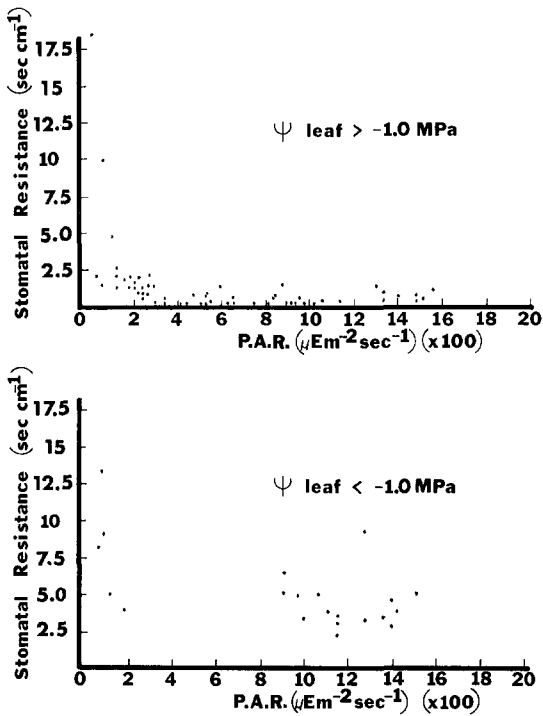


Figure 3. Stomatal light response curves.

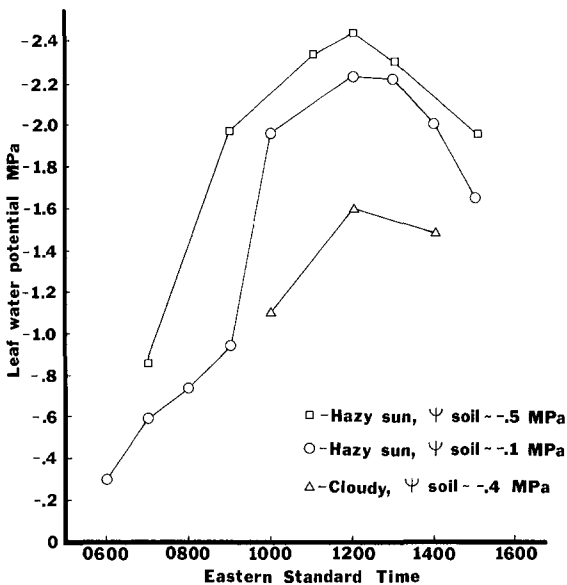


Figure 4. Representative diurnal leaf water potential curves.

about 0.3 MPa. between bagged and exposed leaves. More importantly, stomatal conductance of leaves kept in darkness was not significantly different than that of leaves exposed to morning sunlight. Tobiessen (1976) observed similar behavior in another pioneer species, *Populus tremuloides*. The possibility remains that this response was due to excess heat load imposed by the bag.

Little stomatal responsiveness to low leaf water potentials was observed. There was a gradual decrease in stomatal resistance with decreasing leaf water potential, or perhaps with increasing vapor pressure deficit. No apparent threshold water potential for stomatal closure was found. Mid-afternoon xylem potentials approaching -3.0 MPa . (see Figure 4) were routinely measured coinciding with stomatal conductances less than 10 sec/cm . This behavior has been associated with moist site preference (Tobiessen and Kana 1974, Tobiessen and Buchsbaum 1976) but has also been credited to preconditioning to water stress (Brown *et al.* 1976). In either event, the observation is consistent with Dimitrov's (1968) of uninterrupted assimilation of CO_2 regardless of soil moisture availability.

Stomatal Morphology. Scanning electron photomicrographs of honeylocust abaxial surfaces were made after termination of leaf elongation (Figures 5 and 6). Stomatal length varied by 20% and averaged 15 microns. That value is less than $\frac{1}{2}$ that reported by Davies *et al.* (1973). The differences may be varietal in nature. Stomatal density of 125 stomata/mm^2 agrees well with the 156 stomata/mm^2 reported by Davies *et al.* (1973).

The percentage of epidermis occupied by stomatal opening has been suggested as a good index to relative transpiration capacities (Kochenderfer and Lee 1973; Larcher 1980). The measured stomatal dimensions allow a conservative estimate of 90 microns^2 open stomatal area per stoma. This is just over 1% of an average leaflet abaxial surface, which is nearer the low end of values reported for deciduous species (Kochenderfer and Lee 1973; Larcher 1980). Logically, lower percentages should tend to be associated with drier site adaptation, but this has not been documented. Kramer (1969) observed

that dry site species tend to have high stomatal densities and small stomatal dimensions. Honeylocust has one of the lowest stomatal frequencies reported (Davies *et al.* 1973). This would indicate that honeylocust has more mesic stomatal morphology consistent with its natural range.

Summary and Conclusions

Honeylocust is a pioneer species native to moist bottomlands. But, all species have certain ecological amplitude. Kramer (1980) observed that the success of an organism in a particular environment rarely depends on possession of a single adaptive character, but rather on an optimum combination of characters which minimizes the deleterious effects and maximizes the advantageous effects. Hinckley *et al.* (1978) state that the relationship between maintaining a water status of little or no stress and a positive carbon balance results in a variety of adaptive strategies used by various species.

Adaptations which may provide honeylocust

with a more xeric ecological amplitude are varied. Small leaves provide small boundary layer resistances to the diffusion of heat, water vapor and CO₂ resulting in very high water use efficiency (W.U.E.). The combination of small stomatal dimensions and low stomatal density give honeylocust a low relative transpiration capacity. The crown geometry resulting from leaf folding and wilting minimizes the impact of radiation in driving excess transpiration. Premature senescence by reducing leaf area and conserving water may be a drought resistance character (Begg 1980).

On the other hand, honeylocust exhibits extremely poor stomatal control over water use. There is minimal stomatal responsiveness to plant water potential and no water potential threshold for stomatal closure was observed. Additionally, stomatal function is not totally light dependent. Stomata open very quickly, close very slowly and operate despite imposed total darkness. These characters would seem to be liabilities for survival in dry environments. But at the same time they

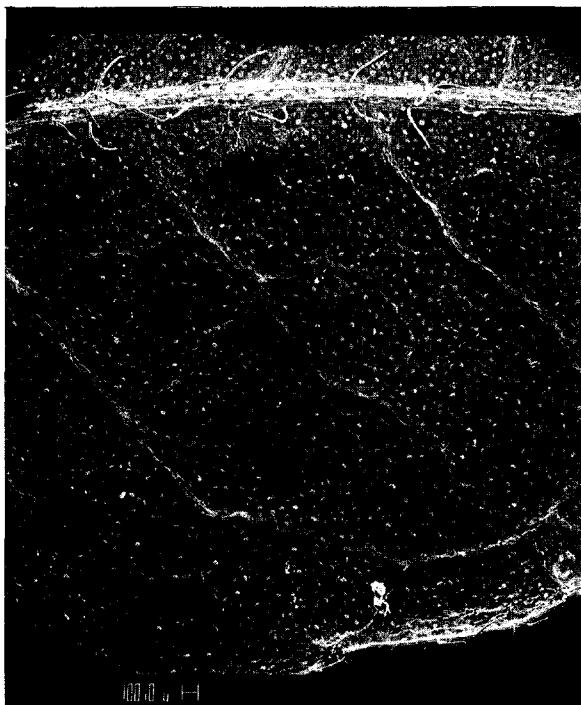


Figure 5. S.E.M. photomicrograph of honeylocust leaflet abaxial surface. (25X)



Figure 6. S.E.M. photomicrograph of honeylocust stomata (2500X)

provide for CO₂ assimilation under water stress. Thus it seems urban honeylocust can maintain a positive carbon balance, at least in the short run, at the expense of a water status of little or no stress.

Many of honeylocust's stress resistance adaptations are reversible. Unfortunately, some are irreversible — growth and yield potential lost by premature senescence does not fully recover with a return to more favorable conditions (Begg 1980). In very xeric environments or where water loss is driven to excess by advection of sensible heat from surrounding man-made surfaces, honeylocust cannot adequately regulate water loss through stomatal control. As a result, despite adaptations which minimize stress, the honeylocust undergoes extended periods of low plant water potential. This probably results in a metabolic imbalance and loss of carbohydrate reserves which may lead to vigor loss and early mortality (Aspinall 1980).

Acknowledgments. This project was supported by the U.S. Forest Service, Northeastern Forest Experiment Station through the Consortium for Environmental Forestry Studies.

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