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Authors: Qi, Yadong*; Favorite, Jammie; Chin, Kit L.; Xiao, Ying

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***Corresponding author:** Dr. Yadong Qi
Professor of urban forestry
Urban Forestry Program
Southern University
Baton Rouge, LA 70813
Phone: 225-771-4408
E-mail: yadong_qi@suagcenter.com

PHYSIOLOGICAL, ANATOMICAL, AND ECOLOGICAL CHARACTERISTICS OF SOUTHERN LIVE OAK

Yadong Qi, Jammie Favorite, Kit L. Chin, and Ying Xiao[1]

Abstract—Gas exchanges of sun-exposed and shaded leaves of southern live oak (*Quercus virginiana* Mill.) were studied monthly from May to September, 2000. Six healthy live oak trees with d.b.h. ranging from 21 to 148 cm on Southern University's campus in Baton Rouge, LA, were selected for the study. Instantaneous gas exchanges were measured during clear sky days from 9 a.m. to 4 p.m. using a portable gas exchange system. Leaf chlorophyll, moisture content, and environmental conditions were also monitored. Anatomy of sun-exposed and shaded leaves was studied in July using a scanning electron microscopy. Sun-exposed leaves had significantly higher net carbon dioxide (CO_2) uptake rate, transpiration rate, and chlorophyll content, and significantly lower internal CO_2 concentration and moisture content than the shaded leaves. The leaf anatomy related well to the leaf physiology. The sun-exposed leaves had a remarkably denser trichome layer and more closely packed palisade mesophyll cells than the shaded leaves. The combined leaf anatomy and physiology indicate that southern live oak possesses a unique ecological advantage of self defense against various environmental stresses.

INTRODUCTION

Southern live oak (*Quercus virginiana*, Mill.) is predominately a landscape and shade tree species that is considered a virtual emblem of the Old South. Live oak is a picturesque native tree found in the lower coastal plain of the Southeastern United States from southeastern Virginia south to Georgia and Florida including the Florida Keys; and west to southern and central Texas with scattered populations in southwestern Oklahoma and the mountains of northeastern Mexico (Harms 1990). Live oak can be seen growing in large yards, as specimen trees in parks, along streets, and overhanging the lanes of historic plantations. Georgia claims the live oak as its state tree. The trees grow on short, thick trunks, reaching a height of 40 to 60 feet at maturity. The live oak is the broadest-spreading of all oaks. Its large canopy will typically spread to nearly twice its height, which means it can shade an area of more than 100 feet. The trunk can grow anywhere from 3- to more than 6-feet-wide with limbs that run horizontally and sometimes sweep the ground under the massive weight (Ball 2003). The leaves are simple, elliptic or oblong, thick, leathery, oval, and dark evergreen. In the spring, this species drops its leaves and grows new leaves within several weeks. The flowers are catkins that occur in the early spring. They are monoecious (both sexes can be found on the same plant) and are pollinated by wind. The fruit is an acorn that occurs in clusters of one to five on peduncles 0.5 to 3 inches long (Odenwald and Turner 1980). The bark is thick, dark brown, and divided into ridges by deep narrow furrows. Southern live oak is intermediate in shade tolerance and once established withstands competition. This species likes moist, well-drained soil and is very drought tolerant and hurricane resistant. Southern live oak is extremely hard to kill because it sprouts vigorously from the root collar and roots (Hardin and others 2001). It is an excellent species for urban and community reforestation, providing maximum ecological and environmental benefits.

The United States is responsible for emitting more than 5 billion tons of carbon dioxide (CO_2) a year (Smith 1996). Increasing levels of atmospheric CO_2 and other greenhouse gases are thought by many to be leading to increased atmospheric temperatures (Nowak 1994a). Trees act as a sink for atmospheric CO_2 by storing carbon (C) through their growth processes. Stored C is used to construct new tissue and repair damage (Landsberg and Gower 1997). Trees in urban areas offer double benefits: (1) by reducing atmospheric CO_2 directly, sequestering and storing it in a form of C; and (2) when located properly, by shading buildings during summer and blocking winter winds, which reduce heating and cooling cost and result in lower CO_2 emissions from fossil-fuel power plants (Nowak 1994b). To maximize C sequestration and other benefits of urban trees, large and long-living shade tree species such as southern live oak should be planted in the suitable urban areas so that more C can be stored and the maximum amount of benefits from urban trees can be achieved.

Several papers pertinent to southern live oak physiology have been published, but they mainly dealt with the seedlings or saplings growing in containers (Beeson 1994; Devitt and others 1993; Devitt and others 1994; Devitt and others 1997; Gresham and others 1991; Levitt and others 1995; Messina and Duncan 1993; Pegoraro and others 2004; Rajashekar and Burke 1996; Tognetti and Johnson 1999a, 1999b). It is not possible to extrapolate the seedling results to mature trees. Except for the early publication by the authors on general leaf anatomy of southern live oak (Qi and Ying 2003), there has been no published information available on comparative physiology and anatomy of sun-exposed and shaded leaves of mature live oak trees. Study of mature trees is necessary for accurate estimation of the canopy level C uptake and transpiration potentials.

The purpose of this study was to investigate the physiological, anatomical, and ecological characteristics of mature southern live oak. The specific objectives included: (1) to compare the CO_2 uptake rate (net photosynthesis), transpiration rate, internal CO_2 concentration, chlorophyll content, and leaf

[1] Professor of Urban Forestry, Southern University and A&M College, Urban Forestry Program, Baton Rouge, LA 70813; Coastal Resources Scientist, Louisiana Department of Natural Resources, Baton Rouge, LA 70804; Professor of Horticulture, Plant and Soil Science Department, Southern University, Baton Rouge, LA 70813; and Research Associate, Socolofsky Microscopy Center, Louisiana State University, Baton Rouge, LA 70803, respectively.

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moisture content of sun-exposed and shaded leaves; and (2) to investigate the anatomical difference between sun-exposed and shaded leaves of mature southern live oak trees. The results obtained will increase scientific knowledge and understanding of the ecology and physiology of southern live oak, which will be useful for modeling and quantification of total C sequestration and water use capacities of the species. It is hoped that the research will increase public awareness of the ecological benefits provided by the urban and community forests.

MATERIALS AND METHODS

Study Site

A study site on Southern University's campus (latitude 30°53' N and longitude 91°19' E) in Baton Rouge, LA, was selected where healthy mature southern live oak trees were found growing. Six trees were chosen to study gas exchange rates monthly from May, 2000, through September, 2000. The base line data on the experimental trees including height, d.b.h., crown radius, leaf area index and total leaf area were collected and summarized in table 1.

Measurements of Gas Exchanges

For each tree, three sun-exposed and three shaded leaves were randomly selected bi-hourly from 9 a.m. to 4 p.m. for measurements of CO_2 uptake and transpiration rates during clear sky days. Two consecutive clear days per month were needed to finish the measurements of all six trees. Instantaneous gas exchange rates of photosynthesis and transpiration were measured using a closed portable gas exchange system (Model LI-6200 with a quarter-liter chamber, Lincoln, Nebraska, USA). This system was programmed to monitor the rate at which CO_2 concentration in the chamber changed over a 40-second interval. The net photosynthesis rate was then calculated using the rate of change and other factors, such as the temperature, pressure, chamber volume, and the amount of leaf area enclosed. Air and leaf temperatures, relative humidity, and photosynthetic active radiation were monitored simultaneously. When a leaf was enclosed in the leaf chamber, the humidity within the chamber tended to rise. This was balanced by the flow of drier air that was returned to the chamber from the analyzer. Transpiration rate was calculated from the change in humidity with time and the flow rate of dry air. For each month, the mean net photosynthesis rate, internal CO_2 concentration, and transpiration rate of sun-exposed and shaded leaves were obtained by averaging the bi-hourly measurements over 2 consecutive days.

Table 1—Baseline data for the southern live oak trees used for gas exchange measurements

Tree no.	d.b.h.	Height	Crown radius	Drip line area	LAI
	cm	- - - - - *m* - - - - -		*m²*	
1	21.20	10.97	3.54	39.27	1.48
2	35.50	10.36	5.83	106.92	2.18
3	43.00	9.75	5.12	82.38	2.03
4	107.00	14.63	12.88	520.99	4.14
5	113.50	14.02	14.55	665.47	2.44
6	148.00	16.46	13.49	571.49	2.06

Measurements of Leaf and Soil Moisture Content

Six sun-exposed leaves and six shaded leaves were sampled from each of the six trees monthly from June to September. The fresh weight was measured immediately after leaves were collected, and the dry weight was measured after drying the leaves at 70 °C in an oven for up to 48 hours. Six soil samples were collected within 0 to 12 inches depth from the areas where the experimental trees grew. The fresh weight of the soil was measured immediately after collection, and the dry weight of the soil was measured after the soil was dried at 70 °C in an oven for up to 72 hours. The formula for obtaining leaf and soil moisture content is: moisture content (%)=$(Wt_{fresh} - Wt_{dry})/Wt_{dry} \times 100$.

Measurements of Leaf Chlorophyll Content

Five sun-exposed and 5 shaded leaves per tree, for a total of 30 sun-exposed and 30 shaded leaves for all 6 trees, were collected monthly. Leaf chlorophyll content was measured with a chlorophyll meter (Spad 501, Minolta Corporation, Japan) in percentage and then converted to the unit of $\mu mol/m^2$ based on an empirical equation (Yadava 1986): chlorophyll($\mu mol/m^2$) = 6.864 + 8.864 x chlorophyll (%).

Scanning Electron Microscopy of Leaves

Six mature sun-exposed and six shaded leaves were collected in July. Each leaf was dissected along the main vein, and three small pieces (5mm x 8mm) were cut perpendicularly to the main vein within the central area of the leaf. The leaf pieces were fixed in FAA (ethanol, glacial acetic acid, and formaldehyde), dehydrated in ethanol series, and dried in CO_2 using Denton DCP-1 critical point drying apparatus. Leaves were then mounted on stubs, coated with 25 nm gold palladium using a Hummer II sputter coater, and examined using a Cambridge S-260 scanning electron microscope.

Statistical Analysis

Data were analyzed using analysis of variance and differences between means were determined using Tukey's Studentized Range (HSD) test, $P \leq 0.05$.

RESULTS AND DISCUSSIONS

Leaf Gas Exchange

Significant differences were detected in photosynthetic rate, internal CO_2 concentration, and transpiration rate between sun-exposed and shaded leaves for each month from May to September (figs. 1, 2, 3). Photosynthetic rates of sun-exposed leaves were significantly higher than the rates of shaded leaves. The sun-exposed leaves took up more than twice the amount of CO_2 than the shaded leaves (fig. 1). Internal CO_2 concentration of sun-exposed leaves was significantly lower than shaded leaves (fig. 2). Internal CO_2 is the amount of CO_2 within the mesophyll tissues, specifically the sponge mesophyll. Because the shaded leaves took up less CO_2, a higher CO_2 level remained within the mesophyll tissues. Transpiration rates of sun-exposed leaves were significantly higher than shaded leaves (fig. 3). Sun-exposed leaves were exposed to direct solar radiation, which was directly responsible for higher transpiration rates. Combining the 5 months measurements showed that under relatively same light and temperature environments, the sun-exposed leaves were significantly different from the shaded leaves in physiological performances including photosynthesis rate, internal CO_2 concentration, and transpiration rate (table 2).

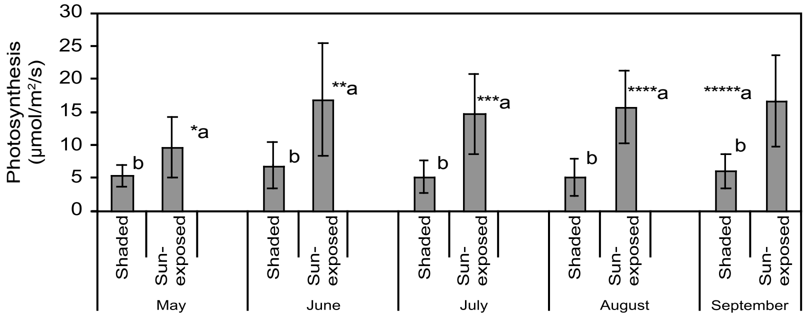

Figure 1—Photosynthesis of sun-exposed and shaded leaves of southern live oak during a growing season. Note: The means with different letters within each month are significantly different. *p=0.001; for all **, ***, ****, and ***** p≤0.0001.

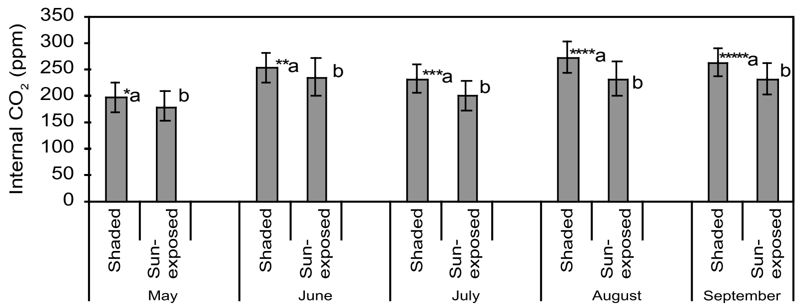

Figure 2—Internal CO_2 of sun-exposed and shaded leaves of southern live oak trees during a growing season. Note: The means with different letters within each month are significantly different; *p=0.0278, **p=0.0078, for all ***, ****, and ***** p≤.0001.

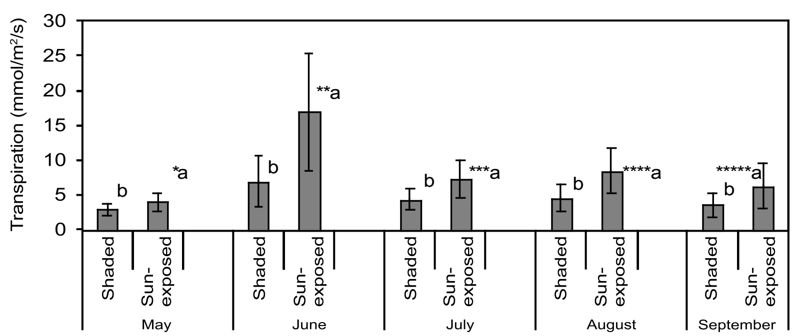

Figure 3—Transpiration of sun-exposed and shaded leaves of southern live oak during a growing season. Note: The means with different letters within each month are significantly different; *p=0.0018, **p=0.0021, for all ***, ****, and ***** p≤0.0001.

Table 2—Comparisons of gas exchange measurements of sun-exposed and shaded leaves

	Sun-exposed leaves[a b]	Shaded leaves[a b]
N(sample size)	295	289
Light (μmol/m^2/s)	1,226.96 ± 431.18 a	1,214.83 ± 438.50 a
Tair (°C)	35.50 ± 3.77 a	36.00 ± 3.75 a
Photosynthesis (μmol/m^2/s)	15.44 ± 6.78 a	5.68 ± 2.84 b
Internal CO_2 (ppm)	220.94 ± 36.42 b	251.78 ± 35.38 a
Transpiration (mmol/m^2/s)	6.81 ± 3.21 a	4.03 ± 1.83 b

[a] Mean ± standard deviation.

[b] Pairs of values followed by the same lowercase letter are not significantly different at the p ≤ 0.05 level.

Leaf Chlorophyll Content and Moisture Content

Chlorophyll contents of sun-exposed leaves were significantly higher than shaded leaves (fig. 4). The data for May and July were not available due to equipment repair. The leaf moisture content was monitored between the months of June through September. Sun-exposed leaves had significantly lower moisture percentages than the shaded leaves in July, August, and September (fig. 5). This could be attributed to the fact that the sun-exposed leaves lost more water due to their higher transpiration rate (fig. 3). Overall, the highest leaf moisture percentage was in June followed by August, July, and September. The leaf moisture level was well-correlated with the soil moisture content, which was also the highest in June (11 percent), followed by August (9.86 percent), July (6.85 percent) and September (6.41 percent).

Leaf Anatomy

The scanning electron micrographs of sun-exposed and shaded southern live oak leaves are illustrated in figure 6. The adaxial (upper) surfaces were covered with cuticle that was smooth in the sun-exposed leaf (fig. 6A) and rough and furrowed in the shaded leaf (fig. 6B). The smooth cuticle layer acts as an uninterrupted film that protects leaves by diminution of water loss and enhancement of reflection of the sunlight. The abaxial (lower) surfaces were covered with flattened, multicellular, shield-shaped trichomes (leaf hairs) that were much denser and fully differentiated in the sun-exposed leaf (fig. 6C) than in the shaded leaf (fig. 6D). The stomata were more exposed and visible in the shaded leaf (fig. 6D), while the thick trichome layer of the sun-exposed leaf (fig. 6C) acts like a carpet to give protection to stomata against desiccation, against various chemical and physical influences, to protect leaves against being fed upon by animals, and against infestation by parasites. The leaf transverse (cross-section) structure shows that the palisade tissue consisted of three layers of parenchyma cells that were clearly defined and more compactly arranged in the sun-exposed leaf (fig. 6E) than in the shaded leaf (fig. 6F). The compact arrangement of the palisade parenchyma cells in the sun-exposed leaves provided more surface area of leaf interior containing chloroplasts. This resulted in higher chlorophyll content per unit of leaf area (fig. 4), and thus increased photosynthesis efficiency and net photosynthesis rate (fig. 1). The shaded leaf had loosely packed palisade cells (fig. 6F) compared to the sun-exposed leaf (fig. 6E). Also, sun-exposed southern live oak leaves were smaller and glossier than shaded leaves (Data not shown here). This agreed with Kozlowski and Pallardy (1997), who concluded that shade-grown leaves of broad-leaved trees are larger and thinner than sun-grown leaves, providing more efficient light harvesting per unit of dry weight invested. Hence, shaded leaves confer a greater potential for plant growth per unit of leaf dry weight and also have fewer palisade layers than leaves grown in the full sunlight.

CONCLUSIONS

The distinctive anatomical differences between sun-exposed and shaded leaves of southern live oak are mainly attributed

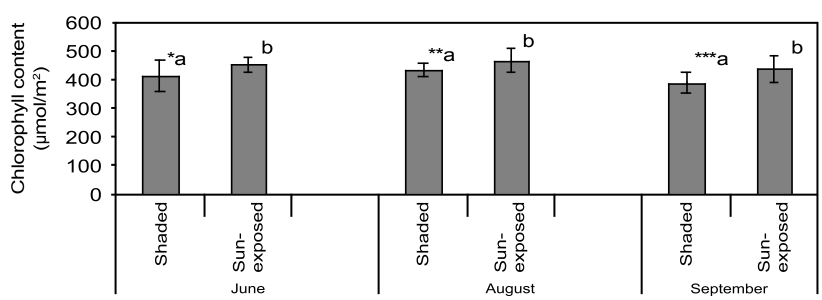

Figure 4—Chlorophyll content of sun-exposed and shaded leaves of southern live oak during a growing season. Note: The means with different letters within each month are significantly different; *p=0.0002, **p=0.0105, ***p=0.0003.

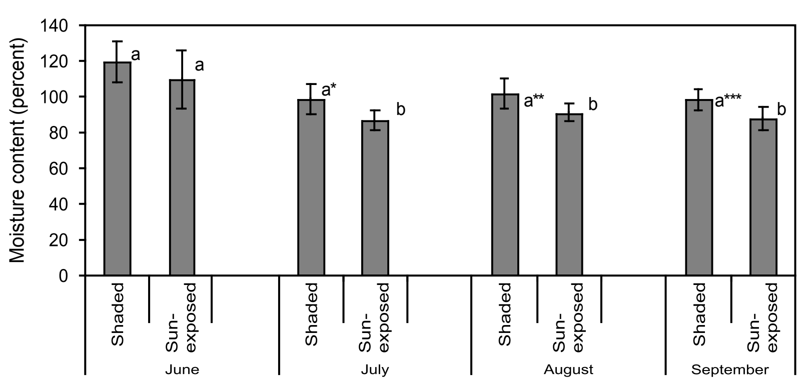

Figure 5—Leaf moisture content of sun-exposed and shaded leaves of southern live oak during a summer season. Note: The means with different letters within each month are significantly different; *p=0.0026, **p=0.069, ***p=0.019.

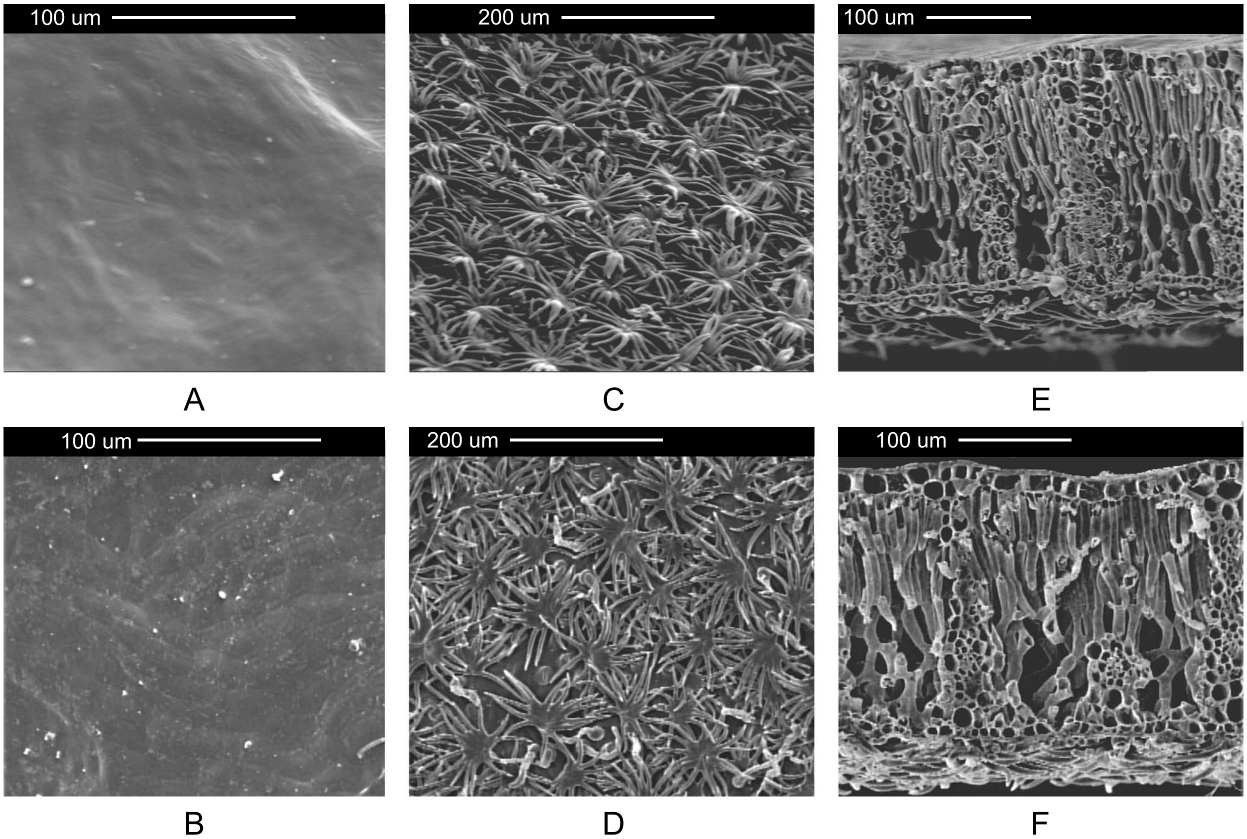

Figure 6—Scanning electron micrographs of sun-exposed and shaded leaves of southern live oak. (A) adaxial surface of a sun-exposed leaf; (B) adaxial surface of a shaded leaf; (C) abaxial surface of a sun-exposed leaf; (D) abaxial surface of a shaded leaf; (E) transverse view of a sun-exposed leaf; and (F) transverse view of a shaded leaf.

to photomorphogenesis and environmental adaptation. Sun-exposed leaves possess a denser trichome layer and highly packed palisade tissues which enhance net CO_2 uptake and chlorophyll content. The trichome layer may function as a mechanical barrier against biotic attack, as an additional resistance to the diffusion of water vapor from leaf interior to the atmosphere, as a reflector reducing the radiant energy absorbed by the leaf, and as an absorber to help screen out harmful UV-B radiation from the sun.

The combined anatomical and physiological characteristics presented in this paper indicate that southern live oaks possess a unique ecological advantage of self-defense against various environmental stresses. The information will be useful to urban forestry and forestry professionals in tree selection for urban and community reforestation. Since live oak is a hardy, evergreen, long-lived, and easily transplanted tree and grows and develops into a mature tree with a large canopy and massive trunk, planting live oak in the right places will provide many ecological and environmental benefits and maximize C storage benefits of urban trees.

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