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Analyzing growth and mortality in a subtropical urban forest ecosystem

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ABSTRACT

Information on urban tree growth, mortality and in-growth is currently being used to estimate urban forest structure changes and ecosystem services such as carbon sequestration. This study reports on tree diameter growth and mortality in 65 plots distributed among four land use categories, which were established in 2005/2006 in Gainesville, Florida, USA and were re-measured in 2009. Models for mortality and in-growth models were developed by grouping species into hardwoods and softwoods. Annual change in tree diameter at breast height growth was analyzed using three tree species groups based on potential height and longevity. Additionally, the four most common tree species in the study area were modeled to explore factors affecting tree growth. The average annual mortality rate in the city was 9.97%. Trees located in Institutional land use/land cover (LULC) had the highest annual mortality rate (19.2%/yr), and commercial had the lowest (3.1%/yr). Overall, growth rates for the study area (0.70 cm/yr) and residential LULC (0.80 cm/yr) were comparable to other studies. Growth rates for trees in forested areas were higher (0.56 cm/yr) than those previously reported. Individual species-level growth rates such as those for *Juniperus virginiana* (1.24 cm/yr) and *Quercus virginiana* (1.08 cm/yr) were different than other species values reported in other studies. Maintenance activities, site conditions, soil properties, tree characteristics, and LULC significantly influenced urban tree growth, mortality, and in-growth. Results can be used to better understand urban forest ecosystem structure and services in medium sized, subtropical cities and to make better decisions regarding planting and maintenance strategies.

1. Introduction

Increased understanding of urban forest structure and its effects on ecosystem services is key to maintaining and enhancing the quality of life in cities. Currently 50% of the world's population resides in cities, so understanding how an urban forest changes over time can provide insights into the socio-ecological dynamics and drivers of these ecosystem services (Petrosillo et al., 2007). For example, urban forest growth and mortality rates are being used to analyze carbon sequestration by urban trees (Escobedo, Varela, Zhao, Wagner, & Zipperer, 2010; Jo & McPherson, 1995), explore land use and climate factors that affect structure (Nowak, Kuroda, & Crane, 2004; Zhao, Escobedo, & Staudhammer, 2010) and to estimate urban wood biomass and waste estimates (MacFarlane, 2009). Information on urban forest mortality can also be used to develop more effective management techniques (Staudhammer et al., 2011).

Growth and mortality of the urban forest is influenced by a number of factors including: species composition, size distribution, condition, site characteristics, human influences, and disturbance (Duryea, Kampf, & Littell, 2007; Escobedo et al., 2010; Heynen & Lindsey, 2003; Rhoades & Stipes, 1999; Staudhammer et al., 2011; Zipperer, Sisinni, Pouyat, & Fresman, 1997). Long-term monitoring of permanent urban forest plots is one method of assessing the individual significance of these factors and their interactions on growth and mortality (Nowak et al., 2004; Staudhammer et al., 2011). Unfortunately, there is little information on long-term changes in subtropical urban forests; what few studies are available focus on northern, temperate regions of the United States (US; deVries, 1987; Jo & McPherson, 1995; Nowak, 1994). Additionally, when information on temperate trees is applied to trees in subtropical climates, estimates of biomass accumulation, tree growth, and subsequent carbon dioxide sequestration might be incorrect (Escobedo et al., 2010; Staudhammer et al., 2011). Therefore, analyzing permanent urban forest plots through re-measurements should provide for more accurate and site-specific mortality, growth, and subsequent biomass estimates that could be used to better understand the climatic, ecological,

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and socioeconomic influences affecting subtropical urban forest ecosystems.

Urban tree mortality has been the subject of relatively few studies, but some studies of street trees in the temperate northeastern and western US and northern England have shown that mortality was related to tree condition, size, age, land use, water and nutrient stress, socio-economic status, community participation, and maintenance practices (Foster & Blaine, 1978; Gilbertson and Bradshaw, 1985; Nowak, McBride, & Beatty, 1990; Nowak et al., 2004; Sklar & Ames, 1985). For instance, Nowak et al. (1990) observed an average morality of 19% for trees along boulevards in Oakland, California, with higher rates (34%) observed adjacent to apartments and public greenspaces. A study of permanent plots in Baltimore, Maryland reported average annual tree mortality of 6.6% and net change in number of live trees of −4.2% (Nowak et al., 2004). Tree size (e.g. small diameter), condition (e.g. poor), and land use/land cover (LULC) contributed to mortality, with the lowest rates occurring in medium- to low-density residential land uses and the highest rates along transportation corridors and on commercial–industrial LULC. In subtropical Houston, Texas the urban forest mortality rate using permanent plots was 3.9%; mortality was significantly higher on developed open land uses versus high intensity land uses, and mortality significantly increased as urban forest tree density increased (Staudhammer et al., 2011).

Growth rates for urban trees have been found to vary substantially depending on land use, bioregion, and species. In a study using trees in public right-of-ways in two Chicago, Illinois (north central US) neighborhoods, diameter growth averaged 1.09 cm/yr for hardwood and 0.51 cm/yr for softwood trees (Jo & McPherson, 1995). Growth rates were reported to average 0.84 cm/yr for Chicago's urban forest (Nowak, 1994) and 0.63 cm/yr for Baltimore, Maryland's urban forest (Nowak et al., 2004). Iakovoglou, Thompson, and Burras (2002) compared growth rates across land uses and city sizes in the US Midwest, and found annual ring width averaged 0.4–0.5 cm (diameter growth of 0.8–1.0 cm/yr), with higher growth rates in city parks followed by residential and commercial sites. Another study by Iakovoglou, Thompson, Burras, and Kipper (2001) found that site, land use, species and age accounted for 49–77% of variation in growth rates of urban trees in the central US and that pavement and bulk density were related to tree growth. A study of 12 *Quercus laurifolia* trees in Florida (subtropical US) reported much higher growth rates of 1.69 cm/yr (Templeton & Putz, 2003). Staudhammer et al. (2011) observed growth rates of 0.44 (*Liquidambar styraciflua*) to 0.90 (*Pinus taeda*) for the most frequently occurring species in Houston, Texas, while the fastest growing tree observed was *Quercus virginiana* (1.2 cm/yr). Land use, tree size and health were found to significantly influence tree growth.

Information on urban tree growth rates are being used in models such as i-Tree ECO/Urban Forest Effects (UFORE; Nowak, Crane, Stevens, & Ibarra, 2002) to estimate urban forest structure and function in subtropical areas (Escobedo et al., 2010). The UFORE model, for example, uses representative diameter growth rates of: 0.87 cm/yr for urban land use, 0.38 cm/yr for remnant natural forests, and 0.61 cm/yr for park-like areas. These urban and park land use growth rates were obtained from the US temperate cities of Chicago, Syracuse, and New York City (deVries, 1987; Nowak, Crane, et al., 2002), and the remnant natural forest growth rates are from the temperate states of Illinois and Indiana also in the US (Smith & Shifley, 1984). However, even within the same climate, growth rates will differ according to genera, site characteristics, and land use classification. Additionally, measured growth rates in urban forests are often greater than those in natural forests, though comparisons among studies are problematic because species composition, methods and age distributions among study sites vary considerably (Staudhammer et al., 2011).

Other vegetation such as nearby trees, shrubs and turf grass can also affect urban tree growth due to space and resource competition (Vrecenak, Vodak, & Fleming, 1989). Urban soil chemical, physical and biological properties such as water stress and low fertility have been reported to affect tree growth (Close, Kielbaso, Nguyen, & Schutski, 1996; Craul, 1999; Kramer & Boyer, 1995; Pouyat, Yesilonis, Russell-Anelli, & Neerchal, 2007; Scharenbroch, Lloyd, & Johnson-Maynard, 2005). Other site conditions such as impervious surfaces beneath the crown, soil compaction and pH affected growth in sugar maples (*Acer saccharum*), and diameter growth was significantly higher in woodlots versus institutional land uses in Michigan, US (Close et al., 1996). Conversely, annual diameter growth was higher for trees of the same species growing on institutional versus natural forest land uses in Virginia, US implying that the effects of soil properties on tree growth are lessened by open-growing conditions (Kramer & Kozlowski, 1979; Rhoades & Stipes, 1999). This effect might be species-specific, however, as growth for several tree species in Florida parking lots declined as impervious area increased, while growth rates for *Q. virginiana* were unaffected by amounts of impervious area (Grabosky & Gilman, 2004).

With few exceptions, long-term studies of the urban forest have been conducted primarily in large cities with temperate climates, and results are being applied to urban forests with differing climates and urban characteristics (Escobedo et al., 2010). Therefore to better address this lack of information, the objective of this study was to measure mortality and growth in a subtropical urban forest in a medium-sized city (population 115,000) using remeasurements of permanent urban forest plots and site-specific data on site characteristics and surface soil properties. This study will explore whether subtropical urban forests are different from temperate ones in terms of growth and mortality rates, and investigate the soil, site and land use/cover factors driving these rates. Specifically, we hypothesize that subtropical urban trees will have greater diameter growth and mortality rates across all urban land uses in comparison to temperate urban trees. Furthermore, growth and mortality rates for subtropical urban forests in smaller cities will be different than those reported in the literature for particular tree species groups and individual species (deVries, 1987; Iakovoglou et al., 2002; Jo & McPherson, 1995; Nowak, 1994; Nowak et al., 2004; Staudhammer et al., 2011).

2. Methods

2.1. Study area

Gainesville has an area of 127 km^2, and is located at 29°39′N and 82°20′W in north-central Florida. The climate is warm, humid, and subtropical with average monthly temperatures of 19.4 °C in January and 33 °C in June, 295 frost-free days per year (Dohrenwend, 1978), and average annual precipitation of 1228 mm (Metcalf, 2004). The elevation is approximately 30 m above sea level and topography varies from gently rolling hills in the northern portion of the study area to nearly level areas in the south that are characterized by seasonally high water tables (Metcalf, 2004; Phelps, 1987). Gainesville lies on the Hawthorne geologic formation in the north and Plio-Pleistocene deposits of the Ocala Uplift lie in the southern part of the study area (Phelps, 1987). Soils are predominantly sandy siliceous, Hyperthermic Aeric Hapludods and Plinthic Paleaquults, which are very sandy (95%), and the rest are composed of different fill material (Chirenje et al., 2003). The study area has many remnant forest patches within city limits that exhibit natural soil and forest characteristics.

2.2. Plot and tree measurements

In 2005 and 2006, 93 randomly located, 0.04 ha plots were established as part of a long-term monitoring study to measure Gainesville's urban forest. In 2009, 65 of the original 93 plots were re-measured (access was denied to 12 plots, and plot center could not be located on 16 others due to landscape changes) following the protocol outlined in Nowak et al. (2004) and Staudhammer et al. (2011). Plot center was re-located using Global Position System coordinates and originally recorded distance and direction to permanent objects (e.g. fire hydrants, sewer caps, telephone poles). Re-measurement errors were minimized by referencing ground-based aerial photos and the measurements of distance and direction to plot center of individual trees within the plot as recorded at the first time of measurement.

All trees located on the plot with a Diameter at Breast Height (DBH; 1.37 m above ground surface) greater than 2.5 cm were measured sequentially starting from due north and rotating clockwise around plot center; direction and distance to each tree from plot center were also recorded. The following data were collected by tree: species, DBH, total tree and tree crown base height, crown ratio (height to crown base over total tree height), crown width in two directions, crown light exposure (CLE) rating (0–5; Bechtold, 2003), percent missing crown, and percent dieback of foliage as a proxy for tree condition. Since tree DBH was of particular interest for this study, a pole marked at 1.37 m was used to reduce measurement error. At a plot level, percent surface cover was visually estimated using the following categories: impervious surfaces, grass, soil, rock (e.g. pervious rock and gravel), water, litter and mulch, herbaceous vegetation (i.e. areas comprised of vegetation that is not grass or shrub cover) and maintained and un-maintained grass (i.e. grassy areas with no indication of mowing or other maintenance). To facilitate analyses, land uses were assigned at the time of first measurement into the following LULC classes: forest (remnants of natural forests), institutional, commercial and residential/vacant. Land use/cover categories were based on urban forest structure, management regime characteristics, and the primary land tenure and use on each plot (Appendix A). Vacant areas without building structures and on-going management were classified as residential when zoned as such by the city.

Sample data from the 2005/2006 and 2009 samples were merged and individual trees present in both samples were matched into a paired tree dataset for growth analyses if they were: (1) at the same direction and distance from plot center, (2) of the same species, and (3) had a greater DBH measurement in 2009 than in 2005/2006. In-growth was defined as the presence of a tree in the 2009 measurement not originally measured in 2005/2006, indicating a new planting or natural in-growth (i.e. a small tree grew above the DBH threshold of 2.5 cm). Mortality, as defined in this study, is the absence of a previously measured tree which was removed or downed since the 2005/2006 sample.

2.3. Soil measurements and analyses

Surface soil characteristics on the plots were sampled during the summer of 2007 using 1.0 m^2 subplots located at plot center. Soil variables such as bulk density, water content, potassium concentration and pH were collected as described in Dobbs (2009). Three soil bulk density samples were collected per subplot to a depth of approximately 10.0 cm using a soil core sampler and slide hammer. Turf and thatch were removed and samples were placed in 5.0 cm diameter, 4.5 cm deep soil tins that were then fresh weighed, oven-dried for 8 h, and then dry weighed. Fifteen randomly located soil cores were collected per subplot from the upper 10 cm of the soil profile to analyze for soil chemical properties by the University of Florida Extension Soil Testing Laboratory using analytical procedures outlined in Dobbs (2009). Soil data were not collected on 17 plots, 8 of which contained no trees and 9 of which had excessive impervious surfaces (i.e. greater than 50%; Dobbs, 2009). Soil variables highly correlated with other parameters were removed to avoid multicollinearity problems. A Principal Components Analysis of urban soil properties indicated that soil pH was highly correlated with soil water content and fertility, and soil potassium with maintenance disturbance (Dobbs, 2009). This result is similar to findings by Scharenbroch et al. (2005) and Kramer and Boyer (1995), who found relationships between soil bulk density, urban morphology, and plant growth. Therefore, soil pH, potassium, bulk density and water content were used in this study to characterize the effects of plot level soil properties on urban forest mortality and growth rates.

2.4. Species groups

Urban forests can have high tree species diversity per unit area (Zipperer et al., 1997). Therefore, analyzing species-level data is impractical due to insufficient sample sizes. To facilitate statistical analyses, all tree species were grouped into three categories based on maximum potential height and longevity as reported in the USDA PLANTS Database (USDA NRCS, 2010): large size-long life span (LL), large size-moderate life span (LM), and medium and small size (MS). A similar protocol was used by Nowak, Stevens, Sisinni, and Luley (2002). Large size trees were those that potentially could attain a height equal or greater than 18.3 m at maturity; medium and small size trees were those that potentially could attain a height less than 18.3 m at maturity. A moderate life span was considered to be less than 250 years and long life span was greater than or equal to 250 years. In addition, four growth models were created for the four most common tree species in the paired tree dataset. Since removed and in-growth tree sample sizes were insufficient for species' groupings, mortality and in-growth models were developed using two classes: hardwoods and softwoods. Palm species were not analyzed due to small sample sizes.

2.5. Diameter growth, mortality and live tree net change rates

Diameter measurements were converted into annual DBH growth rates (cm/yr) by subtracting the 2005/2006 DBH from the 2009 DBH measurement and dividing by the length of time between measurements for each plot. Plots measured in 2006 had an average of 2.83 years between measurements, while plots measured in 2005 had an average of 3.25 years between measurements. Mortality rates were calculated using matched trees as outlined in Nowak et al. (2004) and annualized mortality, m, was calculated as $m = 1 - (N_1/N_0)^{1/t}$ (Sheil, Burslem, & Alder, 1995), where t is the time interval, N_0 is the total number of living trees in matched plots from the 2005/2006 sample, and N_1 is the number of live trees in matched plots that survived to 2009. Rates of annual net change in live trees (Table 1) were calculated similarly, using total populations counts at the beginning and end of the measurement period.

2.6. Statistical analyses

Statistical modeling of growth, mortality and in-growth were conducted using plot level factors from the original 2005/2006 measurements and included LULC type, number of trees per hectare (TPH), basal area per hectare, and percent surface covers on each plot. In addition, tree level factors from the original 2005/2006 measurement and plot level soil pH, potassium, soil bulk density and water content collected in 2007 were also used. Growth models were created for each of the three species groups and for the four most frequent tree species in the dataset. These four species comprised 43% of paired trees and included: *Q. laurifolia* (76 trees), *Quercus nigra* (62 trees), *Pinus elliottii* (62 trees) and *P. taeda* (57 trees). Two mortality and two in-growth models were generated by grouping species into hardwood and softwood types.

The distribution of recorded growth rates was strongly right-skewed, and thus, growth rate values were transformed using a square root function in the species group models and the natural logarithm plus one for individual species models. These transformations stabilized the variance and allowed assumptions underlying statistical models to be met. There were 46 trees (8% of paired trees) that were found to have negative growth rates and were re-assigned a growth rate of zero for modeling purposes and to approximate actual biological growth. These measurements were likely the result of DBH re-measurement error and/or tree stem shrinkage (Pastur, Lencinas, Cellini, & Mundo, 2007). The majority of these 46 trees were hardwoods (98%) from remnant natural forested plots (63%), and most were multi-stemmed, which makes them more prone to measurement errors.

Approximately half of matched plots were sampled with a 3-year interval between measurements and half with a 3–4-year interval. Whether a plot was sampled during the first or second year of the initial measurement period was based on field logistics and efficiency, so we conducted preliminary *t*-tests to test for differences between samples taken in the two measurement intervals. We tested all plot level variables and found minor differences in TPH, soil water content, and soil bulk density between intervals. We also examined the distribution of plots sampled over LULC for the two intervals and found it to be fairly uniform (30–70%) for all categories except forest, which was more heavily sampled (80%) during the 3-year interval. When taking into account LULC in *t*-tests, we found no significant differences between measurement intervals, except with maintained grass in forested plots. Therefore, to ensure that any systematic sampling bias in the data was taken into account, a variable indicating the interval between measurements was added to models.

Growth rates were modeled using the SAS procedure PROC MIXED (SAS Institute Inc., 2008). A general linear mixed model was estimated, using plot and tree level characteristics as predictor variables and a random effect to account for correlations between trees in the same plot. A Kenward–Rogers adjustment was made to the degrees of freedom to better account for the effect of the autocorrelation in the data (Littell, Milliken, Stroup, Wolfinger, & Schabenberger, 2006). Mortality and in-growth models used a generalized linear mixed model with a negative binomial distribution to characterize the response variable. Models were fit with the SAS procedure PROC GLIMMIX (SAS Institute Inc., 2008) using plot level characteristics as predictor variables. While the growth rates modeled implicitly included the period of time between measurements in their calculation, mortality and in-growth were modeled as counts taken over the time between measurements. Therefore, a variable designating time between measurements, as well as its interactions with plot level variables, was included in the mortality and in-growth models.

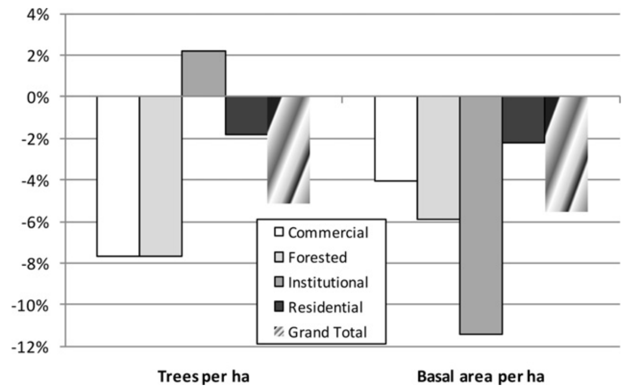

Fig. 1. Average percent net change in live trees per hectare and basal area per hectare by land use/cover and city total for Gainesville, Florida from 2005/2006 to 2009.

Statistically significant effects and their interactions were identified with a type I error level (α) of 0.05, and models were compared with the corrected Akaike's information criteria (AICC; the small sample bias-corrected version of Akaike's information criteria fit statistic). To provide evidence that the data arose from these models, the final estimated models had the lowest AICC values and included only those effects that were significant ($\alpha < 0.05$). To determine significant differences in growth and mortality rates between LULC types, Fischer's Least Significant Difference statistical procedure was used ($\alpha < 0.05$).

3. Results

From 2005/2006 to 2009, the overall average annual mortality was 9.97% (Table 1). When comparing trees within the 65 re-measured plots, there was a net annual loss of approximately 11 live trees (4.26 trees/ha/year) and 0.65 m^2/ha of basal area (0.25 m^2/ha/year). In 2005/2006, 754 trees were measured in these 65 plots and by 2009, 128 (17%) trees were lost through death or removal; most tree loss (64% of the 128 trees) was from forest, followed by residential (26%), commercial (5%), and institutional (5%) LULCs. Plots in 2009 contained a total of 717 trees; 626 of the trees recorded at the time of first measurement were re-measured allowing for matching of individual trees. Twenty nine trees which were dead at the time of the first measurement were matched, but were not used for growth modeling, and 91 new trees were considered in-growth.

On average, the city's live tree density and basal area per hectare decreased by 5% (Fig. 1). Commercial and forest plots had the largest average decreases in trees per hectare (7.7%). Institutional plots had the largest decrease in basal area per hectare (11.4%) but also had a slight increase in trees per hectare (2.2%). Growth rates were highest on residential plots (0.82 cm/yr) and lowest on commercial and forest plots (0.56 cm/yr; Table 1). Growth rates for individual

Table 1
Plot count, average annual growth and mortality rates, and average annual net change in live trees for all re-measured trees between 2005/2006 and 2009 in Gainesville, Florida by land use and cover categories (standard errors shown in parentheses).

Land use	Commercial	Forest	Institutional	Residential	City total
Percent of total number of trees in 2009	5.7%	58.5%	13.2%	22.6%	100%
Number of matched plots	7	15	16	27	65
Number of plots with trees	2	15	11	23	51
Number of live trees in 2009	36	398	93	161	688[a]
Average growth rate (cm/yr)	0.56 (0.05)	0.56 (0.10)	0.67 (0.13)	0.82 (0.08)	0.70 (0.06)
Average mortality rate (%)	3.12% (3.12%)	5.41% (1.31%)	19.2% (12.1%)	9.12% (4.38%)	9.97% (3.28%)
Average annual net change in live trees	2.14% (4.14%)	−2.59% (0.98%)	−5.09% (9.73%)	−3.18% (5.06%)	−3.21% (3.05%)

[a] Does not include 29 dead trees.

Table 2
Top four species ranked by frequency and top eight species ranked by highest average annual growth rate (AGR) for trees in Gainesville, Florida from 2005/2006 to 2009.

Rank	Species (number of trees)	Annual growth rate (cm/yr)	Standard error
By frequency			
1	*Quercus laurifolia* (76)	0.69	0.13
2	*Quercus nigra* (62)	0.77	0.20
3	*Pinus elliottii* (62)	0.68	0.12
4	*Pinus taeda* (57)	0.44	0.09
By growth rate			
1	*Juniperus virginiana* (4)	1.24	0.36
2	*Quercus virginiana* (16)	1.08	0.36
3	*Lagerstroemia indica* (12)	0.98	0.27
4	*Celtis laevigata* (20)	0.85	0.30
5	*Ostrya virginiana* (5)	0.84	0.36
6	*Liquidambar styraciflua* (35)	0.61	0.19
7	*Acer rubrum* (36)	0.58	0.15
8	*Cinnamomum camphora* (19)	0.36	0.12

species were highest for *Juniperus virginiana* (1.24 cm/yr), *Q. virginiana* (1.08 cm/yr), and *Lagerstroemia indica* (0.98 cm/yr) (Table 2).

3.1. Growth rate models

Growth rates for trees characterized as large-size-long life (LL) were influenced by plot level factors for percent maintained and un-maintained grass, as well as average tree crown width and percent missing crown (Table 3). Growth was positively influenced by all factors with the exception of percent missing crown. Growth rates for large size-moderate life span (LM) trees were influenced by plot level factors for basal area, percent maintained grass, soil bulk density, and soil water content. Tree level factors of DBH, average crown width, percent missing crown and CLE also influenced LM trees (Table 3). Overall the LM growth rates were positively influenced by every factor except DBH and percent missing crown. Growth rates for medium- and small-sized (MS) trees were negatively influenced by DBH and positively by CLE (Table 3).

Growth rates for *P. taeda* were negatively influenced by DBH and positively by crown ratio (Table 4). Growth rates for *P. elliottii* were also influenced by DBH and crown ratio, as well as plot level factors for LULC and percent un-maintained and maintained grass (Table 4). There were no *P. elliottii* found in commercial land uses, but its growth rates were influenced by all other LULCs. *Q. laurifolia* and *Q. nigra* growth rates were positively influenced

Table 3
Test of fixed effects for model of annual diameter at breast height (DBH) growth by tree species group in Gainesville, Florida from 2005/2006 to 2009.

Effect	Estimate	Num DF	Den DF	*F* value	*Pr* > *F*
Large potential size, long life span trees (LL), *n* = 126					
%Maintained grass	0.0044	1	121	18.44	<0.0001
%Un-maintained grass	0.0056	1	121	7.06	0.0089
Average crown width	0.0046	1	121	10.24	0.0018
% Missing crown	−0.0018	1	121	4.55	0.0350
Large potential size, moderate life span trees (LM), *n* = 284					
Basal area per hectare	0.0006	1	275	10.28	0.0015
%Maintained grass	0.0041	1	275	23.11	<0.0001
Diameter at breast height	−0.0159	1	275	18.03	<0.0001
Average crown width	0.0075	1	275	18.63	<0.0001
% Missing crown	−0.0015	1	275	6.46	0.0116
Crown light exposure	0.0415	1	275	13.66	0.0003
Soil bulk density	0.2251	1	275	9.38	0.0024
Soil water content	0.0096	1	275	15.59	<0.0001
Medium potential size trees (M), *n* = 120					
Diameter at breast height	−0.0170	1	117	5.80	0.0176
Crown light exposure	0.0707	1	117	17.05	<0.0001

Num DF, numerator degrees of freedom; Den DF, denominator degrees of freedom.

Table 4
Test of fixed effects for model of annual diameter at breast height (DBH) growth of four most frequent tree species in Gainesville, Florida from 2006 to 2009.

Effect	Estimate	Num DF	Den DF	*F* value	*Pr* > *F*
Pinus taeda, *n* = 57					
Diameter at breast height	−0.0084	1	54	6.83	0.0157
Crown ratio	0.3157	1	54	6.22	0.0116
Pinus elliottii, *n* = 62					
Land use/cover – forest	0.2097	2	55	8.01	0.0009
Land use/cover – institutional	0.2508	2	55	8.01	0.0009
Land use/cover – residential	0.0000	2	55	8.01	0.0009
%Maintained grass	0.0050	1	55	29.94	<0.0001
%Un-maintained grass	0.0054	1	55	15.47	0.0002
Diameter at breast height	0.0107	1	55	11.66	0.0012
Crown ratio	0.1721	1	55	4.95	0.0303
Quercus laurifolia, *n* = 76					
Crown light exposure	0.0566	1	74	4.55	<0.0001
Quercus nigra, *n* = 62					
%Un-maintained grass	−0.0143	1	59	8.04	0.0063
Crown light exposure	0.0543	1	59	11.98	0.0010

Num DF, numerator degrees of freedom; Den DF, denominator degrees of freedom.

by CLE. *Q. nigra* growth rates were also negatively influenced by percent un-maintained grass (Table 4). For *Q. laurifolia*, the most frequently occurring tree in Gainesville (13% of all trees), growth rates were found to be greatest, though not significantly, in residential plots (1.07 cm/yr) and lower in commercial (0.59 cm/yr), forest (0.44 cm/yr), and institutional (0.49 cm/yr).

Soil variables resulted in few significant effects in growth models when considering the lowest AICC models. However, models with slightly higher AICC values were explored to further investigate significant effects. For LL trees, a model including significant effects for DBH, soil potassium and soil pH, indicated that soil potassium and percent missing crown negatively influenced growth. In an alternative model for *Q. nigra* with a higher AICC value, growth significantly decreased as trees per hectare, soil bulk density, and soil potassium increased, while growth significantly increased with soil pH.

3.2. Mortality and in-growth models

Two mortality models were developed for hardwood species. Hardwood mortality model 1 indicates that trees per hectare alone significantly influenced mortality (Table 5), with mortality increasing as tree density increased. Hardwood mortality model 2 included LULC, litter and mulch, and plantable space, as well as trees per hectare and maintained grass, which both interacted with the time between measurements. Residential plots had significantly more trees removed versus commercial, forest, and institutional plots

Table 5
Test of fixed effects for model of mortality for hardwood and softwood tree groups in Gainesville, Florida from 2005/2006 to 2009.

Effect	Num DF	Den DF	*F* value	*Pr* > *F*
Hardwood mortality model 1				
Trees per hectare	1	63	18.40	<0.0001
Hardwood mortality model 2				
Land use/cover	3	54	4.62	0.006
Trees per hectare	1	54	16.73	0.0001
Time between measurements	1	54	4.6	0.0365
Trees per hectare × time	1	54	6.21	0.0158
% Maintained grass	1	54	3.39	0.0713
% Maintained grass × time	1	54	4.52	0.0381
Plantable space	1	54	3.7	0.0598
Duff and mulch	1	54	3.88	0.0539
Softwood mortality				
Trees per hectare	1	63	5.03	0.0284

Num DF, numerator degrees of freedom; Den DF, denominator degrees of freedom.

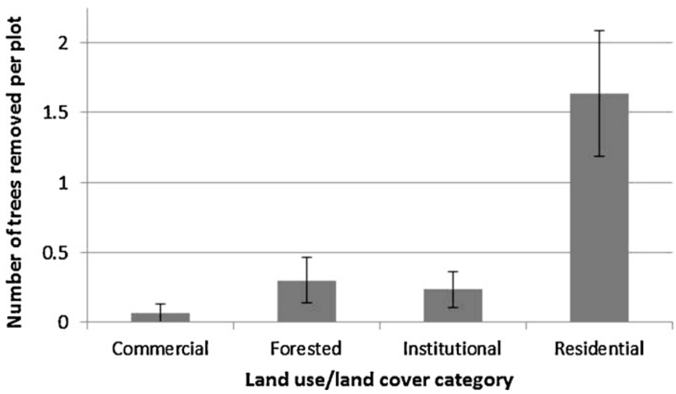

Fig. 2. Least square mean predicted number of trees removed per plot by time between measurements in 2005 and 2006 and land use/cover category in Gainesville, Florida (computed with all other variables in the model adjusted to mean values).

(Fig. 2). There were significantly less trees removed as the percentage of maintained grass increased; however, this trend was only significant when there were 4 years between measurements (Fig. 3a). There were significantly more removals as trees per hectare increased; however, this pattern was only significant when there were 3 years between measurements (Fig. 3b). There were more trees removed as plantable space and area of litter and mulch increased. While the model using trees per hectare had the lowest AICC (174.9 versus 176.9, indicating slightly more evidence that the data arose from this model), the second model is of interest because it indicates that there were significant differences among LULC categories.

There were very few softwood trees removed during the study period (19 trees from 5 plots), so only simple models were explored. The best model of softwood mortality indicated that more trees were removed as trees per hectare increased (Table 5). Individual species models could not be estimated due to the paucity of data in most species; however, annual mortality rates for the most common species in Gainesville were found to range from 0.86% to 6.1% (Table 6).

There were few new softwood trees measured in 2009 (9 plots with 14 total new softwood trees). The best model for the softwood tree group indicated that trees per hectare was the only significant predictor, which positively affected in-growth (Table 7). However, hardwood in-growth model 1 also indicates that, similar to softwoods, trees per hectare significantly and positively influenced hardwood in-growth (Table 7). Hardwood in-growth model 2 shows that trees per hectare, LULC, percent unmaintained grass, and time between measurements influenced in-growth. Land use/cover and percent unmaintained grass both interacted with the time between measurements (Fig. 4). When there were 4 years between measurements, forested plots had significantly less

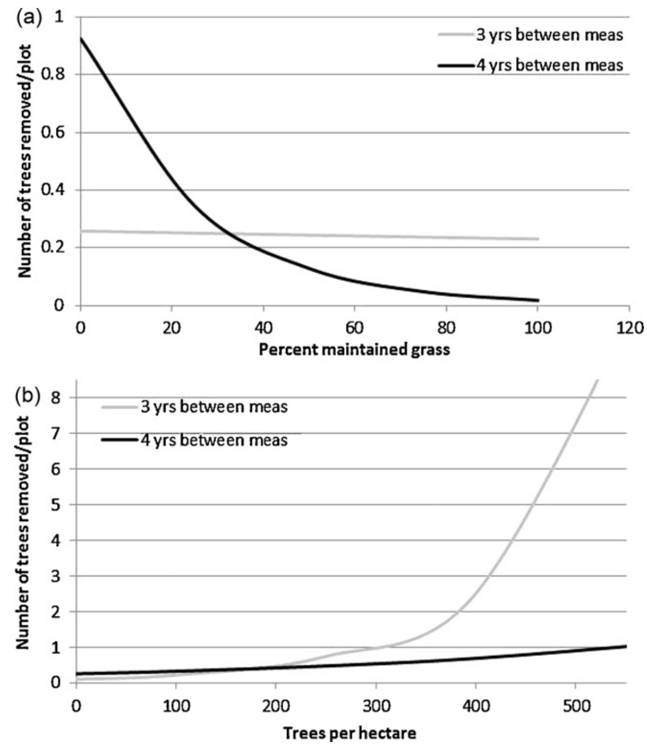

Fig. 3. Least square mean predicted number of trees removed per plot versus (a) percentage maintained grass and (b) trees per hectare, by time between measurements in Gainesville, Florida (computed with all other variables in the model adjusted to mean values).

Table 7
Test of fixed effects for model of in-growth for hardwood and softwood tree groups in Gainesville, Florida from 2005/2006 to 2009.

Effect	Num DF	Den DF	*F* value	*Pr* > *F*
Hardwood in-growth model 1				
Trees per hectare	1	63	14.08	0.0004
Hardwood in-growth model 2				
Trees per hectare	1	54	33.28	<0.0001
Time between measurements	1	54	0.66	0.4209
% Unmaintained grass	1	54	0.00	0.9573
% Unmaintained grass × time	1	54	6.19	0.016
Land use/cover	3	54	4.69	0.0056
Land use/cover × time	3	54	2.99	0.0391
Softwood in-growth				
Trees per hectare	1	63	5.75	0.0194

Num DF, numerator degrees of freedom; Den DF, denominator degrees of freedom.

in-growth versus residential. When the time between measurements was 3 years, forested plots had significantly less in-growth versus institutional and residential plots (Fig. 4). There was significantly more in-growth as the percentage of unmaintained grass

Table 6
Annual mortality rates for the ten most common trees in Gainesville, Florida, ranked by mortality rate.

Rank	Species	Annual mortality rate	Proportion of matched trees in land use/land cover			
			Commercial	Forest	Institutional	Residential
1	*Gordonia lasianthus*	6.10%	0.0%	5.9%	0.0%	0.0%
2	*Prunus caroliniana*	6.05%	3.0%	0.6%	9.2%	16.8%
3	*Nyssa biflora*	4.99%	0.0%	5.3%	3.9%	0.0%
4	*Quercus nigra*	4.88%	0.0%	16.0%	2.6%	2.3%
5	*Quercus laurifolia*	4.05%	36.4%	9.0%	23.7%	10.1%
6	*Celtis laevigata*	3.38%	0.0%	4.2%	0.0%	3.8%
7	*Acer rubrum*	3.26%	0.0%	7.3%	9.2%	15.3%
8	*Pinus taeda*	3.02%	0.0%	11.8%	6.6%	7.6%
9	*Pinus elliottii*	0.97%	0.0%	13.2%	14.5%	3.1%
10	*Liquidambar styraciflua*	0.86%	0.0%	8.7%	0.0%	3.1%

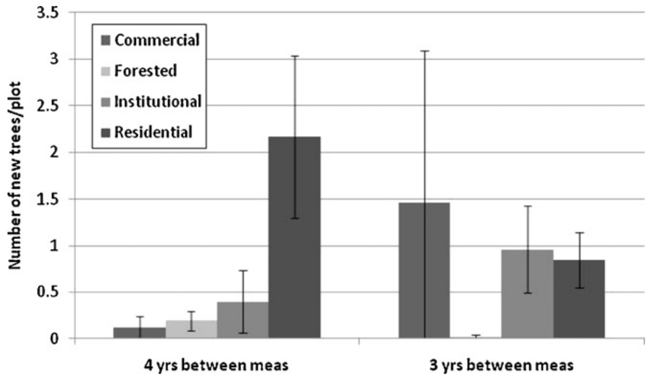

Fig. 4. Least square mean predicted number of new trees per plot (in-growth) by time between measurements and land use/cover category in Gainesville, Florida (computed with all other variables in the model adjusted to mean values).

increased, however this difference was only apparent when examining data that had 3 years between measurements (Fig. 5). While the more parsimonious hardwood in-growth model 1 had a slightly lower AICC (170.7 versus 172.8) – indicating slightly stronger evidence that the data arose from this model – hardwood in-growth model 2 indicates that there were significant differences among LULC and as a result might have implications for the influence of maintenance activities on in-growth.

4. Discussion

Our analyses show that Gainesville's subtropical urban forest had both an overall loss in tree population over time in terms of live tree density and a net decrease in basal area. Commercial and remnant natural forest plots had the highest rates of tree loss and moderate decreases in basal area per hectare (Fig. 1). Conversely, institutional plots were the only LULC to increase in trees per hectare, but had the largest decrease in basal area. This implies that trees were planted or replaced on institutional land uses, while more trees were removed/downed than naturally re-generated on forest plots. This might be due to natural succession in remnant forest patches within urban landscapes, where shade intolerant trees are replaced by dominant, shade intolerant species, and other changing environmental conditions associated with urbanization (Templeton & Putz, 2003; Zipperer et al., 1997).

Growth rates for this study's subtropical urban trees were different than those reported in temperate urban forests in the Midwestern US region by Iakovoglou et al. (2002), where radial growth estimates were higher in city park sites, followed by residential

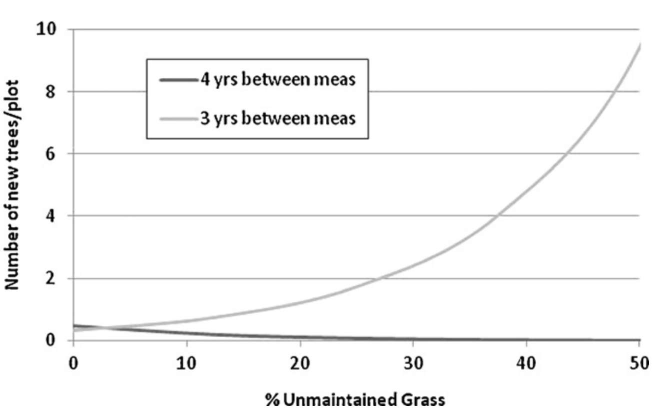

Fig. 5. Least square mean predicted number of new trees per plot versus percentage unmaintained grass by time between measurements in Gainesville, Florida (computed with all other variables in the model adjusted to mean values).

and commercial sites (Table 1). In Gainesville, higher diameter growth rates were found on residential (0.82 cm/yr) and institutional (0.67 cm/yr), with lower rates in forest (0.56 cm/yr), and commercial (0.56 cm/yr) sites. On the other hand, the "manicured" city parks sites studied by Iakovoglou et al. (2002) might have experienced higher amounts of maintenance activities, such as fertilization and pruning, in comparison to the subtropical sites represented in this study. Tree growth rates in this study were also substantially greater for remnant natural forests than those used by the UFORE model (0.38 cm/yr), but contrary to our hypothesis, they were similar to growth rates used in the model for open-grown urban (0.87 cm/yr) and park-like (0.61 cm/yr) land uses (Table 1; Nowak, Crane, et al., 2002). Growth rates for particular tree species in this study were different from other studies. *Q. laurifolia* growth, for example, was estimated at 1.07 cm/yr, which was substantially less than the 1.69 cm/yr reported by Templeton and Putz (2003). Also, growth rates for two other common species in Gainesville, *Q. nigra* (0.77 cm/yr) and *L. styraciflua* (0.61 cm/yr), were greater than those reported in Houston (0.57 and 0.44 cm/yr, respectively; Staudhammer et al., 2011). The higher growth rates reported in this study versus others are likely due to the longer growth season of this subtropical area.

Overall annual mortality rates (9.97%) during the analysis period were higher than those reported in similar studies in Baltimore (6.6%; Nowak et al., 2004) and Houston (4.7%; Staudhammer et al., 2011). Nonetheless, comparisons of this study's mortality rates by size classes to that of Nowak et al. (2004) indicate similar rates. In general, a high mortality was found for small sized trees (0–15.2 cm DBH) and low mortality for medium sized trees (15.3–61.0 DBH). There were significant differences between LULC when comparing mortality rates for hardwood trees (Mortality model 2; Table 5). Overall, this study's average mortality rates were highest in institutional plots (19.2%) and lowest in commercial (3.1%); however, institutional plots actually exhibited a positive net annual change in number of live trees over the study period (Table 1). Our observed mortality rates differ from those reported in Nowak et al. (2004) in Baltimore, where mortality was higher on transportation or commercial–industrial land uses versus on medium to low-density residential land uses. Our results also differ from those reported in Staudhammer et al. (2011), since morality rates in Houston's urban forest were affected by land cover and tree density and were lower in urban high- and low-density residential than in open spaces and wetlands.

Higher mortality rates were found for the two most frequently occurring hardwood species (*Q. nigra* and *Q. laurifolia*) versus those of the two most frequently occurring softwood species (*P. taeda* and *P. elliottii*; Table 6). For both softwood and hardwood species, mortality rates increased as trees per hectare increased (Table 5), though for hardwoods, this trend was only significant when there was a 3-year interval between plot measurements (Fig. 3a). This trend is likely related to the fact that most forested plots were measured at the 3-year interval, and only forested plots were observed to have values greater than 380 trees/ha. This may imply that the relationship between density and mortality was stronger for remnant natural forested areas, a trend that has been observed in studies of natural and urban forest tree mortality (Templeton & Putz, 2003). We also observed a significant decline in hardwood mortality as percent maintained grass increased; however, this relationship was only significant when the time between measurements was 4 years (Fig. 3b). This trend is likely related to the fact that most residential plots were measured at the 4-year interval, and only residential and commercial plots were observed to have percent cover of maintained grass >70%. This may imply that the relationship between maintained grass and removals was stronger for residential and commercial land uses. For hardwood species, least square mean predictions, which take all other variables in the model into account, indicated that residential plots had significantly higher mortality rates than that those from forested plots.

Similar to mortality results, in-growth was significantly and positively affected by tree density, a result similar to that reported in Staudhammer et al. (2011). Institutional plots had the highest increase and residential plots had the lowest decrease in trees per hectare on a net basis, and model-based least square mean predictions of in-growth indicated significantly higher in-growth in residential and institutional plots versus forested plots. The number of new trees was also positively correlated with the percentage of unmaintained grass, but only where 3 years elapsed between measurements (Fig. 5). This trend may be driven by forested plots, which were more often measured at a 3-year interval, and also tended to have higher unmaintained grass percentages. This may imply that the relationship between unmaintained grass and new trees was stronger for remnant natural forested areas, where grass may be an indicator of site quality.

Plot level factors such as soil and tree density in terms of basal area only affected growth in the LM model. However, tree level factors related to crown measurements (e.g. average crown width, percent missing crown, CLE or crown ratio) were significant in all growth models, and CLE and DBH were significant in 4 of the 7 growth models; DBH was significant for the two common *Pinus* species, whereas CLE was significant in the two common *Quercus* species. Iakovoglou et al. (2001) also found that site and land use as well as tree species and age accounted for 49–71% of variation in urban tree growth rates. These authors also reported significant relationships between growth rates and the number of nearby trees and mechanical injury to trees from maintenance activities.

Trees in the LM and M categories and *Quercus* had positive growth effects with higher CLE, indicating better growth rates in open-grown environments. Trees in the LM and M categories and *P. taeda* had lower growth rates with higher DBH, which is to be expected, as trees senesce with age. Growth of *P. elliottii*, on the other hand, was positively related to DBH. This result, however, may have been influenced by a lack of larger individuals in our sample; whereas we sampled *P. taeda* up to a DBH of 71 cm (average DBH = 32.3 cm), *P. ellitottii* in the sample were all less than 56 cm DBH (average = 29.6 cm). If our sample had captured larger individuals, we would have expected to see the same decline in growth associated with tree age. On the other hand, Iakovoglou et al. (2001) did not detect a significant relationship between the number of nearby trees and growth rates in residential trees. These authors suggest that this might be due to the linear arrangement of these trees, which could be indicated by lower CLE as measured in our study.

Results from the LL and *P. elliotii* growth models suggest that once established (i.e. grown to 2.5 cm DBH), tree growth in the urban environment is affected by surrounding surface covers such as the amount of maintained and unmaintained grass. This is possibly due to factors caused by activities associated with lawn and turf maintenance such as increased fertilization and irrigation, as well as the tree's crown size and exposure to light (Dobbs, 2009; Iakovoglou et al., 2001).

The LM growth model results suggest that growth is also affected by maintained grass and crown characteristics like missing crown foliage and crown width. Similar to LL trees, LM growth is positively influenced by soil water content and soil bulk density, basal area and crown diameter. Interestingly, increased growth was associated with increased soil bulk density, however this result was not expected, as decreased bulk density is known to improve soil physical properties such as water infiltration and soil biological processes which are conducive to plant growth (Scharenbroch et al., 2005). On the other hand, increased bulk density was found by Dobbs (2009) on plots with high percent maintained grass which may suggest multicollinearity between these variables that may have neutralized this effect. Moreover, the sandy textures and bulk density values for this study are from the upper 10 cm of the soil profile; therefore these measurements might not reflect the effects on growth by root-soil interactions of trees with deeper roots. Iakovoglou et al. (2001) also found significant relationships between urban tree growth rates and soil bulk density in urban trees in the Midwestern US.

Diameter growth was positively influenced by CLE and initial crown diameter in the MS growth model, suggesting that for these trees, size and the amount of light exposure are more important than other factors that were analyzed and might be related to the tree's growing space and competition with other trees (Vrecenak et al., 1989). Crown light exposure was limited in the average *P. taeda* where only 2 sides out of a possible 5 were exposed to light, possibly explaining why tree crown ratio influenced growth for this LM-categorized specie more significantly since taller, dominant trees have greater potential for increased light which contributes to growth (Templeton & Putz, 2003). For *P. elliottii*, a positive relationship between DBH growth and initial DBH is unusual, especially due to the fact that the average 2005/2006 DBH of *P. elliottii* (29.6 cm) describes a medium-sized tree by size class; however, this might be a reflection of the lack of larger individuals sampled in our study. Iakovoglou et al. (2001) found that proper tree spacing, health and protection from mechanical injury enhanced growth rates for mature urban trees in the central US. Similar to that study, our DBH growth model generated for LL trees (Table 4) indicated that the presence of grassy surface covers – or associated maintenance activities – positively influenced diameter growth in *P. elliottii*. On the other hand, both oak species are categorized as LM trees and both oak growth models were positively influenced by CLE. Plot and tree level characteristics affected diameter growth in all species groups and the individual species model, while plot level characteristics like trees per hectare and LULC affected mortality and in-growth.

Greater sampling intensity would likely have improved growth, mortality, and in-growth models. However, due to limited access and insufficient plot re-location information, this was not possible. An important analysis would have been to show the growth and mortality differences for the same species growing on remnant natural forest and urban LULC conditions in addition to values reported for the entire city, as this might provide useful information on the effects of urban conditions or resource competition dynamics. Unfortunately, the sample size was insufficient for such analyses. In addition, our soil sampling design is likely not capturing the spatial heterogeneity of soils within plots and individual tree-site condition effects (Pouyat et al., 2007). Also, soil samples from the subsurface might have better revealed the effects of soil bulk density on urban forest change. However, given the costs, access issues, and unacceptable ground disturbance activities associated with a more intensive soil sampling design on private properties, our method is a first step towards understanding soil effects on urban forests, and is consistent with methods used in other recent studies of urban soils (Dobbs, 2009).

Another limitation of this study was that re-measurements of diameter at breast height can differ from actual tree growth due to measurement error and changes in tree physiology, especially over short (3–4 years) time intervals (Avery & Burkhart, 1983; Pastur et al., 2007). Changes in the height of mulch and litter below a tree can change the breast height measurement used for subsequent measurements resulting in subsequent measurements being taken at a different height. To account for this, tree core increments are often measured to determine tree growth. However, tree coring in urban areas is usually not appropriate due to damage to private trees and issues of liability.

5. Conclusion

The growth rates presented in this study can be applied to subtropical urban forests of medium-sized cities. Using this study's growth rates in urban forest structural and ecosystem service models could also reduce bias and variance in biomass estimates in subtropical cities with high tree cover and those with greater amounts of remnant natural forests. However, care should be taken when assuming that growth and mortality rates can simply be explained by landuse and climate (e.g. rain, length of growing season). Our results suggest that there are complex underlying processes responsible for growth and mortality, though mortality rates were comparable by size class and land use to similar studies (Nowak et al., 2004; Staudhammer et al., 2011). On the other hand, growth estimates for individual species, in particular for many of the more common species in our subtropical study area, were very different from those used in the UFORE/ECO model (Nowak, Crane, et al., 2002).

This study provides information on how tree and site characteristics affect urban and peri-urban tree growth in subtropical Gainesville, Florida according to tree size and longevity. Both plot and tree level characteristics can be used to estimate diameter growth except for MS trees, which were found to be only influenced by tree level characteristics. Maintained grass, as an alternative to other ground cover vegetation types, might enhance growth rates in many types of urban trees because understory vegetation does not compete for light and might additionally be associated with maintenance activities that contribute to the growth of surrounding trees such as irrigation, fertilization, and edging of new vegetation or vines that can grow around a tree's stem. However, issues related to turf management such as over-fertilization and watering as well as other community values (e.g. use of native species) should be considered (Dobbs, 2009).

Results from this study could also be used to analyze carbon sequestration in subtropical urban forests (Escobedo et al., 2010), generate improved post-hurricane urban forest debris estimates (Staudhammer et al., 2011), and develop site-specific supply curves for urban green waste generation for bionenergy applications (Dobbs, 2009; MacFarlane, 2009). Growth information could also be used in the development of urban tree planting strategies such as in selecting trees with appropriate crown sizes or the optimal trees appropriate for specific sites (i.e. soils and available light source) since many plot and tree level factors affect tree growth. Additional insights could be provided into identifying factors that influence tree canopy and crown size and subsequent shading which reduces building energy use and ambient air temperatures, thus decreasing the need for energy from fossil-fuel-based power plants (Pandit & Laband, 2010). Results from this study can be used to manage urban forests in a way that optimizes their provision of ecosystem services and to better understand the factors that maximize urban forest growth and minimize mortality.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.landurbplan.2011.10.004.

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