INFLUENCE OF CHINESE PRIVET (*LIGUSTRUM SINENSE* LOUR.) ON RIPARIAN FORESTS OF THE SOUTHERN PIEDMONT: NET PRIMARY PRODUCTIVITY, CARBON SEQUESTRATION, AND NATIVE PLANT REGENERATION

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DISSERTATION ABSTRACT

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The spread of invasive, nonnative vegetation in the Southeast has been identified as a critical concern for the maintenance of ecosystem biodiversity and impacts on the forest industry. One example of such a species is Chinese privet (*Ligustrum sinense* Lour.), whose rapid expansion in riparian forests of the Southeast has been reported. Unfortunately, there has been minimal research on impacts of this species to forest functions and processes such as net primary productivity (NPP), carbon sequestration and native plant regeneration.

Research plots were selected in the Piedmont physiographic province of western Georgia that represented a continuum of understory Chinese privet invasion from 0-100%. Above- and belowground net primary productivity (NPP) and standing crop biomass was estimated. Additionally, leaf, stem, and fine root carbon concentrations were determined to estimate carbon sequestration trends. Lastly, the proportion of native plants in the regeneration forest layer was determined. Each of these forest functions and processes was compared with the proportion of Chinese privet found in the understory.

Understory Chinese privet invasion (25-79% of total stems) was accompanied by a significant increase in total NPP and carbon sequestration that was strongly influenced by belowground NPP. The initial increase in total NPP and carbon sequestration was followed by a numerical, but not significant, decrease when >80% of total understory stems were Chinese privet. This trend was likely influenced by the lack of a diverse forest stratum found under dense mid-story Chinese privet. When the understory was composed of 40% Chinese privet, it appeared to suppress native plant regeneration to below 50% of total. This has implications for long-term impacts on the replacement of native canopy trees, NPP, and carbon sequestration. Overall, the results suggest that processes and functions such as net primary productivity and carbon allocation will ultimately be diminished in Southeastern riparian forests invaded by Chinese privet due to the loss of large, native canopy trees that are not replaced due to limited native species regeneration.

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CHAPTER I

INTRODUCTION

Invasive, Nonnative Plants

Landscape alterations induced by invasive, nonnative plants are of growing concern to land managers, scientists, and concerned citizens. The economic impacts of invasive, nonnative plants and animals may be as great as $120 billion per year (Pimentel et al. 2005). Moreover, Wilcove et al. (1998) noted that invasive, nonnative plant species are the second highest threat to threatened and endangered species in the United States after habitat loss. Because they have been introduced into areas outside of their natural range, nonnative plants lack natural enemies such as insects and diseases that tend to keep populations in balance (Miller 2003). For example, Morse et al. (1995) estimated that 5,000 nonnative plant species have become invasive, displacing native vegetation in natural ecosystems found in the United States.

Nonnative trees, shrubs, vines, grasses, ferns and forbs invade forests and fields, decreasing forest productivity, hampering forest use and degrading diversity and wildlife habitat (Miller 2003). Impacts by nonnative, invasive plants to forest ecosystems, especially related to recruitment of native plant seedlings and general ramifications for succession, native biodiversity, and ecosystem structure, may be both short- and long-term (MacDonald et al. 1989, Gordon 1998, Katz and Shaforth 2003, Ens and French 2008). Better understanding the shifts in composition and structure that result from suppression of native plant regeneration, and how this may drive changes in productivity and biogeochemistry is imperative (Katz and Shaforth 2003, Valery et al. 2004), especially as management priorities and solutions are sought for nonnative, invasive plants.

Many of the invasive, nonnative plant species in the Southeast U.S. were introduced from far eastern and subtropical Asia (Stapanian et al. 1998). Chinese privet (*Ligustrum sinense* Lour.), a member of the Olive family (Oleaceae), was introduced from China and Europe in the early to mid-1800s as an ornamental plant and has become naturalized throughout the Southeast as well as along the east coast to New England (USDA 2008). It is an aggressive, invasive semi-evergreen to evergreen woody shrub that forms dense thickets in riparian forests and along fencerows (Miller 2003). In particular, Chinese privet invades floodplain forests because of its reproductive and competitive adaptations that include seed dispersal by birds, root suckering, shade tolerance, and wide-ranging soil nutrient requirements (Langeland and Burkes 1998). Although it becomes established easily in disturbed areas, Chinese privet also has the capability to invade understories of undisturbed forests (Langeland and Burkes 1998, Merriam and Feil 2002), explaining its rapid expansion across the Southeast.

Due to Chinese privet's capacity to out-compete and displace native vegetation, large-scale ecosystem modifications may occur (Merriam and Feil 2002, USDA 2008). For example, in regions where Chinese privet invasions have occurred, the usual pattern of species succession is halted and dense stands of Chinese privet form in the place of native hardwood regeneration (Merriam and Feil 2002). Furthermore, Chinese privet may diminish timber production, may impact carbon sequestration and export, and may alter the nutrient transformation capacity of riparian forests.

The rate and extent of invasive, nonnative plant dispersal is strongly influenced by current landscape characteristics and past land uses, especially related to shifts in land use from agriculture to urban / suburban (Hutchinson and Vankat 1997, Ward 2002, Loewenstein and Loewenstein 2005, Burton and Samuelson 2007). For example, Loewenstein and Lowenstein (2005) found that urban plots in Columbus, Georgia were characterized by greater numbers of nonnative species, including Chinese privet. Developing and rural plots in west Georgia also had abundant Chinese privet, perhaps related to remnant populations from past land use. Lundgren et al. (2004) reported that past land use was the strongest predictor of invasive, nonnative cover and richness and that current land development and physical soil characteristics were strongly correlated with invasive, nonnative cover and richness. Similarly, abandoned agricultural fields and home sites were closely tied with expansion of Chinese privet in the Oconee River basin in north Georgia (Ward 2002).

Net Primary Productivity

Net primary productivity (NPP) describes increases in organic material after losses to respiration over a unit of time. Rates of NPP influence cycling of nutrients, yield of merchantable timber, and carbon sequestration. Plants allocate NPP aboveground or belowground in response to limited resources, such as nutrients and water. Differences in allocation may assist a plant in maintaining balances between carbon and other nutrients and between leaf area, available sunlight, moisture, and nutrients to that leaf area (Kimmins 2004). As an example, in poor soil conditions, plants may increase root biomass at the expense of stem productivity to provide increased potential for exploration of nutrients and water resources (Keyes and Grier 1981). Aboveground NPP (ANPP) includes changes in stem increment and the production of litterfall, including both leaves and reproductive structures. Belowground NPP (BNPP), or changes in fine root production, is less well studied, but is an important component of total NPP (Vogt et al. 1986). For example, fine roots are variable in their response to water and nutrients and can serve as sensitive bioindicators of disturbance effects on ecosystem structure and function (Fahey et al. 1999, Cavalcanti and Lockaby 2005).

Invasion of forest ecosystems by nonnative species may alter availability of nutrients, water, and light (Crooks 2002) that, in turn, may directly influence NPP. Ehrenfeld (2003) noted that invasive plant species frequently increase a community's biomass and net primary production. For instance, net primary production of Chinese tallow (*Sapium sebiferum* (L.) Small) forests has been reported to be comparable to that of many native deciduous forests in the southern United States (Cameron and Spencer 1989) and double that of coastal prairies (Harcombe et al. 1993). No research on the influence of Chinese privet on riparian forest NPP has been found.

Carbon Allocation and Sequestration

The carbon cycle may be described as the movement of carbon between the biosphere, atmosphere, oceans, and geosphere. Carbon is stored in sinks, processed, and released back into the cycle. Net primary productivity of vegetation acts as a sink of carbon with plants absorbing carbon dioxide from the atmosphere during photosynthesis and releasing it to the atmosphere during respiration. Forests, especially in the temperate zone, have been identified as the potential missing sink in the global climate carbon balance (Sedjo 1990). Another source of carbon is decomposition of soil organic matter (leaf litter, coarse woody debris) in the forest floor. Carbon allocation by plants regulates forest ecosystem carbon cycling through the shifting of photosynthesis products between respiration and biomass production, short-lived and long-lived tissues, and aboveground and belowground components (Litton et al. 2006). Carbon sequestration is the process through which carbon dioxide (CO_2) from the atmosphere is absorbed by trees, plants and crops through photosynthesis, and stored as carbon in biomass (tree trunks, branches, foliage and roots) and soils (US EPA 2008).

Carbon cycling in floodplains and wetlands is of great interest not only because it is responsible for the main energy inputs into small order streams (Fisher and Likens 1973), but also because of the growing body of knowledge on carbon sequestration and global climate change impacts. Wetlands, including riparian corridors, have the ability to sequester carbon due to their high productivity and large belowground stocks of organic carbon (US Climate Change Technology Program 2003).

Carbon is stored both above- and belowground in living and dead plant and animal materials. Carbon modelers categorize soil organic carbon into three pools: (1) an active pool, including fresh plant material and root exudates with residence times of about a year, (2) a slow pool that includes microbes and decomposes with residence times of 1 – 100 years, and (3) a passive pool that includes microbes and decomposes with residence times of 100 – 1000 years (Parton et al. 1987).

A change in type of vegetation may result in changes to root distribution patterns and aboveground community structure (Reynolds et al. 1997, Sala et al. 1997, Jackson 1999). These biomass allocation changes may influence carbon, nutrient, and water cycling. Consequently, study of both above- and belowground biomass and production is necessary in order to fully describe ecosystem changes. At the watershed level, shifts in species composition in a floodplain may also impact associated stream ecosystems in regard to carbon input and export. Ziegler and Brisco (2004) compared carbon dynamics in a forested versus agricultural watershed. They determined that both organic matter source and nutrient concentrations significantly impact bioavailable carbon in small streams.

There is limited information on amounts of carbon sequestered by wetlands, including riparian areas (US Climate Change Technology Program 2003). Ecosystem function and diversity can be better estimated with increased knowledge of biomass, net primary productivity, and soil carbon storage, especially amid global climate change concerns (Clark et al. 2001).

Native Plant Regeneration

When a nonnative plant is introduced into a community, its effects may range from competitive replacement of one or more species to the loss or reduction of entire strata (Lundgren et al. 2004). Invasive, nonnative plants that are successful in becoming established in new ecosystems have demonstrated their ability to out-compete and replace native vegetation (Merriam and Feil 2002, Reinhart et al. 2006, Galbraith-Kent and Handel 2008). There are many examples of shifts in native species regeneration due to nonnative species invasion and these include Green Sri Lanka privet (*Ligustrum robustum walkeri* Decne.) in the forests of La Reunion Island (Lavergne et al. 1999), Nepalese browntop (*Microstegium vimineum* Trin. A. Camus) in southeastern forests of the USA (Loewenstein and Loewenstein 2005, Oswalt et al. 2007), Cinnamon (*Cinnamomum verum* J. Presl.) in tropical forests in the Seychelles (Kueffer et al. 2007), Amur honeysuckle (*Lonicera maackii* (Rupr.) Herder) in eastern North America (Gorchov and Trisel 2003), Norway maple (*Acer platanoides* L.) in northeastern forests of the USA (Galbraith-Kent and Handel 2008), and Chinese privet (*Ligustrum sinense* Lour.) in southern forests (Merriam and Feil, Loewenstein and Loewenstein 2005, Burton et al. 2005).

The loss of native species recruitment may have long-term impacts including a decrease in species diversity (Wilcove et al. 1998, McKinney and Lockwood 1999, Lundgren et al. 2004), a loss of habitat that may be detrimental to native flora and fauna (Wilcove et al. 1998), a reduction of forest structural complexity (Luken and Thieret 1996, Burton et al. 2005), and diminished NPP and carbon sequestration potential (Naeem et al. 1994, Hector et al. 1999, Costanza et al. 2007). Conversely, invasions by nonnative species may result in enhanced NPP, increased standing crop biomass, and increased nitrogen mineralization (Ehrenfeld 2003). The need to better understand impacts of Chinese privet on native plant regeneration in riparian forests is critical due to its rapid expansion across the Southeast, its likely impacts on habitat diversity, ecosystem processes, and merchantable timber regeneration, and the need for targeted management of Chinese privet invaded areas. Although some invasive, nonnative species appear to proliferate after small-scale and large-scale disturbances (Parker et al. 1993, Davis et al.

2000, Meekins and McCarthy 2001, Bartuszevige et al. 2007), Chinese privet has the potential to become readily established with or without disturbance due to its bird assisted seed dispersal (Langland and Burks 1998). Brown and Pezeshki (2000) noted that invasive species such as Chinese privet may be tolerant of environmental conditions such as dense shade and flooding and pose a prominent threat to bottomland ecosystems by disrupting natural competition and succession.

Objectives

Although its impact is expanding across the Southeast, the influence of Chinese privet on riparian system functions and processes has not been well studied. A 2.5 year study was undertaken in an effort to better understand modifications to net primary productivity, carbon sequestration and allocation, and native vegetation regeneration accompanied by varying levels of Chinese privet invasion. Specifically, the objectives were:

1) To determine how increasing densities of Chinese privet influence above- and belowground net primary production;
2) To determine Chinese privet's impact on carbon sequestration in riparian systems; and
3) To document the influence of Chinese privet on native vegetation regeneration.

This dissertation is divided into three main topics: net primary productivity, carbon sequestration and allocation, and native plant regeneration with each topic comprising an individual chapter. Chapter 2 describes changes in riparian forest productivity along a continuum of understory Chinese privet invasion (0-100% of total understory stems). Forest productivity was estimated using litterfall, annual increases in stem biomass, and fine root productivity. Leaf area index, soil bulk density, nitrogen mineralization (Mitchell 2008), and water chemistry measurements were also collected to identify relationships with forest productivity. Relationships between reference conditions, medium (25-79% of total understory), and high levels of Chinese privet invasion (>80% of total understory) are explored.

Chapter 3 investigates the relationship between understory Chinese privet invasion and corresponding levels of carbon sequestration and changes in carbon allocation. Carbon concentrations (mg kg^{-1}) for litterfall, stems, and fine roots were used to estimate carbon allocation and sequestration, based on standing crop biomass and net primary productivity, respectively. Significant curvilinear relationships between understory Chinese privet and carbon sequestration in litterfall and fine roots are described.

Additionally, the influence of Chinese privet on native plant regeneration is discussed in Chapter 4. Specific thresholds related to native plant suppression are correlated with proportion of understory Chinese privet, numbers of Chinese privet stems per hectare, and total basal area. Lastly, Chapter 5 presents a synthesis of the research and results contained in each chapter. Suggestions for future research are also provided.

METHODS

Study Plot and Design

A total of sixteen 0.04 ha circular plots were established in six watersheds located in Muscogee and Harris Counties in the Piedmont physiographic province, western

Georgia, USA (Fig. 1, Table 1). The underlying geologic formation among research plots was similar and soils in the research watersheds included Chewacla (Fine-loamy, mixed, active, thermic Fluvaquentic Dystrudepts), Vance (Sandy-clay-loam, fine, mixed, semiactive, thermic Typic Hapludults), and Toccoa (Coarse-loamy, mixed, active, nonacid, thermic Typic Udifluvents) (NRCS 2008). Research plots were occupied by uneven-aged deciduous forests that were composed of vegetation species typical of southern Piedmont forests and that were similar among research plots (Table 1). The climate of the study site is humid with temperatures ranging from winter lows of 0º C to summer highs of greater than 32º C (cdo.ncdc.noaa.gov/dlyp/DLYP). Annual precipitation is approximately 127 cm (Franklin et al. 2002).

Research plots were selected to represent a continuum of 0 to 100% Chinese privet stems in the understory (Fig. 2). Plots were separated into three categories based on the proportion of Chinese privet: Reference, Medium, and High plots having 0, 25-79 and >80% respectively. These categories were partitioned into ranges of understory privet invasion that allowed for comparisons between differing stages of invasion and where significant statistical differences were detected. Additionally, predominant land use for each research watershed was characterized using percent impervious surface as described by Crim (2007). Land use classifications were forested, rural, developing, and urban (Table 1).

One subplot of 5 m x 5 m was established at each research plot to study understory dynamics and one subplot of 3 m x 3 m was established to sample fine roots (Fig. 1). Data were collected from November 2004-May 2007. Period 1 and 2 results report the first 15 months (annualized) and the final 15 months (annualized) respectively.

Separating results in this manner allowed for the capture of growth at the beginning and end of growing seasons from 2004-2007. Periods were analyzed in combination, as well as separately, to discern differences that may have occurred due to variability in rainfall or other factors. If no statistical differences existed between sampling years, results are reported as years combined.

Temperature and Light

Precipitation data were obtained from the National Oceanic and Atmospheric Administration weather station located at the Columbus, GA airport (http://cdo.ncdc.noaa.gov/dly/). Relative moisture conditions were determined using the Palmer drought index (http://www.drought.noaa.gov/palmer.html) for each week from November 2004 through April 2007. This index calculated drought or excess moisture conditions on average temperature and precipitation of the area.

Two StowAway TidbiT Temp Data Loggers (Onset Computer Corporation, Pocasset, MA) were deployed per plot, one on the soil surface and one approximately 5 cm below the soil surface within the sub-plot for belowground productivity. Sensors collected data hourly from April 2005 through April 2007. One HOBO Light Intensity Data Logger (Onset Computer Corporation, Pocasset, MA) was installed 1.5 m above the soil surface in the center of each plot. Light measurements were recorded every 35 minutes for the duration of the study.

Bulk Density

Bulk density was determined using the method described by Blake and Hartge (1986). A known volume (cm^3) of mineral soil in the upper 11 cm of soil profile was collected at three systematically selected locations within the 0.04 ha plot. The sample was then dried at 105º C for 48 hours or until constant mass was achieved, weighed, and bulk density was calculated as Mg / m^3.

Leaf Area Index

Canopy and mid-canopy foliage from the most common trees found at each 0.04 ha plot was collected in July of 2006. The Delta T video imaging system was used to measure leaf area index (LAI) (Delta-T Devices LTD, Burwell, Cambridge, England). Foliage was oven-dried for 72 hours at 70º C and dry weight was recorded. LAI was calculated by multiplying sampled leaf area by the annual foliar litterfall production.

Chinese Privet Dry Weight Equation

Chinese privet dry weight equations were developed since this species was a primary focus and no equations were available. Chinese privet stems ranged in size from 4.8 – 15.24 cm DBH and were sampled during the height of the growing season (July 2005 and 2006). All stems collected were located under a closed canopy on the campus of Auburn University. Auburn University is located in the same ecoregion as the research plots. In the field, trees were cut at the base, measured for height, and separated into foliage and woody biomass and weighed. A sub-sample of foliage and stems was dried and weighed to correct field weights for moisture content. The dry weight equation derived by sampling Chinese privet stems was used to estimate Chinese privet contribution to carbon dynamics, $y = 0.1214x^{2.4919}$ ($R^2=0.97$, $p<0.001$) (Fig. 3).

Table 1. Research plots and watershed characteristics.

Watershed	Research Plot (% Understory Chinese privet)	Dominant Species	Predominant Land Use (% Impervious Surface)
Blanton Creek	BLN 1 (0) BLN 2 (0) BLN 3 (0)	*Acer rubrum* *Liquidambar styraciflua* *Liriodendron tulipifera* *Ostrya virginiana* *Carpinus caroliniana* *Fagus grandifolia* *Cornus florida* *Morus rubra*	Forested (1.41)
Mulberry Creek	MU1-1 (91) MU1-2 (76) MU1-3 (29)	*Ligustrum sinense* *Carpinus caroliniana* *Liquidambar styraciflua* *Acer negundo* *Quercus nigra* *Ulmus alata* *Diospyros virginiana*	Rural (3.77)
Roaring Branch	RB1 (35) RB2 (82) RB3 (92)	*Ligustrum sinense* *Acer rubrum* *Ostrya virginiana* *Quercus nigra* *Ulmus alata* *Prunus serotina* *Prunus caroliniana* *Liquidambar styraciflua* *Liriodendron tulipifera* *Platanus occidentalis*	Urban (30.30)
Standing Boy	SB2-1 (86) SB2-2 (88)	*Ligustrum sinense* *Carya spp.* *Ostrya virginiana* *Liquidambar styraciflua* *Quercus nigra* *Liriodendron tulipifera* *Acer negundo*	Developing (3.41)
Standing Boy	SB4-1 (99) SB4-2 (100) SB4-3 (98)	*Ligustrum sinense* *Carpinus caroliniana* *Liriodendron tulipifera* *Acer rubrum* *Acer negundo* *Ilex americana*	Developing (3.33)
Sand Creek	SC1 (65) SC2 (48)	*Ligustrum sinense* *Liriodendron tulipifera* *Acer rubrum* *Prunus serotina* *Liquidambar styraciflua* *Quercus nigra*	Rural (1.24)

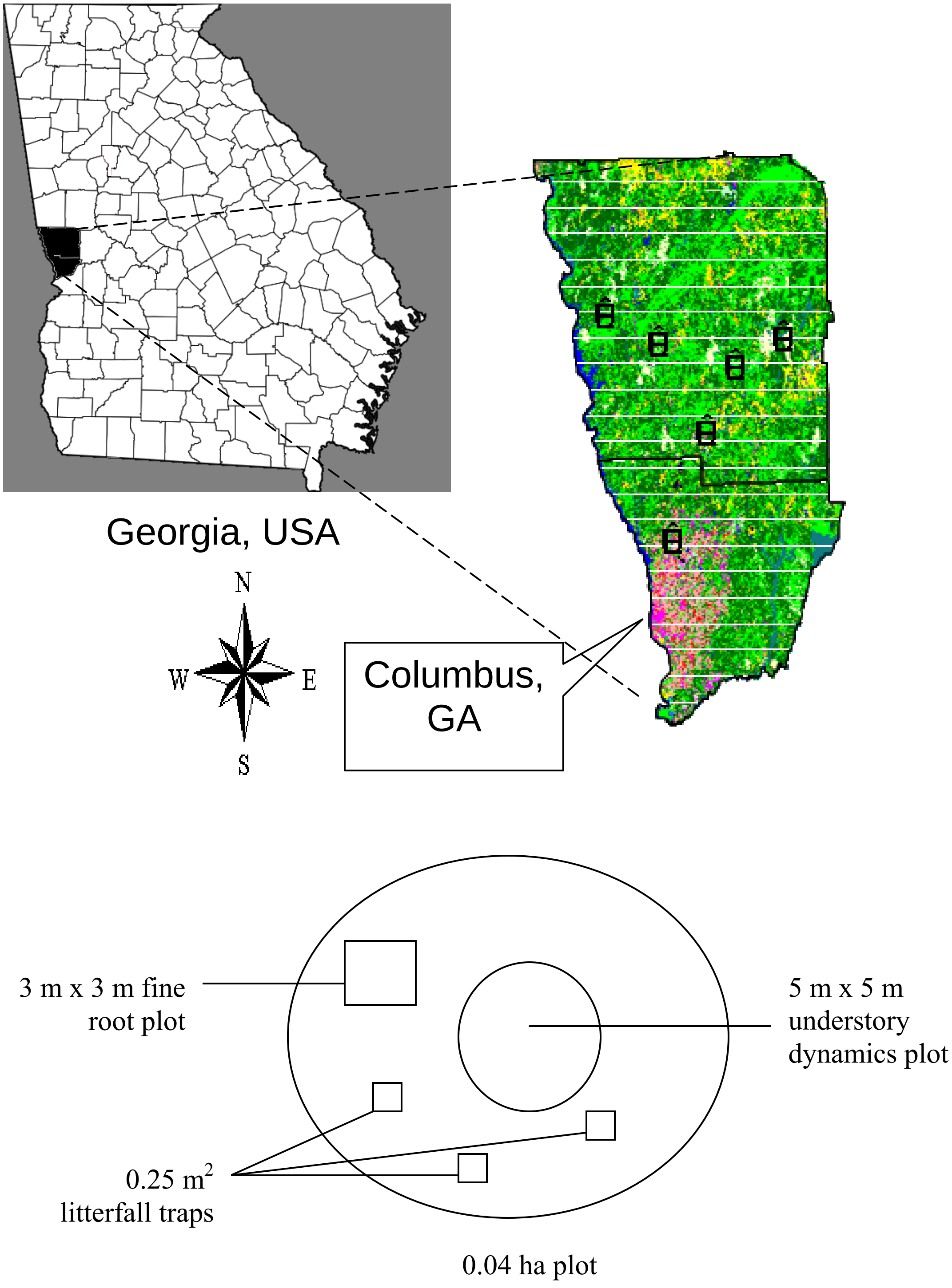

Figure 1. Location of research watersheds in West Georgia and plot layout.

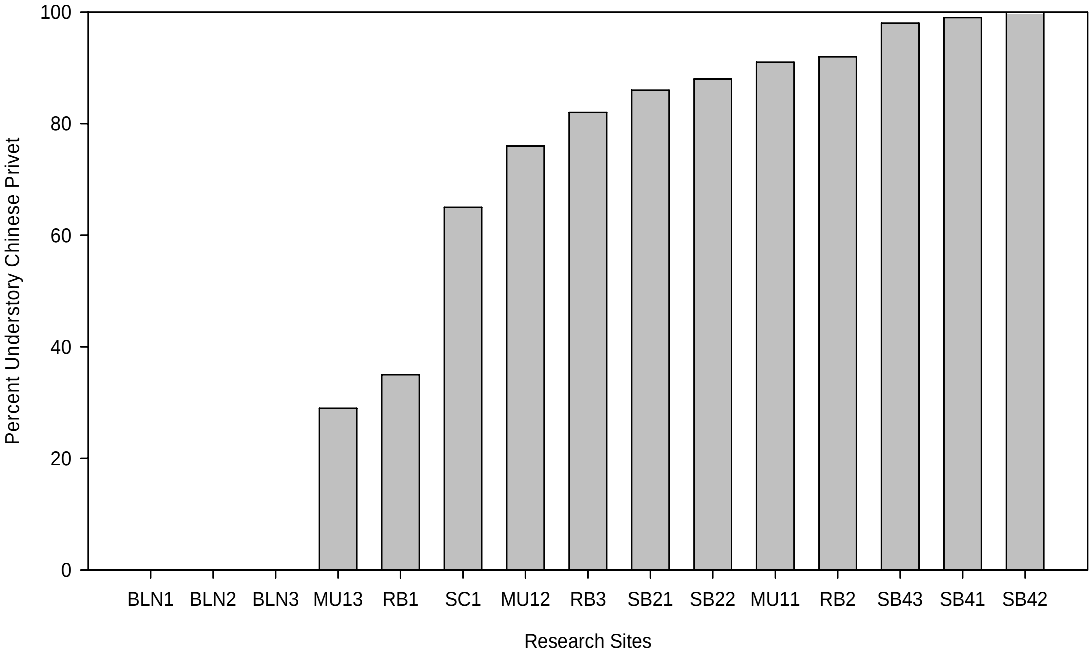

Figure 2. Percent Chinese privet occupying understory at each research plot.

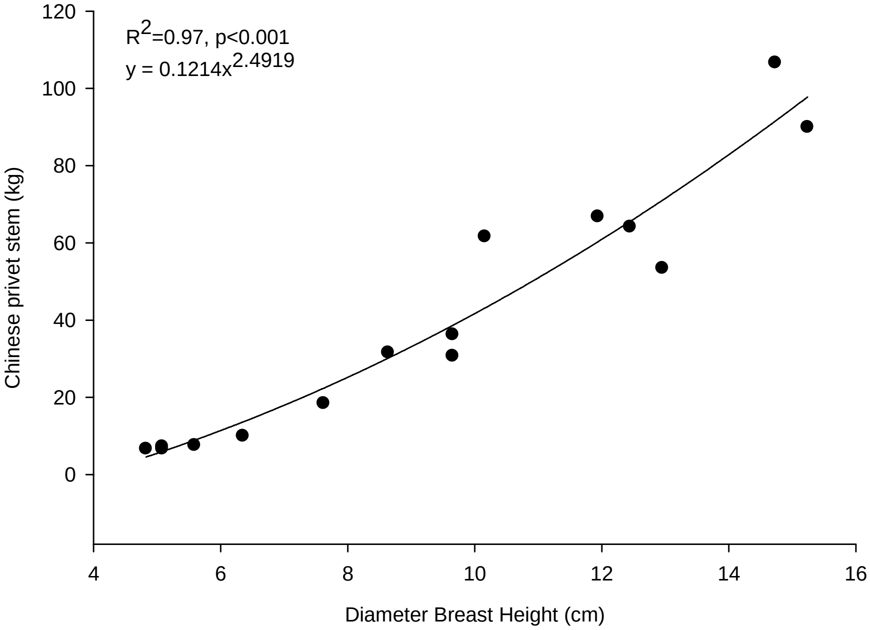

Figure 3. Significant regression relationship between Chinese privet stem mass and DBH.

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CHAPTER II

INFLUENCE OF CHINESE PRIVET ON PRODUCTIVITY OF RIPARIAN FORESTS OF THE SOUTHERN PIEDMONT

INTRODUCTION

Invasive, nonnative plants

Nonnative trees, shrubs, vines, grasses, ferns, and forbs invade forests and fields, decreasing forest productivity, hampering forest use, and degrading diversity and wildlife habitat (Miller 2003). Morse et al. (1995) estimated that 5,000 nonnative plant species have become invasive, displacing native vegetation in natural ecosystems found in the U.S. Economic impacts of invasive, nonnative plants and animals may be as great as $120 billion per year (Pimentel et al. 2005). In spite of the magnitude of the problem, we do not clearly understand how critical forest processes and functions are altered by successful invasions. Understanding the ecological basis for the success of invasives is particularly critical in riparian forests since these encompass a broader array of functions than many other forest ecosystems. We have some insights regarding impacts of invasives on regeneration of native plant species and general ramifications for succession, native biodiversity, and ecosystem structure (MacDonald et al. 1989, Gordon 1998, Katz and Shaforth 2003). We can postulate that shifts in composition and structure drive changes in productivity and biogeochemistry (Katz and Shaforth 2003, Valery et al.

2004). Consequently, the totality of impacts from aggressive invasive, nonnative species is profound and underscores the importance of better understanding the functional ramifications of that proliferation.

Many of the invasive, nonnative plant species in the Southeast were introduced from far eastern and subtropical Asia (Stapanian et al. 1998). Chinese privet (*Ligustrum sinense* Lour.) is an aggressive, invasive, shrub that forms dense thickets in riparian forests and along fencerows (Miller 2003). The species was introduced from China and Europe in the early to mid-1800s as an ornamental plant and has become naturalized throughout the Southeast as well as along the east coast to New England (USDA www.invasivespeciesinfo.gov). It is a semi-evergreen to evergreen member of the Olive family (Oleaceae) that may grow to 9 m in height. Chinese privet successfully invades floodplain forests because of reproductive and competitive adaptations that include seed dispersal by birds, root suckering, shade tolerance, and wide-ranging soil-nutrient requirements (Langeland and Burkes 1998). Although it becomes established easily in disturbed areas, Chinese privet also has the capability to invade understories of undisturbed forests (Langeland and Burkes 1998, Merriam and Feil 2002), explaining its rapid expansion across the Southeast.

Woody plant species in a minimally disturbed, Southern Piedmont floodplain forest typically include river birch (*Betula nigra* L.), sycamore (*Platanus occidentalis* L.), sweetgum (*Liquidambar styraciflua* L.), winged elm (*Ulmus alata* Michx.), and green ash (*Fraxinus pennsylvanica* Bush.). If succession is allowed to proceed without disturbance, a stable community of regional oak-hickory (*Quercus – Carya*) species will appear (Hodges 1998). However, in regions where Chinese privet invasions have occurred, the usual pattern of species succession is halted and dense stands of Chinese privet form in the place of native hardwood regeneration (Merriam and Feil 2002).

Due to Chinese privet's capacity to out-compete and displace native species, large-scale ecosystem modifications may occur (Merriam and Feil 2002, USDA www.invasivespeciesinfo.gov). Alteration of floodplain ecosystem processes impacts floodplain functions, potentially decreasing the value of floodplains to society. As an example, it is possible that Chinese privet may cause major reductions in timber production, may impact carbon sequestration and export, and may alter the nutrient transformation capacity of riparian forests.

Current landscape characteristics and past land uses influence the rate and extent of invasive, nonnative plant dispersal, especially related to shifts in land use from agriculture to urban / suburban (Hutchinson and Vankat 1997, Ward 2002, Loewenstein and Loewenstein 2005, Burton and Samuelson 2007). Loewenstein and Lowenstein (2005) found that urban plots in Columbus, GA were characterized by greater numbers of nonnative species, including Chinese privet. Developing and rural plots in west Georgia also had abundant Chinese privet, perhaps related to remnant populations in place from past land uses such as home sites or abandoned agricultural fields. Developing plots were designated based on land use change from agriculture or forest to urban or suburban cover with 9-23% transitional land use. Rural plots were characterized by a predominant land use of second growth mixed forest, pine plantations, and pasture with few dwellings and small communities. Lundgren et al. (2004) reported that past land use was the strongest predictor of invasive, nonnative cover and richness. They also noted that current land development and physical soil characteristics were strongly correlated with invasive, nonnative cover and richness. Similarly, abandoned agricultural fields and home sites were closely tied with expansion of Chinese privet in the Oconee River basin in north Georgia (Ward 2002).

Net Primary Productivity

Net primary productivity (NPP) describes increases in organic material after losses to respiration over a unit of time. Rates of NPP influence cycling of nutrients, yield of merchantable timber, and carbon sequestration. Plants allocate NPP aboveground or belowground in response to limited resources, such as nutrients and water. Differences in allocation may assist a plant in maintaining balances between carbon and other nutrients and between leaf area, available sunlight, moisture, and nutrients to that leaf area (Kimmins 2004). As an example, in poor soil conditions, plants may increase root biomass at the expense of stem productivity to provide increased potential for exploration of nutrients and water resources (Keyes and Grier 1981). Aboveground NPP (ANPP) includes changes in stem increment and the production of litterfall, including both leaves and reproductive structures. Belowground NPP (BNPP), or changes in fine root production, has been less studied, but is an important component of total NPP (Vogt et al. 1986). For example, fine roots are variable in their response to water and nutrients and can serve as sensitive bioindicators of disturbance effects on ecosystem structure and function (Fahey et al. 1999, Cavalcanti and Lockaby 2005).

Invasion of forest ecosystems by nonnative species may alter availability of nutrients, water, and light (Crooks 2002), that in turn may directly influence NPP. Ehrenfeld (2003) noted that invasive plant species frequently increase a community’s biomass and net primary production. As an example, NPP of Chinese tallow (*Sapium sebiferum* (L.) Small) forests has been reported to be comparable to that of many native deciduous forests in the southern United States (Cameron and Spencer 1989) and double that of coastal prairies (Harcombe et al. 1993). No research on the influence of Chinese privet on riparian forest NPP has been found.

Objective and Hypotheses

The objective of this research was to determine how increasing densities of Chinese privet influence above- and belowground NPP. It is hypothesized that, as Chinese privet understory stem densities increase, aboveground NPP will decline due to changes in stand structure (fewer large overstory trees). However, BNPP in the upper 11 cm of soil is expected to increase as a result of higher fine root densities associated with dense clumps of Chinese privet.

METHODS

Forest Productivity

Total NPP was estimated by summing total aboveground and belowground productivity. Aboveground productivity was estimated as total litterfall plus stem production. Total litterfall was estimated as the sum of leaf litter plus reproductive litter. Finally, BNPP was estimated by summing all increases in fine root biomass (0.1-3.0 mm diameter) occurring between sampling increments.

Aboveground Productivity

Litterfall was collected monthly from November 2004 until April 2007 in three 0.25 m^2 littertraps located systematically in each 0.04 ha study plot as described by Schilling and Lockaby (2005). Twigs were not included in the litterfall data since they are accounted for in the dry weight equations for standing crop biomass. Litterfall traps were made of treated lumber and lined with 2-mm nylon mesh. Litterfall was dried at 70° C until constant mass was achieved. Biomass for total litterfall, reproduction, and miscellaneous pieces was recorded for each trap. Samples were ground in a Wiley Mill to pass a 20 mesh sieve and analyzed for carbon and nitrogen by thermal combustion (Perkin-Elmer 2400 series II CHNS/O analyzer; Perkin-Elmer Corp., Norwalk, CT). Annual litterfall production was estimated by summing average monthly litterfall biomass.

Annual woody productivity was estimated by recording diameter at breast height (DBH) of trees greater than 10 cm DBH on each 0.04 ha plot. These data were collected annually in December 2005, 2006, and 2007. Aboveground woody dry weights were calculated for hardwood species using regression equations of Clark et al. (1985) that utilized DBH as the independent variable. Woody productivity was calculated as the difference in woody dry weights between years. Basal area was estimated using a wedge prism with a basal area factor of 10 used at plot center. Stand age was estimated by taking 3-7 increment cores at DBH from canopy and mid-story trees on each plot.

Belowground Productivity

Two fine root samples were collected in the 3 m x 3 m sub-plot on each plot every 6-8 weeks from February 2005 to April 2007 using the soil coring method described by Vogt and Persson (1991) and Anderson and Ingram (1993) and summarized by Bledsoe et al. (1999). Soil cores 5-7 cm in diameter were collected to a depth of 11 cm, transported in a cooler, and stored at 4º C to preserve live roots. Pin flags were placed at each sampling location to avoid re-sampling a disturbed location. Because more than 50% of fine roots are found in the top 10 cm of soils (Baker et al. 2001), sampling to a depth of 11 cm ensured the majority of fine roots were collected. It has been noted that sequential coring does not capture root growth and mortality between sampling periods and is therefore likely to be a conservative estimate (Fahey et al. 1999). However, frequent sequential coring with replications at each plot provides an acceptable representation of fine root production and turnover (Baker et al. 2001, Calvacanti and Lockaby 2005). Fine roots were separated from soil and organic matter and then into live and dead fractions. Fine root samples were sorted within one month of collection in order to differentiate between live and dead roots.

Root dry weight was determined by diameter class: very fine (0.1-1 mm), intermediate (1.1 – 2.0 mm), and coarse (2.1 – 3.0 mm). Live and dead roots were dried at 55-70º C until constant mass was achieved and weighed to report g m^{-2} of each diameter class. Fine root production was estimated by summing positive differences in mean fine root biomass between sample dates (Fogel 1983), allowing for seasonal comparison. Fine roots were ground in a Wiley Mill to pass a 20-mesh sieve and analyzed for C and N by thermal combustion (Perkin-Elmer 2400 series II CHNS/O analyzer; Perkin-Elmer Corp., Norwalk, CT) (Nelson and Sommers 1996).

Water Chemistry

Streams that influenced the research plot floodplains were located adjacent to research plots, but did not intersect the plots. Water chemistry grab samples were collected mid-stream at mid-depth and placed on ice in a cooler for transport to the laboratory. Before each collection, polypropylene bottles were conditioned by rinsing three times with stream water. Water samples were analyzed within five days after collection. Anions and cations (NO_3^-, Cl^-, SO_4^-, Na^+, NH_4^+, K^+) were analyzed using a Dionex DX-120 ion chromatograph (Dionex Corporation, Sunnyvale, CA).

Water chemistry data from February 2005 – January 2006 was used for Period 1 data comparisons (Crim 2007). Period 2 data comparisons are based on monthly water samples collected from August 2006 – May 2007. Summer data are absent from Period 2 comparisons. However, there was little rainfall and stormwater runoff that would have influenced stream water chemistry during this period.

Nitrogen Mineralization

Nitrogen mineralization was estimated using the *in situ* method of Hart et al. (1994). Samples were collected at random locations within the 0.04 ha plot at approximately 2-month intervals between November 2005 and April 2007. For each sample, two randomly located soil cores were taken at a depth of approximately 7.5 cm within the same quadrant of each plot (an area approximately 0.01 ha). After removal of coarse roots, the soil from each core was divided between two polyethylene bags (about 150 mL of soil in each bag), one of which was reburied to a depth of about 7.5 cm and incubated for approximately 30 days. Pre-incubation and post-incubation samples were put on ice and returned to Auburn University for processing. Soil moisture content was measured gravimetrically for each collection date using 10-g sub-samples dried at 105° C for 48 hours. An additional 10-g subsample was extracted using 100 mL 2 *M* potassium chloride (KCl). The soil-KCl suspension was shaken for 1 hour and then filtered and frozen. Samples were then thawed prior to analysis. Extracts were evaluated for NH_4-N and NO_3-N using a BIO-RAD Model 450 microplate reader for NH_4-N and NO_3-N. Mineralized N was estimated by calculating the difference in total N (sum of NH_4-N and NO_3-N) between pre- and post-incubation values. Data were converted to a per-hectare basis using the soil bulk density value for each site.

Statistical Analysis

SAS software version 9.1 (SAS-Institute 2002-2003) was used for all statistical analyses. Regression analysis was used to assess relationships between independent variables, such as percent understory Chinese privet, and dependent variables, such as productivity (PROC REG, SAS Institute 2002-2003). Mean comparisons of productivity, leaf area index, and standing crop were performed using analysis of variance (ANOVA) (PROC GLM, SAS Institute 2002-2003). Tukey's HSD means comparison test was used as a posthoc test and all differences significant above the 90 percent confidence level were reported. Data sets were analyzed to ensure normality assumptions were met and were log transformed when necessary. Medians were used in the analysis of water chemistry data because these data represented a departure from normality.

RESULTS

Research Plots and Percent Understory Chinese privet

The percentage of understory occupied by Chinese privet was significantly different ($p < 0.0001$) among predominant current land uses for each watershed (Fig. 4). Developing watersheds had the greatest percentage of Chinese privet in the understory. There was no difference between urban and rural watersheds, and no difference in stand age among the Chinese privet categories (Fig. 5).

Precipitation Patterns

Precipitation was variable during the 30 month study period (Fig. 6) with less than normal rainfall occurring during much of the second period (September 2005 – May 2007). Monthly measured rainfall ranged from 16.9 cm above the 30-year average to 8 cm below the 30-year average. The Palmer Drought Index indicated drought conditions starting in April 2006 and persisting throughout the study (Fig. 7).

Temperature and Light

There were no differences for mean air temperatures among Chinese privet categories (Fig. 8). Similarly, no significant differences were found for soil temperatures among Chinese privet categories (Fig. 8). Light intensity maximums and means were not significantly different among Chinese privet categories either (Fig. 9).

Overall Productivity

Period 1. Sand Creek 2 watershed plot data were omitted from all analyses of NPP because of unusually low productivity values, probably due to an atypical soil texture. Table 2 lists NPP means for each Chinese privet category and overall ranges in Period 1. Total NPP ranged from 1506 to 3195 g m^{-2} yr^{-1} in Period 1 and was significantly greater in Medium plots than in Reference plots ($F=3.05$, $p<0.0847$) (Fig. 10).

Belowground productivity (BNPP) was the major contributor to the significant differences in Total NPP for Period 1 and means ranged between 304 and 987 g m^{-2} yr^{-1}. Medium and High plots had significantly more BNPP than Reference plots ($F=6.69$, $p<0.0112$) (Fig. 11). There was no significant difference among Chinese privet categories for aboveground NPP (ANPP), estimated as woody productivity plus total litterfall (Fig.12). Period 1 ANPP ranged from 907 to 2244 g m^{-2} yr^{-1}. Annual woody productivity was also not significantly different among Chinese privet categories and ranged from 386 to 1418 g m^{-2} yr^{-1} (Fig. 13). No significant differences were detected among Chinese privet categories for total litterfall, leaf litter, or reproductive litter (Figs. 14, 15, 16). Annual leaf litter production ranged between 471 and 826 g m^{-2} yr^{-1} and annual reproductive litter production ranged between 39 and 106 g m^{-2} yr^{-1} in Period 1.

BNPP did not significantly differ by season. However, when root size class diameters are considered, BNPP dynamics are revealed. Very fine roots (0.1-1.0 mm) exhibited significant relationships between BNPP and LAI ($R^2=0.50$, $p<0.0032$). BNPP means for very fine roots ranged between 81 and 675 g m^{-2} yr^{-1}. Furthermore, intermediate roots (1.1-2.0 mm) had stronger significant relationships with bulk density in Period 1 (R^2=0.31, p<0.0311) when compared with very fine roots (R^2=0.23, p<0.0708). Means for intermediate fine root production ranged between 92 and 322 g m^{-2} yr^{-1}. In addition, coarse fine root production (2.1-3.0 mm) means ranged between 161 and 667 g m^{-2} yr^{-1} and did not exhibit a significant relationship with nitrogen mineralization, bulk density or LAI.

Period 1 Regression Relationships. For many of the productivity measures there was an overall trend toward increased productivity in the medium category of understory Chinese privet invasion. The regression relationship between BNPP and percent understory Chinese privet was significant in Period 1 (R^2=0.53, p<0.0112) (Fig. 17). There was no significant relationship between percent understory Chinese privet and total litterfall, leaf litter, or reproductive litter in Period 1 although productivity tended to be greatest in the Medium category of Chinese privet (Figs. 18, 19, 20). Lastly, no significant relationship between woody productivity and understory Chinese privet was detected.

Period 2. Fewer overall significant differences were detected among Chinese privet categories in Period 2 compared with Period 1. Although no significant difference among privet categories was found for total NPP, ANPP, or woody productivity (Figs. 10, 12, and 13), total litterfall in the Reference plots was significantly less than both Medium and High Chinese privet plots (Fig. 14). This was driven primarily by significant differences in the reproductive litterfall component. The Reference category had the least and the High category had the greatest amounts of reproductive litter

(F=4.30, p<0.0391) (Fig. 16). Annual reproductive litter production ranged between 58 and 145 g m^{-2} yr^{-1}. On the contrary, there was no difference in annual leaf litter production among Chinese privet categories in Period 2 (Fig. 15). Annual leaf litter productivity ranged between 430 and 568 g m^{-2} yr^{-1} in Period 2. Overall ranges for total NPP, ANPP, woody productivity, and total litterfall were 1,363 to 2,769 g m^{-2} yr^{-1}, 934 to 1,971 g m^{-2} yr^{-1}, 379 to 1296 g m^{-2} yr^{-1}, and 487 and 682 g m^{-2} yr^{-1}, respectively (Table 3).

BNPP ranged from 369 to 808 g m^{-2} yr^{-1} in Period 2 and no significant difference among Chinese privet categories was found (Fig. 11). However, very fine roots (0.1-1.0 mm) displayed significant relationships between BNPP and nitrogen mineralization (R^2=0.42, p<0.0088) and LAI (R^2=0.3233, p<0.0270). Means for very fine root production ranged between 71 and 388 g m^{-2} yr^{-1}. Moreover, intermediate fine roots (1.1-2.0 mm) had significant relationships with bulk density (R^2=0.28, p<0.0427) as opposed to very fine roots (no significant relationship in Period 2). BNPP means for intermediate fine roots ranged between 95 and 324 g m^{-2} yr^{-1}. Finally, coarse fine root production (2.1-3.0 mm) ranged between 193 and 481 g m^{-2} yr^{-1} and there was no significant relationship with nitrogen mineralization, bulk density or LAI.

Period 2 Regression Relationships. As in Period 1, regression relationships in Period 2 suggest increased productivity in the Medium Chinese privet category. Significant regression relationships were found between percent understory Chinese privet and total litterfall (R^2=0.58, p=<0.0058), leaf litter (R^2=0.49, p<0.0183), and reproductive litter (R^2=0.42, p<0.0367) (Figs. 18, 19, 20). There was no significant regression relationship in Period 2 between BNPP (Fig. 17) or woody productivity and percent understory Chinese privet.

Between Period Comparisons. Comparisons between years were made to detect possible responses to climate differences, especially drought conditions. A Student's T-test detected significantly more total NPP in Period 1 compared with Period 2 in the Medium Chinese privet category ($p<0.0603$) (Fig. 21). However, there was no significant difference between Period 1 and Period 2 total NPP in the Reference and High Chinese privet categories. Even though significant differences were detected between years for total litterfall in the Medium category, BNPP likely exerted a stronger influence on total NPP in the Medium Chinese privet category. For example, a Student's T-test between years revealed that BNPP was significantly greater in Period 1 than Period 2 in the Medium plots ($p<0.0284$), but not in the Reference or High plots (Fig. 22).

There was significantly more total litterfall (leaf litter + reproductive litter) in Period 1 for each of the Chinese privet categories: Reference ($p<0.04$), Medium ($p<0.09$) and High ($p<0.06$) (Fig. 23). This was influenced strongly by significant differences between sampling years for leaf litter productivity. Period 1 leaf litter production was significantly greater in each of the Chinese privet categories: Reference ($p<0.0376$), Medium ($p<0.0296$) and High ($p<0.0155$) (Fig. 24). However, more reproductive litter was found in Period 2 for each of the Chinese privet categories. This difference was only significant in the High category ($p<0.0008$) (Fig. 25).

Chinese Privet NPP

Chinese Privet Leaf Litter. Mean annual Chinese privet leaf litter production ranged between 0.06 and 88 g m^{-2} yr^{-1}in Period 1 and 0.02 and 126 g m^{-2} yr^{-1} in Period 2. The proportion of total leaf litter composed of Chinese privet leaves varied from 0.01% to 18.7% in Period 1 and 0% to 28.2% in Period 2.

Unlike total leaf litter, which fell predominantly in the fall, Chinese privet leaf litter was collected primarily in the spring. Significant differences varied among Chinese privet categories and between years. In Medium plots, the spring season had significantly more Chinese privet leaf litter production in Period 1 than summer or fall, but was not different from winter (F=4.36, p<0.0102) (Fig. 26). Similarly, Period 2 Chinese privet leaf litter production was significantly greater in the spring than all other seasons (F=4.41, p<0.0003) (Fig. 27). High plots were more variable in Chinese leaf litter production across seasons for both sampling years (Fig. 26). In Period 1, spring Chinese privet leaf litter production in High plots was significantly greater than summer and fall, but not winter. Similar to Period 1, Period 2 High plots had significantly more Chinese privet leaf litter production in the spring than all other seasons. An ANOVA revealed no significant differences in Chinese privet leaf litter production between the sampling years when compared by seasons (Fig. 27).

Chinese Privet Woody Biomass Productivity. The contribution of Chinese privet to woody productivity ranged from 0 to 596 g m^{-2} yr^{-1} in Period 1 and 0 to 363 g m^{-2} yr^{-1} in Period 2. This represented 0-44% and 0-29% of overall woody productivity in Years 1 and 2, respectively. Number of Chinese privet stems greater than 5 cm DBH ranged from 0 to 1125 stems per hectare (Reference<Medium<High). A majority of the Chinese privet

were considered understory stems less than 10 cm DBH, so they were not included in measures of woody productivity. Understory Chinese privet stems ranged in number from 0 to 118,800 stems per hectare and composed a majority of understory stems in the Medium (60%) and High (95%) Chinese privet categories. A Student's t-test revealed no significant difference in Chinese privet woody NPP between years among Chinese privet categories.

Leaf Area Index

Total stand LAI ranged from 7 to 12 and had a significant quadratic relationship with percent understory Chinese privet ($R^2=0.21$, $p<0.001$) (Fig. 28). LAI in the Reference plots (6.7) was significantly different from the Medium (8.2) and High (9.1) categories ($F=10.38$, $p<0.0001$) (Fig. 29).

Total stand LAI and total litterfall (leaf litter + reproductive litter) were significantly related in Period 1 ($R^2=0.41$, $p<0.0106$) and in Period 2 ($R^2=0.27$, $p<0.0454$) (Figure 30). The Period 1 significant regression relationship was strongly influenced by the significant relationship between leaf litter and LAI ($R^2=0.39$, $p<0.0135$) (Fig. 31). Reproductive litter and LAI were not significantly related in Period 1 ($R^2=0.10$, $p<0.2610$) (Fig. 32).

Conversely, the Period 2 regression relationship had the opposite pattern with leaf litter not having a significant relationship with LAI ($R^2=0.14$, $p<0.1771$) (Fig. 31), but reproductive litter having a significant relationship with LAI ($R^2=0.31$, $p<0.0324$) (Fig. 32). BNPP was significantly related to LAI in Period 1 ($R^2=0.42$, $p<0.0086$) and Period 2 ($R^2=0.21$, $p<0.0884$) (Fig. 33). LAI and Chinese privet leaf litter had a significant quadratic regression relationship that suggested greater Chinese privet leaf productivity in the middle ranges of LAI: Period 1 (R^2=0.61, p<0.0036) and Period 2 (R^2=0.80, p<0.0001) (Fig. 34).

Total Stand Basal Area

Basal area ranged from 11.6 to 41.8 m^2 ha^{-1} and was significantly different among all Chinese privet categories (Reference>High>Medium) (F=64.39, p<0.0001) (Fig. 35). Additionally, basal area was significantly related to percent understory Chinese privet (R^2=0.64, p<0.0001), exhibiting a reverse J-shape with higher basal area values in plots with low and high understory Chinese privet invasion (Fig. 36). Lastly, basal area and Chinese privet leaf litter exhibited a significant negative linear regression in Period 1 (R^2=0.45, p<0.0064) and Period 2 (R^2=0.40, p<0.0118) (Fig. 37).

Nutrient Influences

Nitrogen Mineralization. Nitrogen mineralization rates were not estimated during Period 1. Annual rates of nitrogen mineralization in Period 2 were positively correlated with Total NPP (R^2=0.57, p<0.0011) and ANPP (R^2=0.33, p<0.0255) (Figs. 38 and 39). These significant relationships were mainly influenced by leaf litter productivity, woody productivity, and BNPP. Figure 40 illustrates the significant positive relationship between Period 2 total litterfall and annual nitrogen mineralization rates (R^2=0.46, p<0.0051). This relationship was strongly influenced by a significant relationship between leaf litter and nitrogen mineralization rates (R^2=0.44, p<0.0075) (Fig. 41). However, there was not a significant relationship between reproductive litter and nitrogen mineralization (R^2=0.13, p<0.1942). Woody production had a weak, but significant positive relationship to nitrogen mineralization (R^2=0.25, p<0.0576) (Fig. 42). BNPP was strongly and positively correlated to annual rates of nitrogen mineralization in Period 2 (R^2=0.66, p<0.0004) (Fig. 41). LAI was also significantly related to nitrogen mineralization (R^2=0.40, p<0.0108) (Fig. 44).

Live Fine Root Nutrients. Nitrogen concentrations did not differ significantly by Chinese privet category in Period 1. However, the Reference category had significantly greater concentrations of nitrogen than the Medium or High categories in Period 2 (F=5.27, p<0.0054) (Fig. 45). Nitrogen content ranged from 64-121 g m^{-2} in Period 1 and 66-87 g m^{-2} in Period 2. Period 1 nitrogen content was more variable than Period 2 among the categories. For example, there were significant differences among all three Chinese privet categories with Medium having the greatest nitrogen content (F=14.97, p<0.0001). In Period 2, only the Reference category exhibited significantly lower nitrogen content than either Medium or High categories (F=2.60, p<0.0753) (Fig. 46).

Carbon concentration means for in Period 1 and Period 2 are presented in Table 4 and 5. Carbon concentration was significantly less in the Reference category than the Medium and High categories in Period 1 (F=4.26 p<0.0146). There was no significant difference in carbon concentration among Chinese privet categories in Period 2 (Fig. 47). However, carbon content was significantly different among all Chinese privet categories in both Period 1 (F=27.85, p<0.0001) and Period 2 (F=14.76, p<0.0001) (Fig. 48). Carbon content means ranged from 2,959-5,975 g m^{-2} in Period 1 and 2,990-4,860 g m^{-2} in Period 2 (Tables 4 and 5).

The C:N ratio ranged from 61-70 in Period 1 and 69-80 in Period 2. The Reference category had a significantly lower C:N ratio of 61 compared with the Medium or High category ratios of 70 and 69 respectively in Period 1 (F=3.04, $p<0.0488$). There was no significant difference among Chinese privet categories for C:N ratio in Period 2 (Fig. 49).

Root nutrient seasonal patterns were not significantly different between Period 1 and 2. Additionally, there were no significant seasonal differences within Chinese privet categories; therefore, both years of root nutrient data and Chinese privet categories were combined to describe seasonal patterns (Fig. 50). Nitrogen concentrations were significantly greater in the winter than in other seasons (F=19.04, $p<0.0001$). Similarly, nitrogen content was significantly greater in the winter compared to summer and fall (F=5.74, $p<0.0007$). Fall carbon concentration and C:N ratio were significantly greater than other seasons (F=25.95, $p<0.0001$ and F=19.15, $p<0.0001$ respectively). There was no significant difference between seasons for carbon content.

Dead Fine Root Nutrients. Nitrogen concentrations Chinese privet category means in dead roots ranged from 1.03-1.07 mg kg^{-1} in Period 1 and 0.91-0.94 mg kg^{-1} in Period 2 (Tables 4 and 5). There was no significant difference detected among Chinese privet categories for nitrogen concentrations in Period 1 or Period 2. Nitrogen content ranged from 7.1-11.4 g m^{-2} in Period 1 and 9.2-16.3 g m^{-2} in Period 2 and varied among Chinese privet categories in Period 1 (F=2.98, $p<0.0522$) and Period 2 (F=63.12, $p<0.0096$). The Reference category had significantly less nitrogen than the Medium category, while the Medium and High categories were not significantly different in either year (Fig. 51).

Period 1 carbon concentration means ranged from 43.4-45.5 mg kg^{-1} and carbon concentrations in Period 2 ranged from 44.3-45.9 mg kg^{-1} (Tables 4 and 5). There was significantly greater carbon concentration in the Medium category than Reference or High categories in Period 1 ($F=5.00$, $p<0.0072$) (Fig. 52). In Period 2, carbon concentrations in the Medium category were significantly greater than in the Reference; however, there was no difference between Reference and High or Medium and High category concentrations ($F=62.73$, $p<0.0001$) (Fig. 52). Furthermore, carbon content Chinese privet category means ranged from 316.2-507.9 g m^{-2} in Period 1 and were significantly different between Reference and Medium categories ($F=2.67$, $p<0.0707$). However, the High category was not significantly different from Reference or Medium categories. Period 2 carbon content means ranged from 496.4-870.0 g m^{-2} and the Reference category was significantly lower than Medium and High categories ($F=62.23$, $p<0.0001$) (Fig. 53).

C:N ratios ranged from 45-47 and 57-62 in Years 1 and 2 respectively. While the C:N ratios were numerically greatest in the High category for Period 1 and numerically greatest in the Medium category for Period 2, these differences were not statistically significant.

Some seasonal differences were also detected for dead roots (Fig. 54). However, there were no significant seasonal differences between years or among Chinese privet categories. Nitrogen concentration was significantly greater in the winter compared with summer and fall ($F=12.04$, $p<0.0001$). However, there was no significant difference between seasons for nitrogen content. Dead roots had significantly greater carbon concentrations in the fall than other seasons ($F=9.01$, $p<0.0001$) and winter carbon content was significantly less than other seasons ($F=2.40$, $p<0.0667$). C:N ratios were significantly greater in the fall as compared with other seasons ($F=18.51$, $p<0.0001$).

Water Chemistry and Productivity. Median concentrations for K, Cl, Fl, NO_2, NO_3, NH_4, and SO_4 in stream water were compared to total litterfall (leaf + reproductive litter) and BNPP. Total litterfall and BNPP both exhibited positive significant relationships with K, Cl, NO_3, and SO_4 mg L^{-1} medians (Figs. 55 and 56).

Land Use Influences

ANOVA revealed significantly higher total NPP in Period 1 in watersheds that were predominantly urban ($F=8.64$, $p<0.0031$) (Fig. 57). In Period 2, urban watersheds had significantly higher total NPP compared with forested watersheds ($F=3.33$, $p<0.0603$) (Fig. 57). Period 1 means for forested, rural, developing, and urban were 1,613, 2,125, 2,080, and 2,963 g m^{-2} yr^{-1} respectively. Forested, rural, developing and urban means in Period 2 were 1,561, 1,770, 1,911, and 2,324 g m^{-2} yr^{-1} respectively.

DISCUSSION

The results suggest Chinese privet influenced riparian forest processes such as above- and belowground NPP. Vitousek (1990) and Ehrenfeld (2003) also noted that invasive, nonnative vegetation has the potential to influence ecosystem processes and functions such as nutrient cycling, hydrology, and productivity. Furthermore, the results support research findings that the extent of invasive, nonnative species' impacts may be exacerbated in combination with anthropogenic disturbances such as intensive land use and development (Burton and Samuelson 2007, Loewenstein and Loewenstein 2005, Lundgren et al. 2004, Luken and Thieret 1996) and increased nutrient loading in urban streams (Aguiar et al. 2007, King and Buckney 2000). Overall, Chinese privet is especially a threat to riparian forest ecosystems in the Southeast (Burton and Samuelson 2007, Loewenstein and Loewenstein 2005) where rapid land use change is occurring (Wear 2002).

Total Net Primary Productivity

Total NPP (aboveground + belowground) estimates were more variable in Period 1 compared with Period 2. This may be a result of more plentiful rainfall in Period 1 compared with the drier conditions in Period 2 (Fig. 10). Total NPP was significantly greater in Medium Chinese privet plots compared with the Reference plots in Period 1. Interestingly, High Chinese privet plots had less NPP than Medium plots in Period 1. The Medium plots had dense understories of Chinese privet stems while the Reference and High categories had less dense understories.

Ishii et al. (2004) noted understory tree species play a significant role in enhancing stand productivity. Sunlight may be captured and used more efficiently when a diversity of vertical structure exists, leading to increased stand productivity (Kira et al. 1969, Hartley 2002). Brinson (1990) noted that up until 20 years of stand age, most of the accumulation in biomass and volume in riverine forests is due to recruitment into the >2.5 cm DBH size class (understory) and that a steady state is achieved after 70 years. The average age of stands in this study ranged between 38 and 42 years which is less than the age of steady state, but is greater than the period of time when recruitment of understory stems typically impacts standing crop biomass. The ability of Chinese privet to invade established stands with closed canopies seems to have extended the period of time that understory stems >2.5 cm contribute to NPP. A study of Wax myrtle (*Morella cerifera*), a shrub that formed dense thickets along a Virginia barrier island, had similar findings of rapid shrub growth (increased NPP) in stands in the early stages of shrub invasion (Young et al. 1995).

Ultimately, a loss in species richness with the increase of Chinese privet understory stems may influence overall stand productivity. Several studies have suggested that a reduction in species richness may lead to less efficient gathering of resources which lowers production of biomass and sequestration of CO_2 (Naeem et al. 1994, Hector et al. 1999, Costanza et al. 2007).

Aboveground Net Primary Productivity

Total ANPP values were consistent with ranges found in other floodplain forests (Johnson and Bell 1976, Lugo et al. 1990, Mitsch et al. 1991, Clawson et al. 2001), but higher than estimates reported by Burton and Samuelson (2007) for similar watersheds in West Georgia. It was hypothesized in the current study that ANPP would decrease with increasing densities of understory Chinese privet stems. There was a numerical trend toward increased productivity in the Medium category of understory Chinese privet invasion. However, productivity decreased numerically, but not significantly, in the High Chinese privet plots (>80% understory Chinese privet). Although these differences were not significant between Chinese privet categories (Fig. 11), they suggest that productivity is greatest when the understory is composed of 25-79% understory Chinese privet. This pattern may be a result of decreased regeneration (Chapter 4 - Influence Of Chinese Privet On Native Plant Regeneration In Riparian Forests Of The Southern Piedmont), small changes in light availability with heavy Chinese privet understories, or a loss of forest structure diversity under dense Chinese privet mid-story shrubs. Ehrenfeld (2003) noted that invasion by nonnative species in most cases resulted in higher net primary productivity.

*Total Litterfall. A*nnual total litterfall was slightly greater than values reported in other studies conducted in floodplain forests (Mitsch et al. 1991, Clawson et al. 2001), but within ranges of floodplain productivity described by Cavalcanti and Lockaby (2006) and Lugo et al. (1990). As was the case with ANPP, there was a numerical, but not significant, trend towards increasing total litterfall productivity in the Medium Chinese privet plots followed by a decrease in High Chinese privet plots (Fig. 12). One explanation may be that Medium Chinese privet plots tended to retain diversity of forest structure, i.e., herbaceous layer, shrubs, mid-story, and canopy. Conversely, High Chinese privet plots were characterized by a main canopy, as well as greater numbers of mid-story Chinese privet stems, but lacked the presence of developed herbaceous and shrub layers. This was consistent with other studies where researchers reported that well established mid-stories of Chinese privet severely reduced herbaceous species and completely suppress regeneration of native species (Merriam and Feil 2002). This loss of a regeneration layer may be partially responsible for the decrease in total litterfall productivity in High Chinese privet plots.

Significantly less total litterfall was produced in Period 2 than Period 1 for all Chinese privet categories (Fig. 23). This may be a result of drought conditions in Period 2 (Figs. 6 and 7). A decrease in productivity due to drought conditions has been previously documented by Dickson and Broyer 1972, Bollinger et al. 1991, and Newman et al. 2006. During the drought in Period 2, Reference plots had significantly less litterfall than the Medium and High Chinese privet plots. Invasive, nonnative species may be better adapted to adverse environmental conditions such as summer drought (Grotkopp and Rejmanek 2007), and consequently the higher levels of Chinese privet may have sustained litterfall.

Leaf Litter. Leaf litter productivity made up the majority of total litterfall and was less abundant in Period 2 than Period 1 (Fig. 24). As discussed previously, this is likely due to drought conditions and a lack of available water in Period 2. As was the case with total litterfall, Medium Chinese privet plots had a trend toward higher leaf litter productivity in both years. However, this trend was not significantly different among Chinese privet categories (Fig. 15). Perhaps the light-mass nature of Chinese privet leaves makes detecting a significant difference between Chinese privet categories difficult. LAI was a strongly correlated to leaf litter productivity in Period 1, but was not significantly related in Period 2 perhaps due to drought conditions (Fig. 31).

Reproductive Litter. Unlike total litterfall and leaf litter, reproductive litter had a trend towards greatest productivity in the High Chinese privet plots (Fig. 15). Period 2 Reference plots had significantly less reproductive litterfall than both the Medium and

High Chinese privet plots. Invasive, nonnative plants have been noted to have reproductive characteristics that include short generation time, small seed mass, and long fruiting periods (USDA 2008). Moreover, Chinese privet has been noted to produce about 1,300 fruits per square meter of canopy (Burrows and Kohen 1986). High percentages of understory Chinese privet stems were positively correlated with high rates of reproductive litterfall, especially in Period 2 (Fig. 20), supporting the suggestion that Chinese privet has voluminous reproductive capability.

Reproductive litterfall production was greatest in the spring for both years in all Chinese privet categories. This is consistent with the reproductive litterfall timing of native Piedmont forest understory species such as red maple (*Acer rubrum* L.) and winged elm (*Ulmus alata* Michx.) (USDA 2008). Native species such as water oak (*Quercus nigra* L.), tulip poplar (*Liriodendron tulipifera* L.), and sweetgum (*Liquidambar styraciflua* L.) that tended to occupy the main canopy had fruit / seed periods in the summer or fall (USDA 2008).

Interestingly, unlike total litterfall and leaf litter, reproductive litterfall was greater in Period 2 than Period 1. High Chinese privet plots had significantly greater reproductive litter in Period 2 compared to Period 1 (Fig. 25). The timing of stress plays an important role in the subsequent response by plants (Mooney et al. 1991). Plants may respond to stress such as drought conditions by decreasing or increasing reproductive litter production or by exhibiting no change (Foulds 1978, Archaux and Wolters 2006, Ogaya and Penuelas 2007). Perhaps Chinese privet was not negatively affected by drought conditions in Period 2 resulting in a plentiful crop of berries. Conversely, Chinese privet may have responded to drought conditions by increasing reproductive litterfall in a ‘now or never’ situation for reproduction (Mooney et al. 1991).

Woody Productivity. There was no significant difference in either period among Chinese privet categories. Annual woody productivity was within ranges described by Lugo et al. (1990) and Clawson (2001) for floodplain forests. Period 1 stem productivity was greatest in the Medium Chinese privet plots and Period 2 stem productivity was greatest in the High Chinese privet plots (Fig. 12). Moreover, there was no significant difference in stand ages among Chinese privet categories. Perhaps the similarity among Chinese privet categories in woody productivity is attributed to the similarity in stand age, that is, the dominant canopy tree species are increasing in woody productivity at about the same rate. During this study, Chinese privet did not exert a strong influence on existing annual stem increment. However, Hartman and McCarthy (2007) reported strong evidence for growth reductions in overstory hardwood trees when the invasive, nonnative shrub Amur honeysuckle (*Lonicera maackii* (Rupr.) Herder) occurred in the understory. Dendrochronological methods revealed significant radial and basal growth reductions at approximately 6 years after invasion with the greatest frequency of negative growth changes occurring 20 years after Amur honeysuckle invasion. Perhaps stem increment in the current study would have been higher if Chinese privet was not present. Additionally, the lack of native species regeneration under stands of Chinese privet (Merriam and Feil 2002, USDA 2008) may eventually lead to significant decreases in annual woody productivity as dominant tree mortality occurs and replacements are not recruited. Each of the plots in the current study had a closed canopy of native tree species and mortality of these overstory trees had not yet occurred.

Basal area was similar to other estimates in west Georgia watersheds (Burton and Samuelson 2007) and other forested wetland areas (Lugo et al. 1990). However, there was a dramatic difference in basal area among Chinese privet categories (Figs. 35 and 36). Reference plot basal areas were significantly greater than in Medium and High Chinese privet plots. Medium Chinese privet plots had significantly lower basal areas than High Chinese privet plots. The differences among Chinese privet categories was largely due to the obscured prism view of larger stems considered as 'in' by the numerous understory Chinese privet stems. Other studies have reported an overall decline in basal area as invasive, nonnative woody species invade. For instance, in plots invaded by Amur honeysuckle, shrub density was reported to be negatively correlated with basal area (Hutchinson and Vankat 1997, Bartuszevige et al. 2006). Mascaro and Schnitzer (2007) noted no difference in basal areas between plots invaded by common buckthorn (*Rhamnus cathartica* L.), an invasive, nonnative shrub, and plots dominated by native species in Wisconsin. However, total woody stem density at the common buckthorn plots was more than twice that of native plots. A decrease in basal area in plots that have been invaded by nonnative shrubs may signal the potential for long-term decrease in woody productivity as well as a harbinger for suppressed native stem regeneration. Without regeneration of native tree species, a shift in stand structure is likely to occur. Replacement of native large overstory trees that make up the canopy layer will be greatly diminished. Instead, these canopy trees will be replaced by a dense mid-story composed of Chinese privet. This shift in stand structure will negatively impact NPP as well as standing crop biomass, carbon allocation, and carbon sequestration (Chapter 3, Influence of an Invasive, Nonnative Tree Species on Carbon Allocation and Sequestration in Riparian Forests of the Southern Piedmont).

Belowground Net Primary Productivity

It was hypothesized that belowground NPP (BNPP) in the upper 11 cm of soil would increase with increasing densities of Chinese privet. Period 1 BNPP had a trend similar to total litterfall (Reference<Medium>High) with the Reference category having significantly less BNPP than both Medium and High categories. Period 2 BNPP exhibited the hypothesized trend (Reference<Medium<High), but there was no significant difference between Chinese privet categories (Fig 16). BNPP values were consistent with BNPP estimates reported by Cavalcanti and Lockaby (2005) in ephemeral stream catchments in the Coastal Plain (82.7-1261.5 g m^{-2} yr^{-1}), Powell and Day (1991) in a rarely flooded mixed hardwood community (354-989 g m^{-2} yr^{-1}), and Symbula and Day (1988) in a *Nyssa-Acer* swamp (645 g m^{-2} yr^{-1}). Other researchers have reported lower estimates of BNPP that may be attributed to use of different size classes for fine roots (Clawson et al. 2001) and distinct differences in flooding regimes from the current study (Powell and Day 1991, Clawson et al. 2001). Clawson et al. (2001) estimated BNPP between 56.2-211.1 g m^{-2} yr^{-1} in varying levels of soil moisture. Powell and Day (1991) estimated BNPP between 68-308 g m^{-2} yr^{-1} in a cypress community that experienced prolonged winter flooding.

Estimates of BNPP in Period 1 were significantly greater than Period 2 in the Medium and High Chinese privet plots. There was no difference between Period 1 and

Period 2 in the Reference plots (Fig. 22). Perhaps the Reference plots did not reflect significantly less BNPP during the droughty conditions in Period 2 due to the predominance of larger native tree species that have tap roots able to reach moisture lower in the soil that is unavailable to smaller plants (Kimmins 2004). Chinese privet was observed to have a shallow root system that may have limited its ability to access water in the drier Period 2, which resulted in significantly less BNPP. Soil moisture has a strong influence on root development and distribution (Fisher and Binkley 2000). Frank (2007) reported a large reduction in BNPP in Yellowstone National Park following a drought. Similarly, Konopka et al. (2007) noted that simulated drought dramatically reduced fine root production of Japanese cedar (*Cryptomeria japonica* (L. f.) D. Don.). Drought impacts were greater in the surface soils (0-5cm) than in deeper soils, suggesting fine roots near the surface were more vulnerable to drought.

Percent of understory composed of Chinese privet was significantly related to BNPP, exhibiting similar patterns as litterfall with a trend of increased productivity in the Medium Chinese privet plots and decreased BNPP in the Reference and High plots (Fig. 17). A decrease in BNPP in the High plots may be related to an increased dense mid-story that tended to shade out herbaceous and shrub layer vegetation.

Chinese Privet Leaf Litter Productivity. Chinese privet leaf litter productivity contributed between 0 - 28% of overall litter productivity (High>Medium>Reference). Unlike overall leaf litter productivity, the greatest amount of Chinese privet leaf litter was collected in the spring season for both Medium and High Chinese privet plots (Fig. 26). Ehrenfeld (2003) notes that when a nonnative species is introduced, its effects on nutrient cycling depend on how different it is from the existing native plant species. Differences in litter quality, decomposition rates, and microclimate present at the timing of litterfall all contribute to altered nutrient cycles in other systems (Vitousek 1990, Ehrenfeld 2003, Kimmins 2004). The timing of Chinese privet litterfall suggests potential for shifts in nutrient cycling (Mitchell 2008). There was no significant difference in Chinese privet leaf litter productivity between sampling years (Fig. 27). This suggests that the drought conditions in Period 2 did not reduce Chinese privet leaf litter productivity. In fact, the spring season in Period 2 had greater amounts of litterfall than in Period 1. Chinese privet is highly desirable as an ornamental species due to its ‘tenacious constitution’ that allows it to flourish in harsh conditions such as concrete crevices, back alleys, and floodplains along rivers (Dirr 1998). Moreover, the increase in litterfall in Period 2 could be a relic of plentiful rainfall from the previous year, that is, the ‘lag effect’ meant the drought impact (Newman et al. 2006) was not exhibited immediately by Chinese privet.

Chinese privet leaf litter productivity tended to be higher in the middle ranges of LAI and decreased in the upper ranges of LAI (Fig. 34). This suggests that although Chinese privet is able to thrive in shaded conditions, there is some decrease in productivity with increasing LAI and decreasing available light. This may be attributed to decreasing efficiency in net photosynthate production in systems with high LAI (Kimmins 2004).

The increase in understory Chinese privet stems and accompanying increase in research plot leaf area may be linked to a decrease in detectable plot basal area. For example, Chinese privet leaf litter productivity decreased significantly with decreasing basal area (Fig. 37), suggesting that plots with high basal areas are likely not heavily invaded by Chinese privet that obscures detection of basal area with a prism, and therefore have less Chinese privet leaf litter productivity. Hutchinson and Vankat (1997) and Bartuszevige et al. (2006) also reported negative correlations between invasion of Amur honeysuckle, a nonnative shrub, and basal area.

Leaf Area Index. LAI values observed in this project were similar to other LAI values for a piedmont forest ranging from 4.5-7.4 (Hedman and Binkley 1988) and LAI values in a shrub thicket of wax myrtle ranging from 9.8 and 12.5 (Brantley and Young 2007), but greater than estimates from similar watersheds in West Georgia (e.g., 2.8 – 5.97) (Burton and Samuelson 2007). LAI was positively correlated with ANPP that may be attributed to an increase in annual net photosynthesis and shifts in the spatial distribution of LAI (Fassnacht and Gower 1997, Bolstad et al. 2001). Alternatively, Kimmins (2004) reported increasing LAI values also correspond with increasing shade that contributes to less efficient net production of photosynthate. As the percent of Chinese privet increased in the understory, LAI also increased (Fig. 28). Reference plots had significantly less LAI than Medium and High Chinese privet plots (Fig. 29). Chinese privet tends to form dense thickets that, along with many small, semi-evergreen leaves, contribute to the increased LAI values.

LAI and litterfall production were positively correlated, as seen in previous studies (Fassnacht and Gower 1997, Bolstad et al. 2001). Greater LAI appears to translate into increased capture of sunlight for photosynthesis, which in turn, increases productivity (Leith 1975). LAI and BNPP were positively correlated, with a stronger relationship in Period 1 than Period 2 (Fig. 33). Increased LAI may provide increased potential for a plant to allocate more resources to belowground biomass (Fassnacht and Gower 1997, Bolstad et al. 2001).

Nutrient Influences

Nitrogen Mineralization. Annual rates of nitrogen mineralization were closely correlated with total NPP, ANPP, litterfall productivity, leaf litter, and woody productivity during Period 2 (Figs. 38, 39, 40, 41, 42). Interestingly, LAI was also closely correlated with nitrogen mineralization this same year (Fig. 44). A trend between nitrogen availability and ANPP was also documented by Newman et al. (2006), suggesting that ANPP was N limited in their study. Although it has been noted that invasive, nonnative species may cause shifts in nutrient availability (Vitousek 1990, Ehrenfeld 2003), percent understory Chinese privet and annual rates of nitrogen mineralization were not significantly related in research conducted by Mitchell (2008).

BNPP was strongly and positively correlated with annual rates of nitrogen mineralization (Fig. 43), suggesting nitrogen was a limiting factor in West Georgia riparian forests. This follows a similar trend exhibited by nitrogen mineralization and litterfall productivity. Newman et al. (2006) found that soil moisture, rather than nitrogen availability, was the best predictor for BNPP in a temperate mixed deciduous forest.

Fine Root Nutrients. Content of nitrogen and carbon in live roots was linked to fine root biomass rather than concentration differences (Reference<Medium<High) (Tables 2 and 3, Chapter 2, Influence of Chinese privet on Carbon Allocation and Sequestration in Riparian Forests of the Southern Piedmont). Cavalcanti and Lockaby

(2005), Clawson et al. (2001), and Schilling et al. (1999) also noted that nitrogen and carbon contents were strongly influenced by root biomass. Nitrogen content was more variable in Period 1 than Period 2 (Fig. 46) and was higher than ranges of 0.48-1.38 g m^{-2} reported by Cavalcanti and Lockaby (2005) on reference floodplain plots in the coastal plain of southwest Georgia. However, carbon content was variable in both sampling years with significant differences between Chinese privet categories (Fig. 48). Additionally, carbon content was higher than ranges of 22.67-60.6 g m^{-2} reported by Cavalcanti and Lockaby (2005) in a southwest Georgia coastal plain system.

Nitrogen concentrations (mg kg^{-1}) in live roots were not significantly different across Chinese privet categories in Period 1, but were significantly greater in the Reference plots in Period 2 (Fig. 45). Nambiar (1987) noted that prolonged drought had only minor impacts on root nutrient concentrations. Instead, this difference in concentrations may have been driven by the lower nitrogen and carbon content in the Reference plots for Period 2. Live root nitrogen concentration less than the 1.1 mg kg^{-1} has been reported by Gordon and Jackson (2000) and the range of 1.3-1.68 mg kg^{-1} has been reported by Borken et al. (2007). Carbon concentration in this study was similar to the 48 mg kg^{-1} level reported by Gordon and Jackson (2000), but less than the range of 47.5-51.2 mg kg^{-1} reported by Borken et al. (2007). Carbon concentration was not significantly different among Chinese privet categories in either year of this study.

Mean C:N ratios ranged from 61-70 and 69-80 for Years 1 and 2, respectively. The Reference C:N ratio was less than Medium and High categories both years, but significant at the 0.10 level only for Period 1 (Fig. 49). C:N ratios in this study were greater than values of 46, 54, and 56 reported in the literature by Jolley (2008) for live roots in West Georgia coastal plain watersheds and a mean value of 43 summarized from live root studies by Gordon and Jackson (2000) for live roots < 2mm. On the contrary, C:N ratios were similar to the mean value of 79 summarized by Gordon and Jackson (2000) for 2-5 mm live roots.

Although retranslocation of nutrients by roots prior to senescence has been debated (Nambiar 1987), the significant increase in root nitrogen concentration and content during winter suggests retranslocation of nitrogen from the shoot to the roots (Fig. 50). Carbon concentration was significantly greater in the fall than other seasons, whereas carbon content, a reflection of root biomass, was not different between seasons. The lack of a difference among seasons for carbon content contrasts with other studies and suggests that root turnover was of little magnitude in this study. Schilling et al. (1999), however, reported a peak in fine root biomass during the spring and autumn. Clawson et al. (2001) also noted that an intermediately drained floodplain community reached a biomass peak in September. Cavalcanti and Lockaby (2005) reported a decline in root biomass during the fall. C:N ratio was significantly greater in the fall than other seasons (Fig. 50), reflecting the greater carbon concentration and lower nitrogen concentration reported in fall.

Dead root nitrogen concentrations were not different among Chinese privet categories and were similar to the concentrations of 1.1 mg kg^{-1} reported by Gordon and Jackson (2000). However, dead root nitrogen content was significantly less in Reference plots for both years (Fig. 51) and was greater than ranges of 0.2-0.7 g m^{-2} reported for reference floodplains in the coastal plain of southwest Georgia (Cavalcanti and Lockaby

2005). Lower nitrogen content was likely due to the significantly lower carbon content in Reference plots for both years. Medium plots had significantly greater carbon concentrations for dead roots than Reference and High plots in Period 1 (Fig. 52). In Period 2, the Medium plots had significantly greater carbon concentrations than Reference plots, but did not differ from High plots. This suggests riparian areas with 25-79% Chinese privet in the understory had root detritus that was richer in carbon than areas without Chinese privet or floodplains with >80% understory Chinese privet. This may be attributed to retention of a regeneration and herbaceous layer along with rapidly growing understory Chinese privet stems on the Medium Chinese privet plots. Carbon content for dead roots was significantly greater in Medium Chinese privet plots than the Reference plots for both years, but no difference was detected between Medium and High plots (Fig. 53). There were no differences in C:N ratios across Chinese privet categories for either year.

Seasonal differences were detected for nutrients in dead roots (Fig. 54). As was the case with live roots, nitrogen concentration and content were significantly greater in the winter compared with summer and fall, suggesting retranslocation of nutrients from shoot to the roots. Carbon concentration was greatest in the fall, similar to live root seasonal trends. Furthermore, carbon content was significantly lower in the winter than spring, summer, and fall. Cavalcanti and Lockaby (2005) reported a bimodal increase in dead root biomass in the fall and spring in West Georgia coastal plain watersheds. However, Jolley (2008) described dead root biomass peaks in fall and winter for West Georgia coastal plain watersheds. Additionally, Burke and Raynal (1994) reported that the season where the greatest amount of dead root biomass was observed was variable for a northern hardwood forest, being greatest one year in the spring followed by a year when it was greatest in the fall. Lastly, Hendrick and Pregitzer (1992) reported that root mortality in a northern hardwood forest was more evenly distributed throughout the year as compared with root production, but increased gradually from summer through fall. In the current study, the C:N ratio of dead roots was significantly greater in the fall than other seasons, reflecting the greater carbon concentration and lower nitrogen concentration at that time.

Water Chemistry. Stream water quality data showed positive correlations with litterfall productivity and BNPP (Figs. 55 and 56). Higher nutrient values were strongly related to higher NPP. Higher levels of nutrients moving through a watershed and being transported to floodplains through overbank flooding or stormwater runoff may have stimulated increased litterfall productivity and BNPP. Numerous studies have documented the exchange of nutrients between streams and floodplains (Brinson 1990, Junk 1997, Tockner et al. 1999) and how they influence floodplain NPP.

Land Use Influence

Predominant land use was based on percent watershed impervious surface, with means of 1.24, 3.68, 3.39, and 30.30 % for forested, rural, developing, and urban land use categories, respectively. Partitioning the research plots' watersheds into predominant land use categories revealed that watersheds with more urban influence had significantly greater Total NPP than developing, rural, and forested watersheds in Period 1 (Fig. 57).

Urban watersheds had significantly greater Total NPP than forested watersheds in Period 2. The Total NPP in Period 2 was less variable than Period 1, which was likely due to lower rainfall and less runoff to adjacent streams. Watershed land use has been shown to strongly influence nutrient levels in streams with urban landscapes, generally contributing more nutrients in baseflow and stormwater runoff than agricultural or forested landscapes (Schoonover 2005, Crim 2007). Other studies have pointed to increased nutrient availability and subsequent runoff events in urban areas contributing to the success of invasive, nonnative species (Vidra et al. 2006, King and Buckney 2000). Vidra et al. (2006) noted that exotic species richness was generally positively correlated to soil fertility in urban settings. King and Buckney (2000) concluded the general increase of nutrients in urban Sydney, Australia stream sediments enhanced nonnative plant invasions and altered stream plant communities. Imhoff et al. (2004) reported that urbanization increased NPP at local and regional scales, especially in resource-limited and cold regions, through localized warming or "urban heat" that contributed to the extension of the growing season. Perhaps the ability of invasive, nonnative plants to rapidly occupy habitats in urban areas was also enhanced by nutrient rich stormwater runoff and an extension of the growing season that translated into greater total NPP rates when compared with more natural systems in the current study.

Percent of watershed impervious surface, a common criterion for delineating urban watersheds, was not related to percent understory Chinese privet in this study. However, overall presence and diversity of invasive, nonnative species was greatest in the urban influenced watersheds. Burton and Samuelson (2007) and Loewenstein and Loewenstein (2005) noted an increase in invasive, nonnative plant species with increasing urban land use in West Georgia. Increases were likely due to a suite of factors, including more edge habitat due to fragmentation of the forests and an abundant seed supply. The significantly high NPP found in urban riparian floodplains was likely due to the cumulative effects of nutrient rich stream baseflow and stormwater runoff, increased nonnative species diversity and presence, and the high rates of NPP exhibited by some nonnative plants (Ehrenfeld 2003).

CONCLUSIONS

Chinese privet influenced forest processes such as above- and belowground productivity. It was hypothesized that, as the density of Chinese privet increased in the understory of riparian forests, there would be a decrease in overall ANPP due to the loss of overstory trees and an increase in BNPP due to increased fine root densities associated with dense clumps of Chinese privet. ANPP did not support the stated hypothesis as there was no significant difference among Chinese privet categories. BNPP supported the hypothesis by being significantly greater in Medium and High Chinese privet plots during Period 1. However, there was no difference among Chinese privet Categories for BNPP in Period 2. Although the loss of large, native overstory trees had not occurred during the current study, differences between Total NPP in research plots were observed. In normal rainfall years, Total NPP at significantly increased and then numerically, but not significantly, decreased with increasing levels of Chinese privet invasion. These changes were strongly influenced by BNPP. Additionally, it was observed that a dense Chinese privet mid-story was accompanied by a loss of forest structure diversity. That is, the regeneration and shrub layers tended to decline under a dense mid-story of Chinese privet, which likely contributed to a decrease in NPP.

The lack of significant differences between Chinese privet categories in Total NPP and ANPP during Period 2 was influenced by a decrease in BNPP. Chinese privet is a shallow rooted plant and may have been negatively impacted during low moisture conditions resulting in decreased BNPP. Additionally, research plots in the current study were dominated by large, native canopy trees that were approximately the same age and likely had similar rates of annual stem increment increase. Since woody productivity rates were the greatest contributor to ANPP and total NPP, similar rates of total NPP and ANPP among Chinese privet categories may be expected. Furthermore, the lack of significant differences in litterfall among Chinese privet categories is likely attributed to the light-mass nature of Chinese privet leaves. Although more leaves may have fallen in the Medium Chinese privet plots, the cumulative mass was not great enough to drive a significant difference.

LAI was significantly greater in the Medium and High Chinese privet categories than in the Reference category. This difference was likely due to the dense thickets formed by understory and mid-story Chinese privet and their associated semi-evergreen to evergreen leaves. Increased LAI may have translated into increased productivity that was reflected belowground in Period 1.

Nitrogen mineralization rates were positively and significantly related to all productivity measures suggesting nitrogen was a limiting nutrient in research floodplains of the current study. Root nutrient content was driven by fine root biomass rather than differences in carbon or nitrogen concentrations among Chinese privet categories.

However, seasonal differences in root nutrient concentrations were detected. For example, the significant increase in live root nitrogen concentration during the winter season suggests retranslocation from the shoot to the roots.

The eventual mortality of large, native overstory trees and the lack of native plant regeneration (Chapter 4, Influence of Chinese Privet on Native Plant Regeneration in Riparian Forests of the Southern Piedmont) will translate into dramatically reduced NPP in riparian forests heavily invaded by Chinese privet. This reduction of NPP will also negatively impact the ability of riparian forests to sequester carbon (Chapter 3, Influence of an Invasive, Nonnative Tree Species on Carbon Allocation and Sequestration in Riparian Forests of the Southern Piedmont). The decrease in total NPP at high levels of understory Chinese privet invasion may be of acute interest to forest managers seeking to maximize productivity.

Understory riparian development is influenced by both flooding and available light (Brinson 1990), and the combination of low light and frequent flooding may limit the proliferation of many herbaceous species (Menges and Waller 1983). Chinese privet has successfully become established in many floodplain understories due to its invasive characteristics of prolific reproduction, rapid growth, and tolerance of shade and flooding. Anthropogenic influences such as increased nutrients in a watershed as a by-product of suburban and urban land use may increase NPP and also make the spread and invasion of riparian forests by invasive, nonnative plants easier. Pimentel et al. (2005) aptly states that the challenge with invasive, nonnative species is not just elucidating their economic and ecological impact, but identifying measures that will prevent future damage to natural and managed ecosystems. These measures most certainly involve education of natural resource managers and the general public of the role people may play in minimizing spread of invasive, nonnative species.

Table 2. Period 1 mean net primary productivity for Chinese privet categories Reference, Medium and High plots and overall range for data. Means in a row followed by different letters are significantly different by Tukey's HSD (α=0.10). Standard errors in parentheses.

Period 1		Privet Category		
Productivity (g m^{-2} yr^{-1})	Reference	Medium	High	Range
Litterfall Total	618.4 (26.2)^{a}	757.6 (55.9)^{a}	703.8 (46.4)^{a}	510-932
Leaf litter	553.7 (31.8)^{a}	684.3 (51.6)^{a}	622.3 (43.7^{a}	471-826
Reproductive litter	64.7 (6.7)^{a}	73.3 (12.3)^{a}	81.5 (7.5)^{a}	39-106
Woody biomass	633.5 (105.1)^{a}	947.7 (133.5)^{a}	881.6 (126.7)^{a}	386-1418
Total Aboveground	1251.9 (117.7)^{a}	1705.3 (183.9)^{a}	1585.4 (157.1)^{a}	907-2244
Belowground	364.3 (38.5)^{b}	793.98 (73.8)^{a}	646.9 (65.5)^{a}	304-987
Total	1616.2 (87.8)^{b}	2499.3 (256.0)^{a}	2232.3 (183.0)^{ab}	1506-3195

Table 3. Period 2 mean net primary productivity for Chinese privet categories Reference, Medium and High plots and overall range for data. Means in a row followed by different letters are significantly different by Tukey's HSD (α=0.10). Standard errors in parentheses.

Period 2		Privet Category		
Productivity (g m^{-2} yr^{-1})	Reference	Medium	High	Range
Litterfall	523.4 (17.4)^{b}	634.8 (26.6)^{a}	605.8 (16.7)^{a}	487-682
Leaf litter	451.8 (9.9)^{a}	525.8 (21.5)^{a}	493.3 (16.9)^{a}	430-568
Reproductive litter	71.6 (7.0)^{b}	109.0 (14.2)^{a}	112.5 (6.8)^{a}	58-145
Woody biomass	586.9 (111.3)^{a}	717.8 (45.2)^{a}	827.7 (116.8)^{a}	379-1296
Total Aboveground	1110.3 (122.9)^{a}	1352.6 (68.6)^{a}	1433.5 (127.0)^{a}	934-1971
Belowground	452.8 (59.1)^{a}	550.8 (41.7)^{a}	573.9 (58.6)^{a}	369-808
Total	1563.1 (107.2)^{a}	1903.4 (32.2)^{a}	2007.4 (163.3)^{a}	1363-2769

Table 4. Analysis of variance (ANOVA) of nutrient concentrations and content in fine roots for Chinese privet categories in Period 1. Different letters represent significant differences in means by Tukey's HSD (α=0.10). Standard errors in parentheses.

Parameter measured		Chinese privet Category	
	Reference	Medium	High
N Content (g m^{-2})			
Live	64.4 (4.4)^{c}	121.6 (8.6)^{a}	102.2 (4.9)^{b}
Dead	7.1 (0.7)^{b}	11.4 (1.2)^{a}	9.4 (0.9)^{ab}
C Content (g m^{-2})			
Live	2958.1 (172.2)^{c}	5975.7 (333.8)^{a}	4903.3 (186.3)^{b}
Dead	316.2 (35.4)^{b}	507.9 (56.1)^{a}	437.1 (43.6)^{ab}
N Concentration (mg kg^{-1})			
Live	0.97 (0.03)^{a}	0.91 (0.03)^{a}	0.90 (0.02)^{a}
Dead	1.06 (0.04)^{a}	1.07 (0.03)^{a}	1.03 (0.02)^{a}
C Concentration (mg kg^{-1})			
Live	45.2 (0.2)^{b}	46.0 (0.2)^{a}	45.5 (0.1)^{a}
Dead	43.4 (0.7)^{b}	45.5 (0.5)^{a}	43.8 (0.3)^{b}

Table 5. Analysis of variance (ANOVA) of nutrient concentrations and content in fine roots for Chinese privet categories in Period 2. Different letters represent significant differences in means by Tukey's HSD (α=0.10). Standard errors in parentheses.

Parameter Measured		Chinese privet Category	
	Reference	Medium	High
N Content (g m^{-2})			
Live	66.4 (6.2)^{b}	86.9 (5.9)^{a}	80.2 (4.4)^{a}
Dead	9.2 (1.0)^{b}	15.6 (1.6)^{a}	16.3 (1.2)^{a}
C Content (g m^{-2})			
Live	2990.8 (180.3)^{c}	4860.3 (259.6)^{a}	4207.5 (166.4)^{b}
Dead	496.4 (54.9)^{b}	853.3 (90.9)^{a}	870.0 (56.7)^{a}
N Concentration (mg kg^{-1})			
Live	0.94 (0.06)^{a}	0.80 (0.03)^{b}	0.80 (0.02)^{b}
Dead	0.91 (0.05)^{a}	0.94 (0.04)^{a}	0.93 (0.02)^{a}
C Concentration (mg kg^{-1})			
Live	45.7 (0.2)^{a}	45.8 (0.2)^{a}	45.6 (0.1)^{a}
Dead	44.3 (0.8)^{b}	45.9 (0.3)^{a}	45.0 (0.2)^{ab}

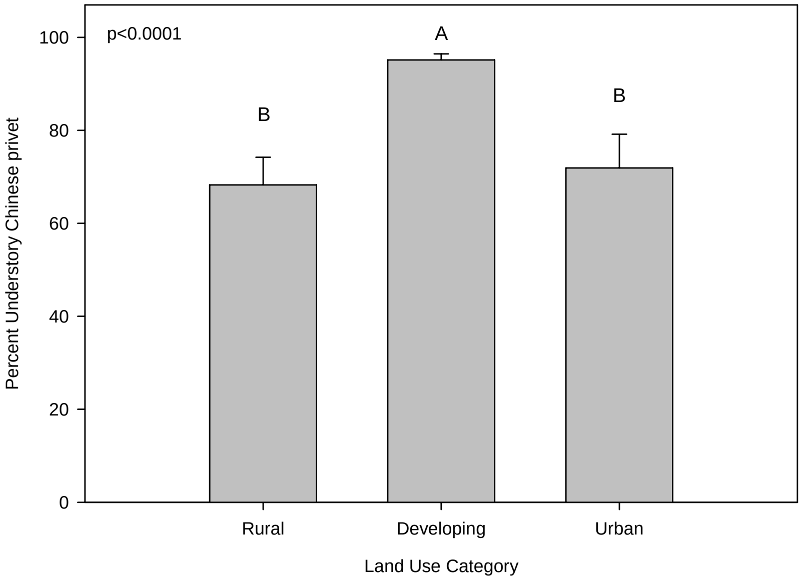

Figure 4. Percent understory occupied by Chinese privet differed significantly by current predominant land use. Letters represent significant difference in means by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

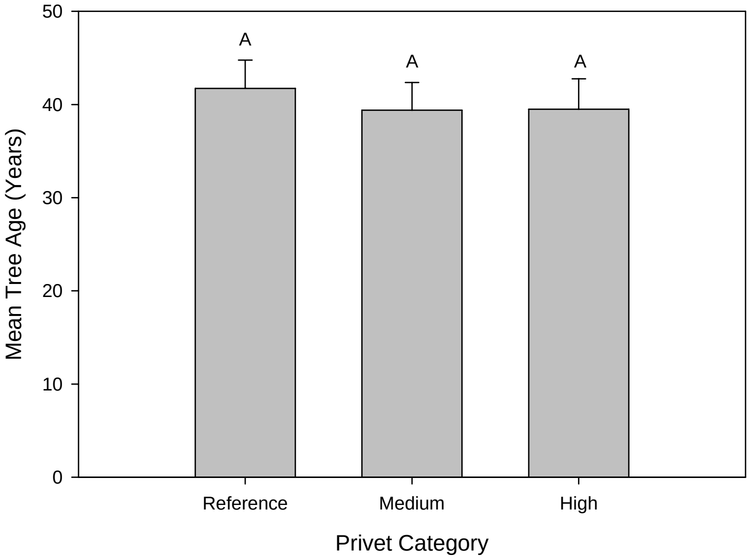

Figure 5. No significant difference in stand age among Chinese privet categories. Letters represent significant difference in means by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

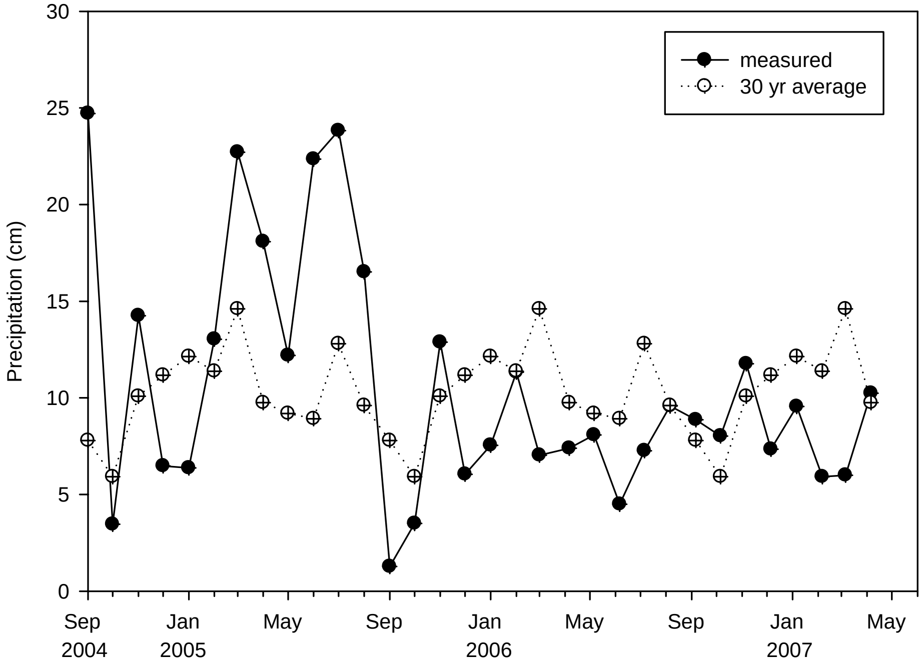

Figure 6. Monthly precipitation and 30-year average for September 2004 – May 2007.

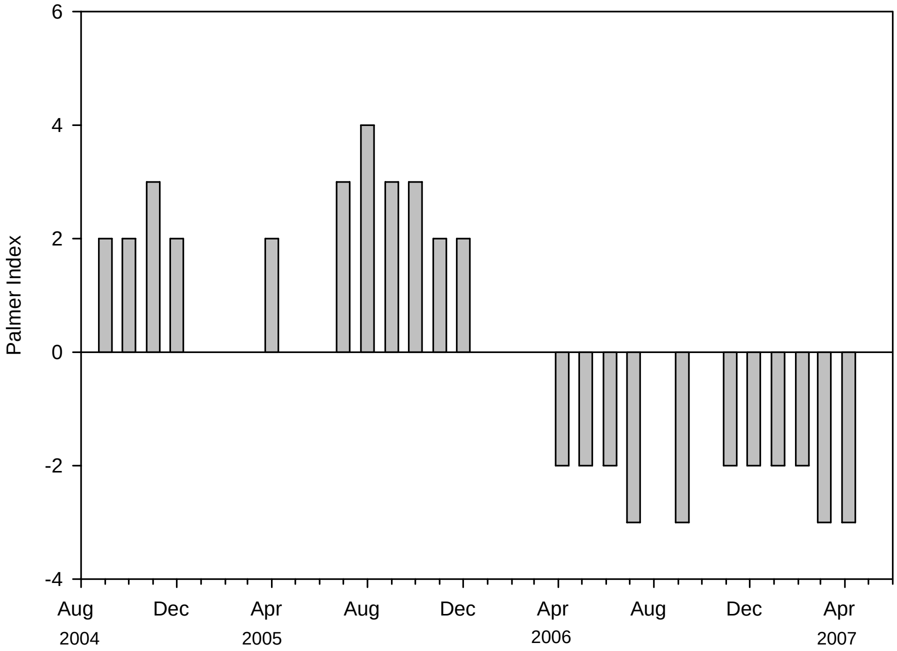

Figure 7. Palmer drought severity indices for September 2004 – April 2007. Positive bars indicate excess moisture, negative bars indicate drought.

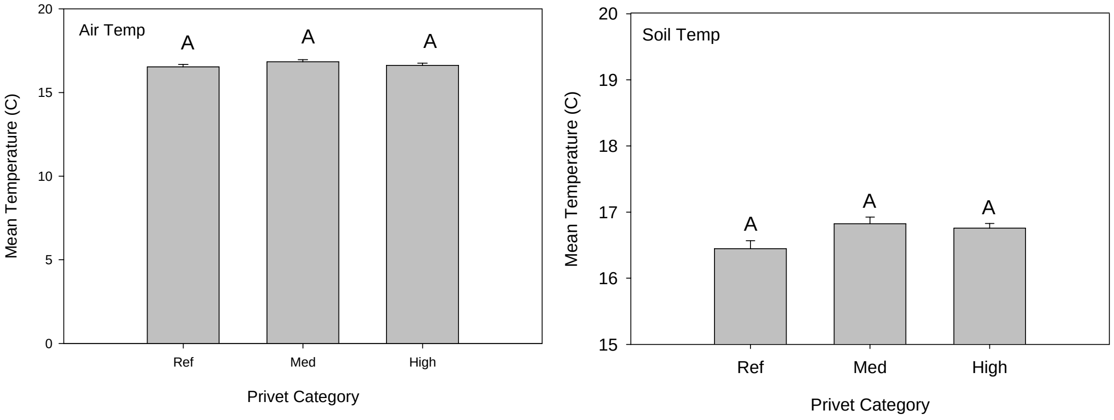

Figure 8. Air and soil temperature measurements by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

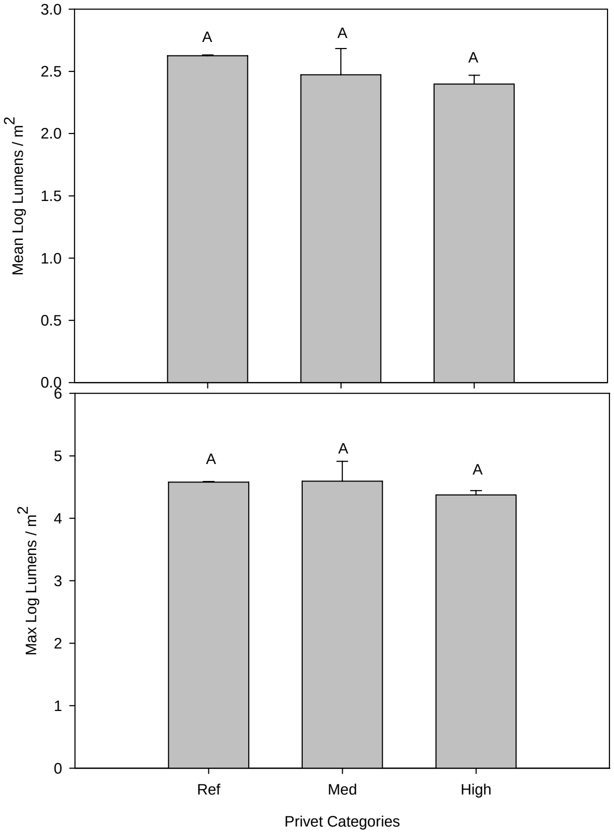

Figure 9. Light measurements by Chinese privet category, mean light intensity (top) and maximum intensity (bottom). Letters represent significant difference in means by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

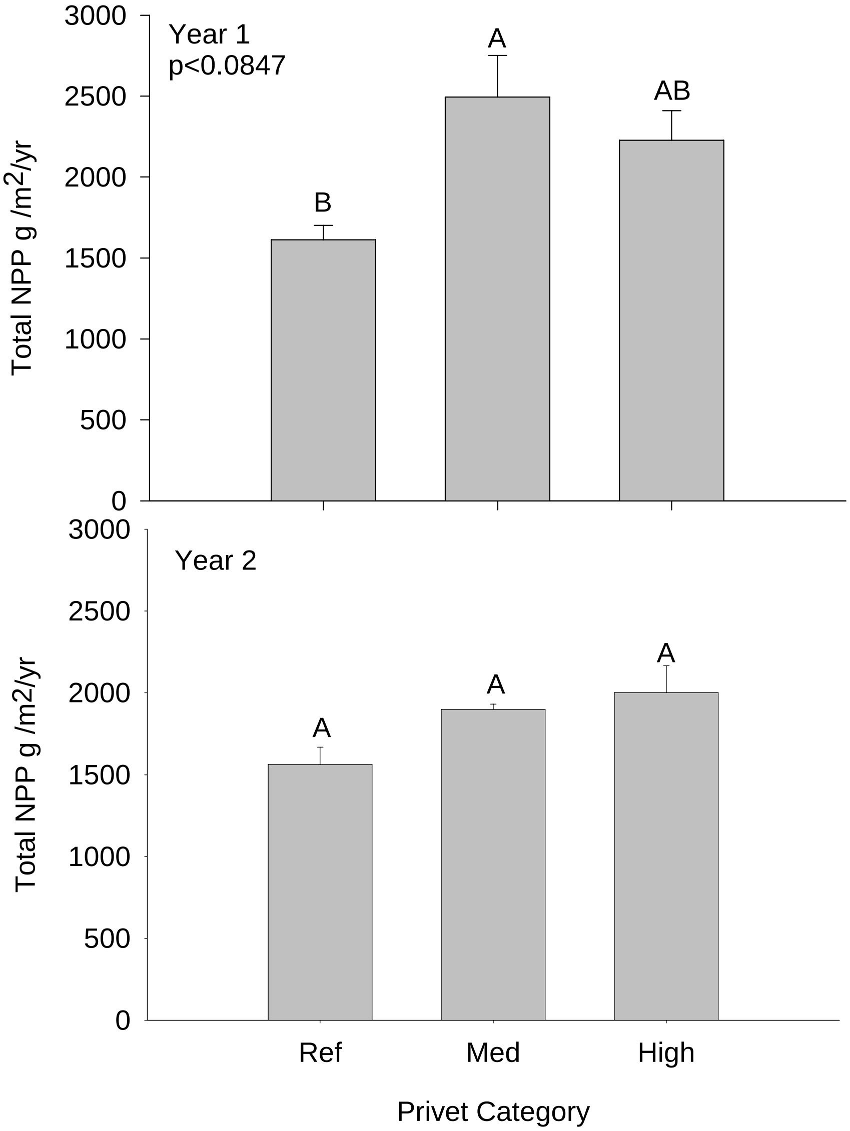

Figure 10. Comparison of total NPP by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

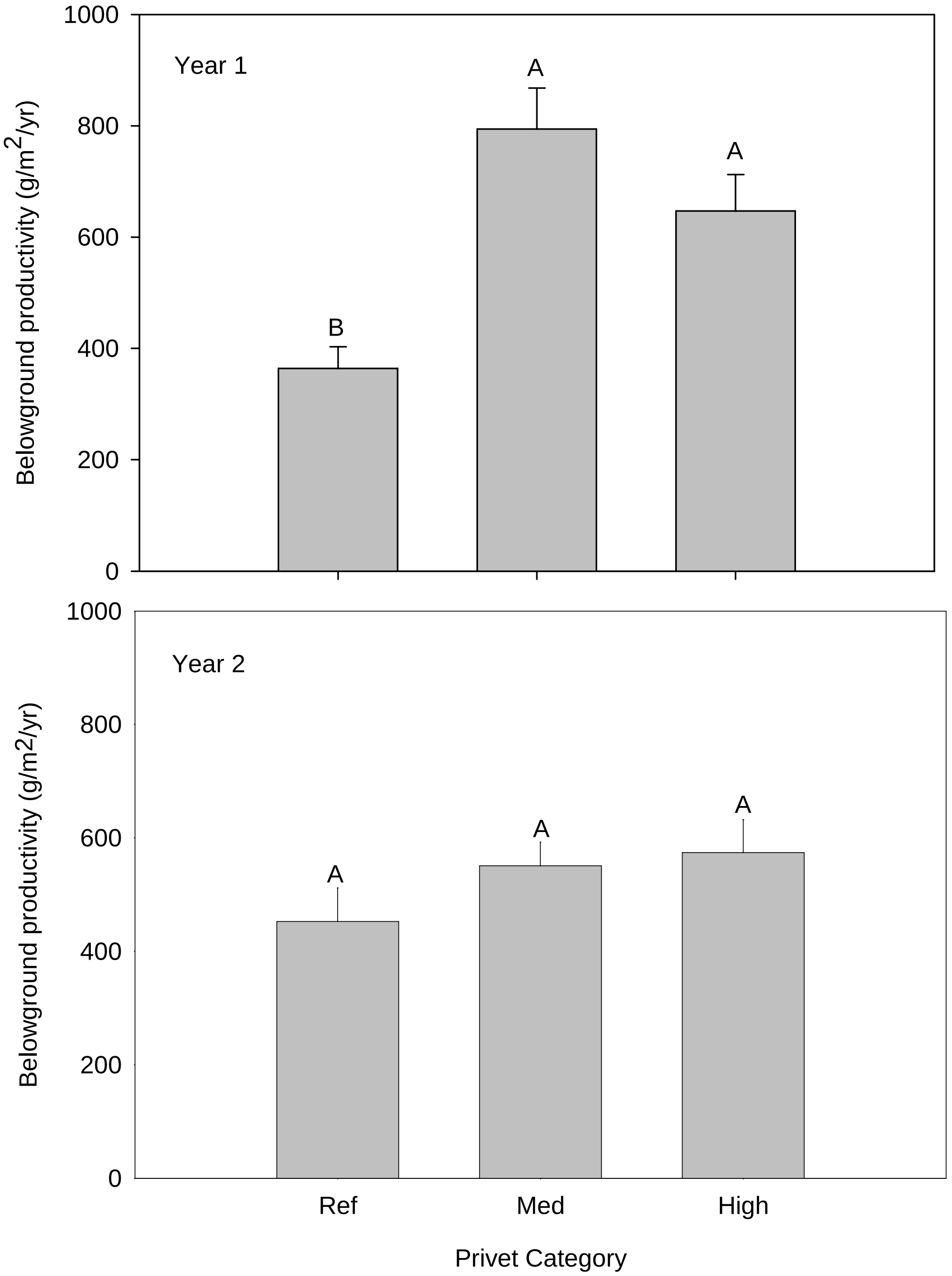

Figure 11. Comparison of belowground productivity by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

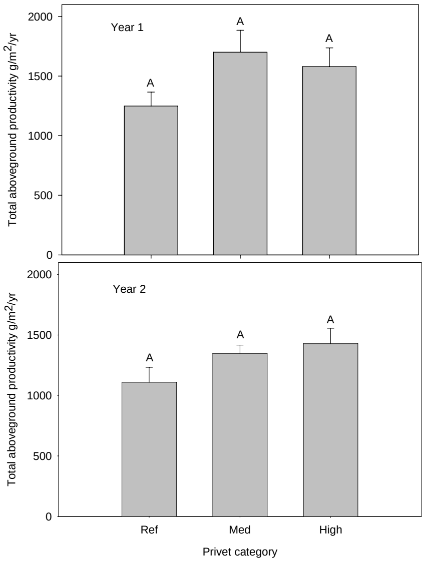

Figure 12. Comparison of total aboveground productivity by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

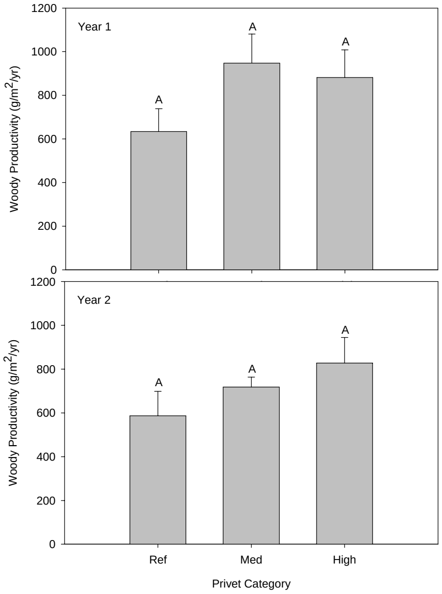

Figure 13. Comparison of woody productivity by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

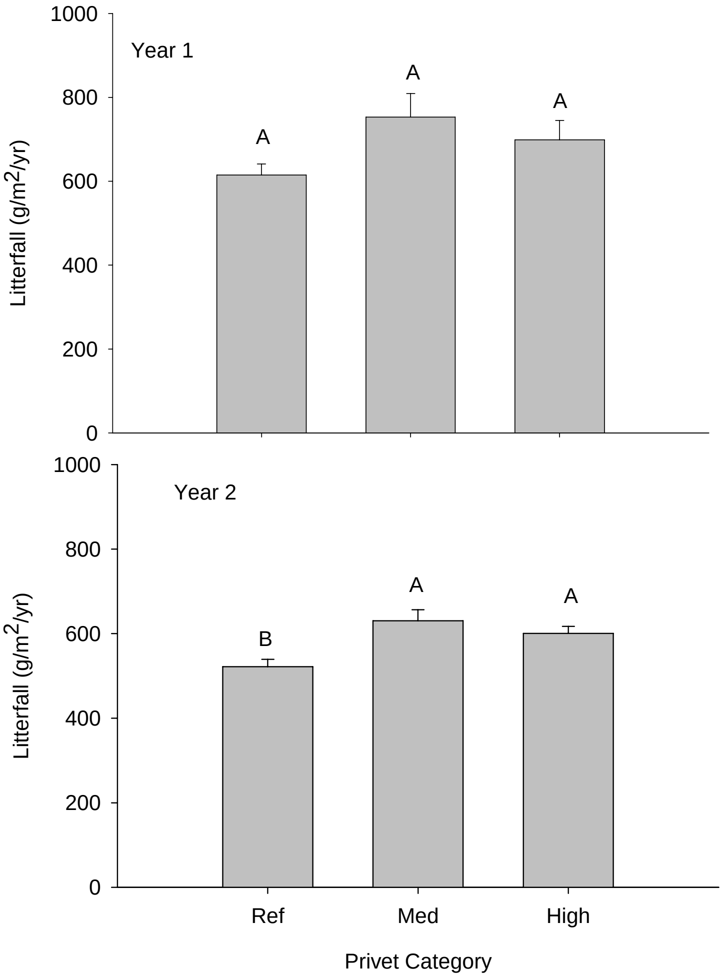

Figure 14. Comparison of annual litterfall production by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

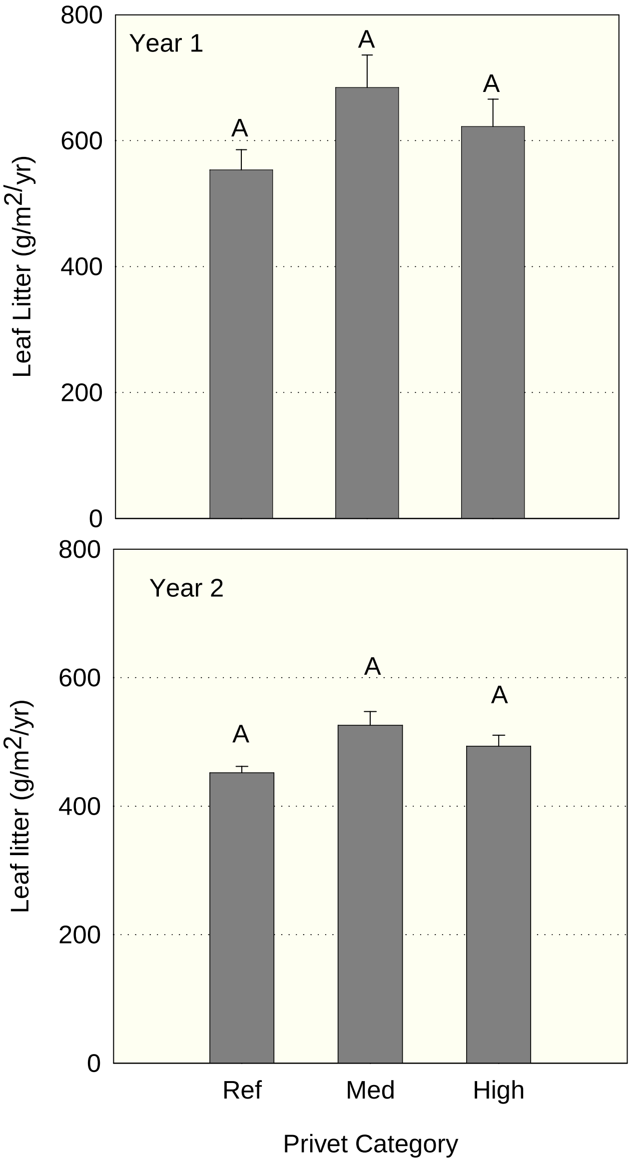

Figure 15. Comparison of annual leaf litter production by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

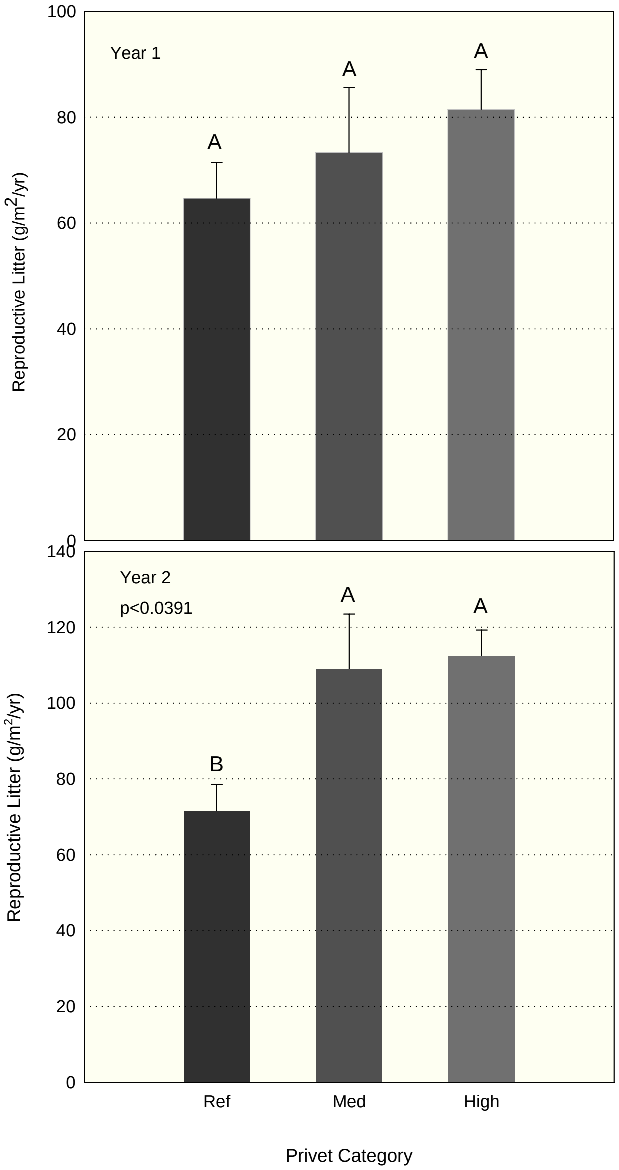

Figure 16. Comparison of annual reproductive litter production by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

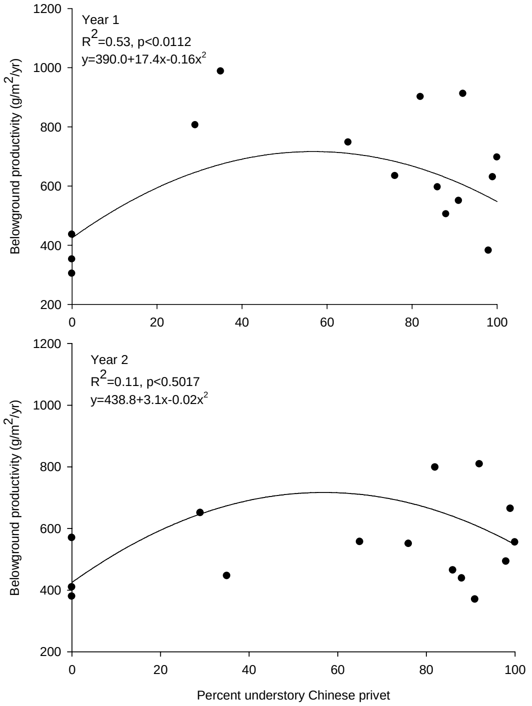

Figure 17. Quadratic regression relationship between belowground productivity and percent understory Chinese privet.

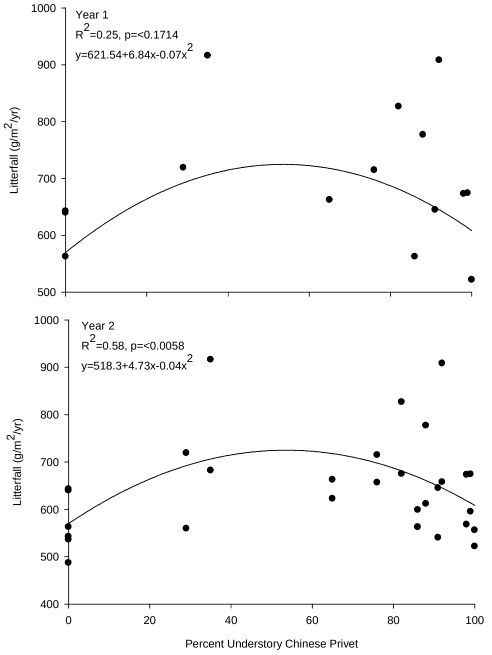

Figure 18. Quadratic regression relationship between percent understory Chinese privet and total litterfall.

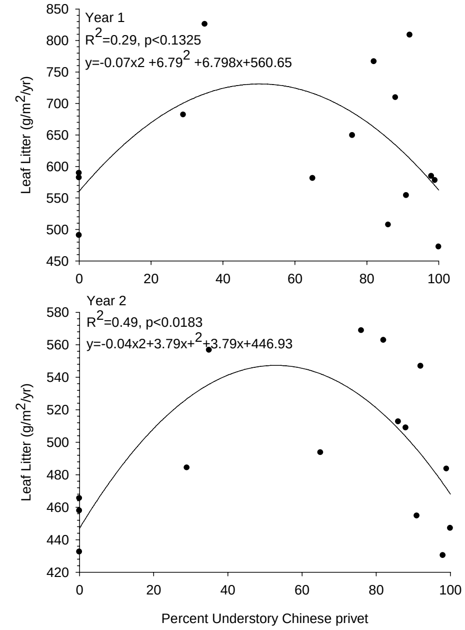

Figure 19. Quadratic regression relationship between percent Chinese privet in understory and leaf litter.

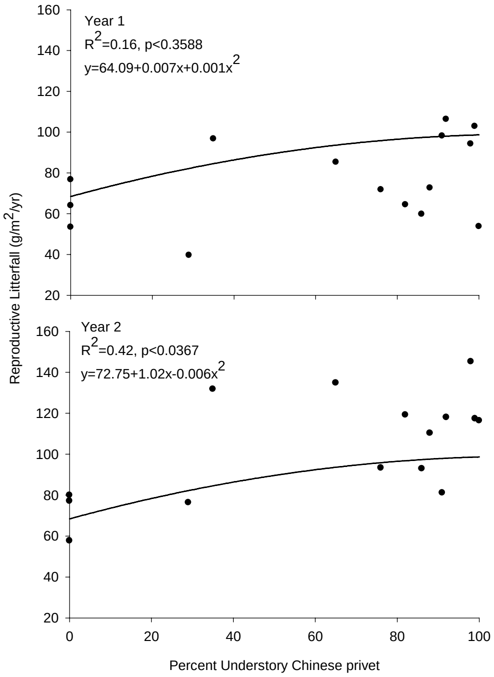

Figure 20. Quadratic regression relationship between percent Chinese privet in understory and reproductive litter.

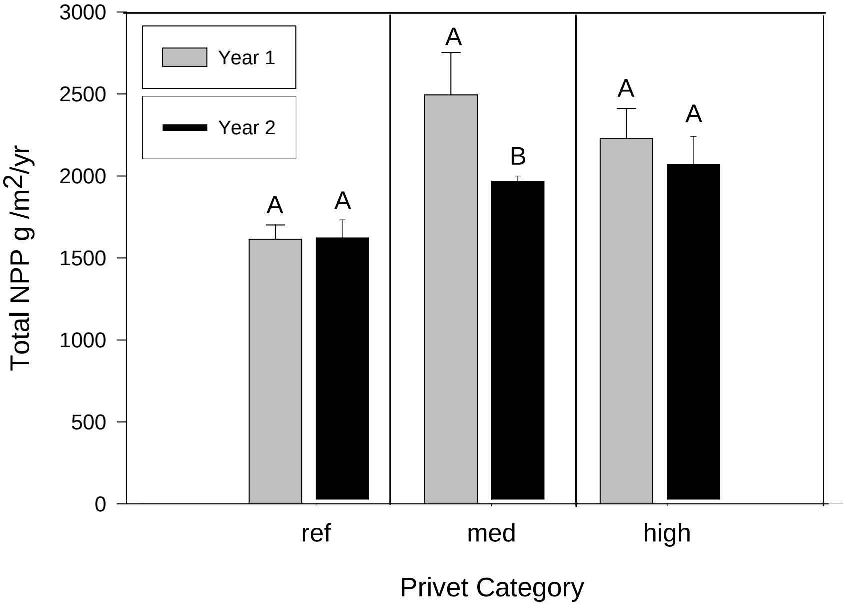

Figure 21. Comparison of total net primary productivity between sampling years by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Medium category significantly different (p<0.0603). Vertical bars indicate standard errors.

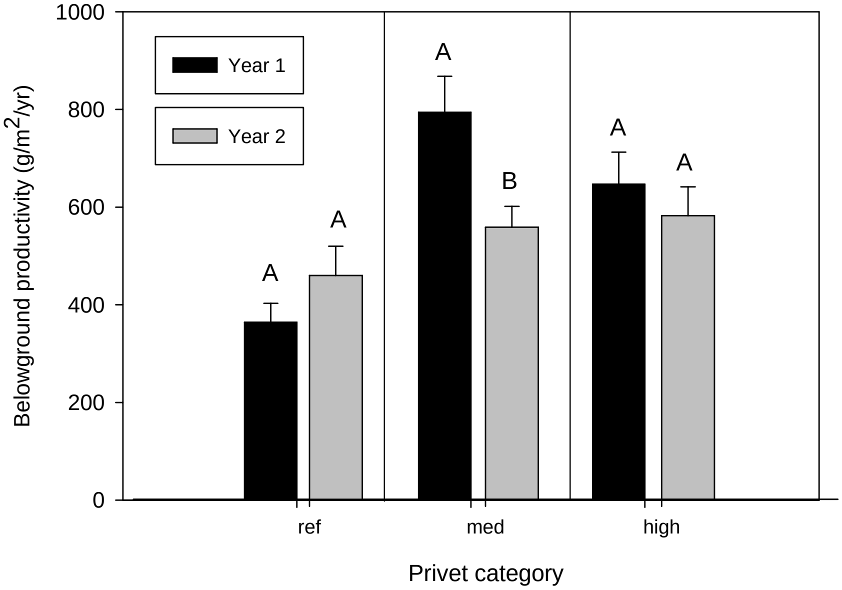

Figure 22. Comparison of belowground productivity between sampling years by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Medium category significantly different (p<0.0284). Vertical bars indicate standard errors.

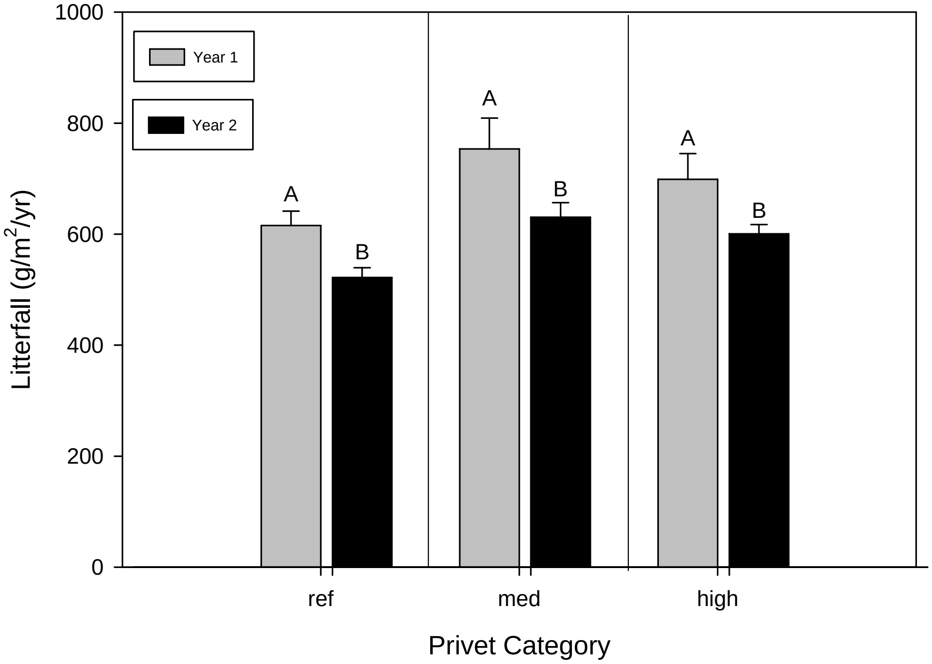

Figure 23. Comparison of total litterfall between sampling years by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10) Reference ($p<0.03$), Medium ($p<0.03$), High ($p<0.02$). Vertical bars represent standard errors.

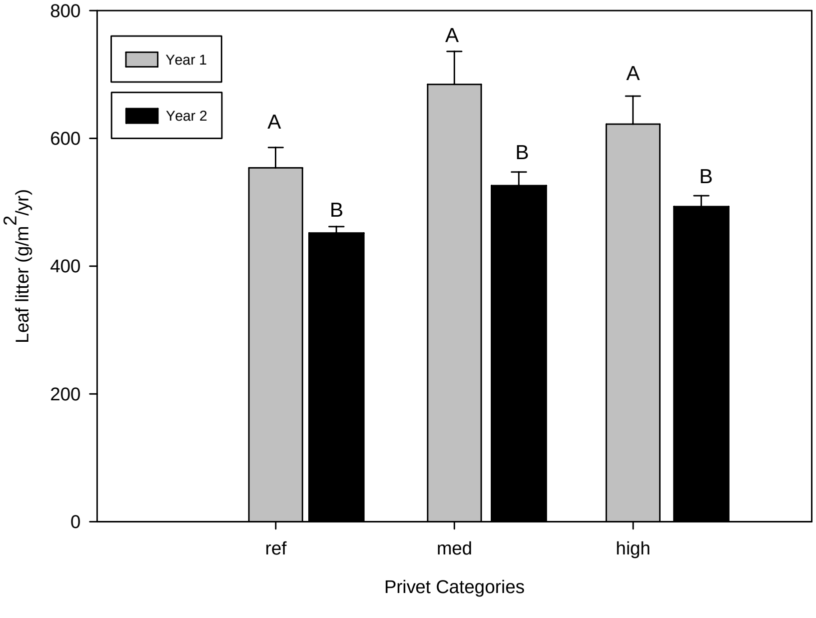

Figure 24. Comparison of leaf litter between sampling years by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10) Reference ($p<0.03$), Medium ($p<0.03$), High ($p<0.02$). Vertical bars represent standard errors.

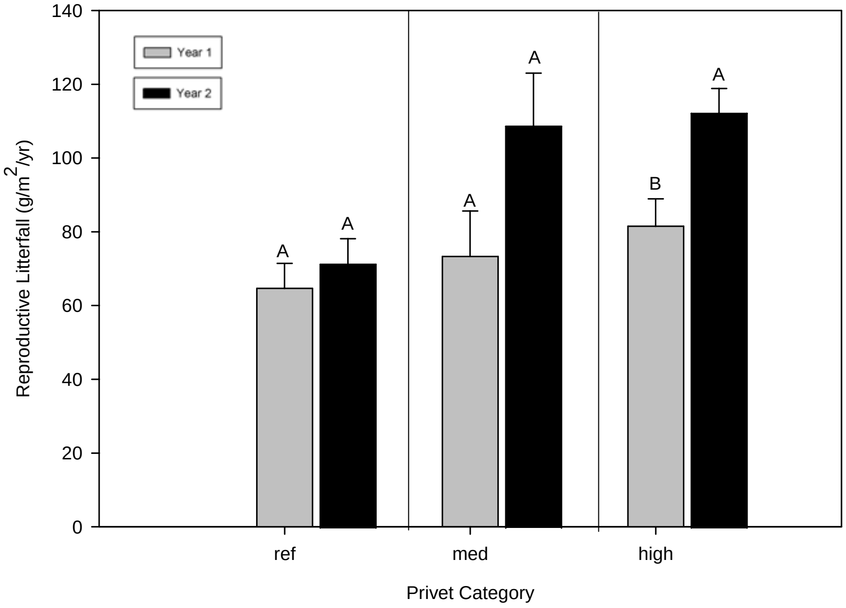

Figure 25. Comparison of reproductive litter between sampling years by Chinese privet category. Means with different letters differ significantly by Tukey HSD ($\alpha=0.10$) Reference ($p<0.5167$), Medium ($p<0.1087$), High ($p<0.00081$). Vertical bars represent standard errors.

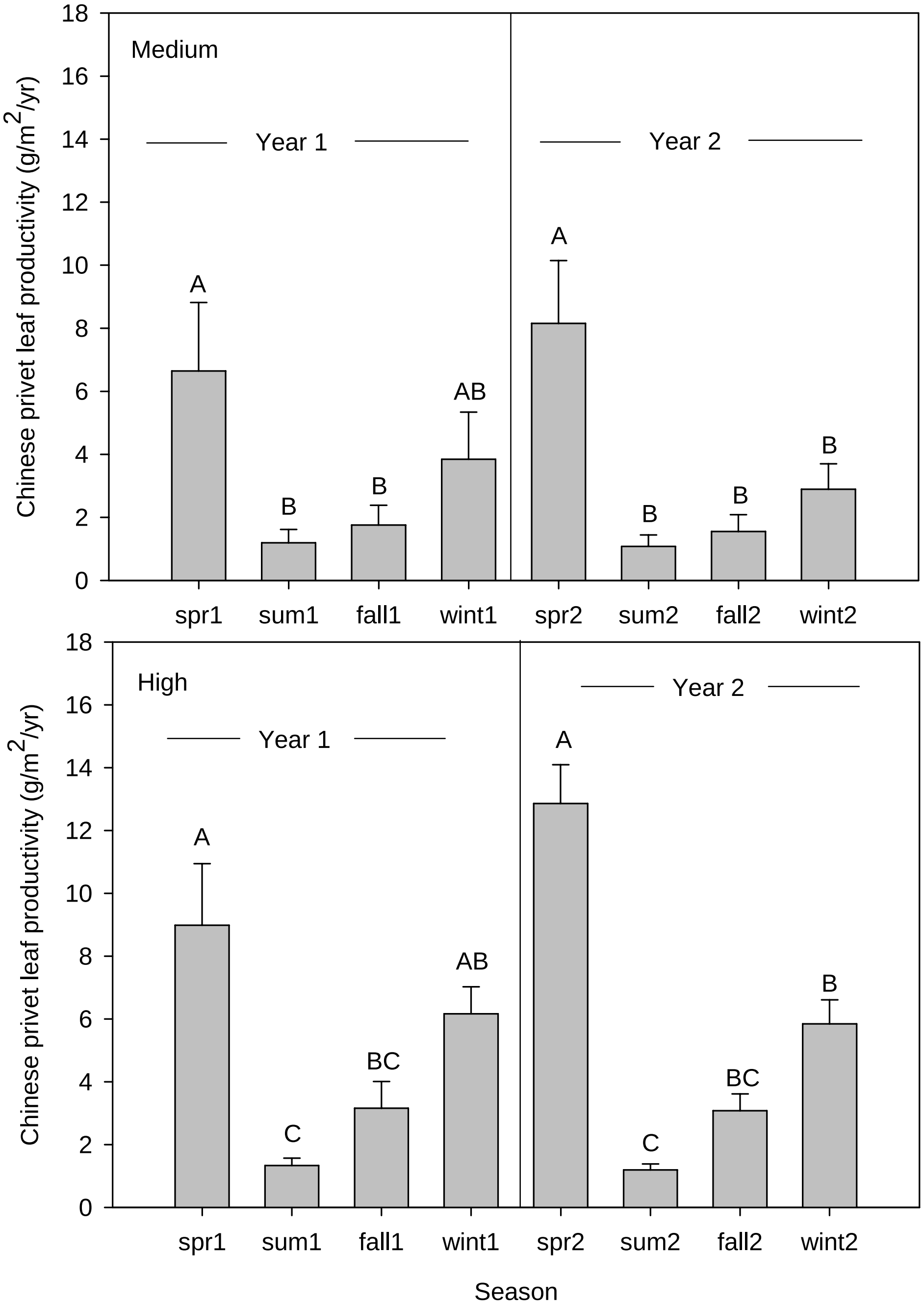

Figure 26. Comparison of Chinese privet leaf productivity across seasons in each sampling year by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

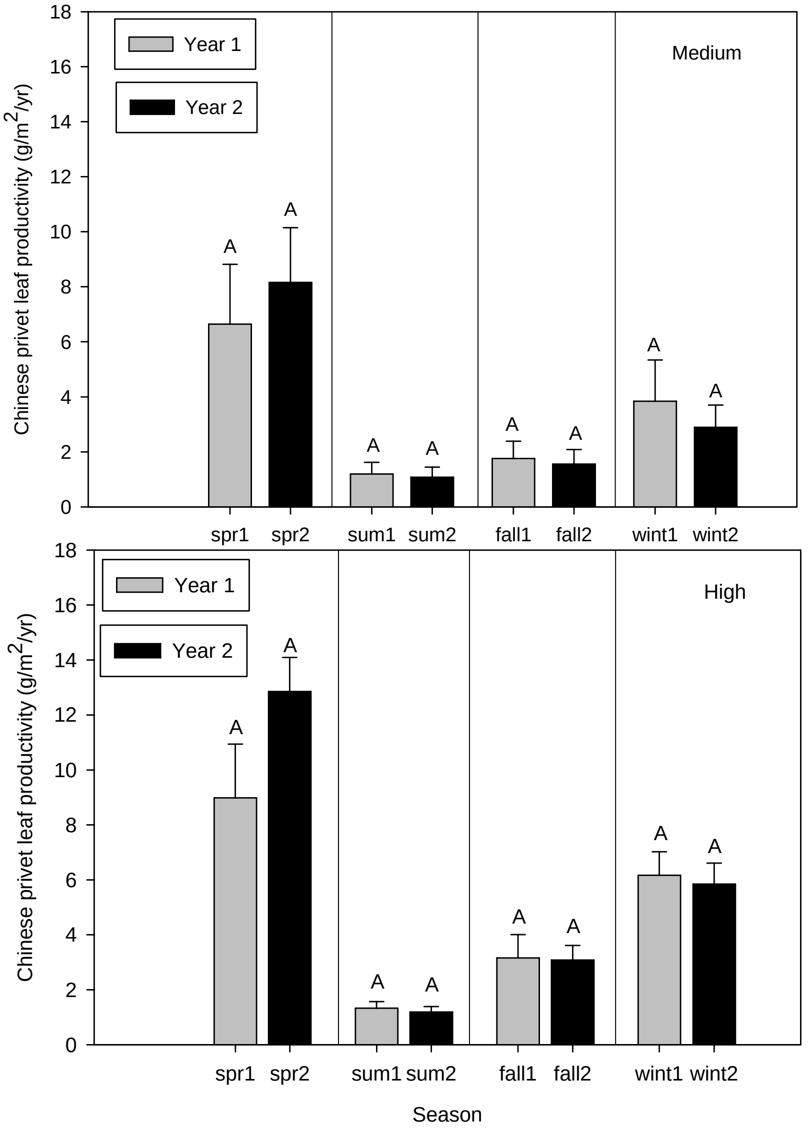

Figure 27. Comparison of Chinese privet leaf productivity across sampling years by season and Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

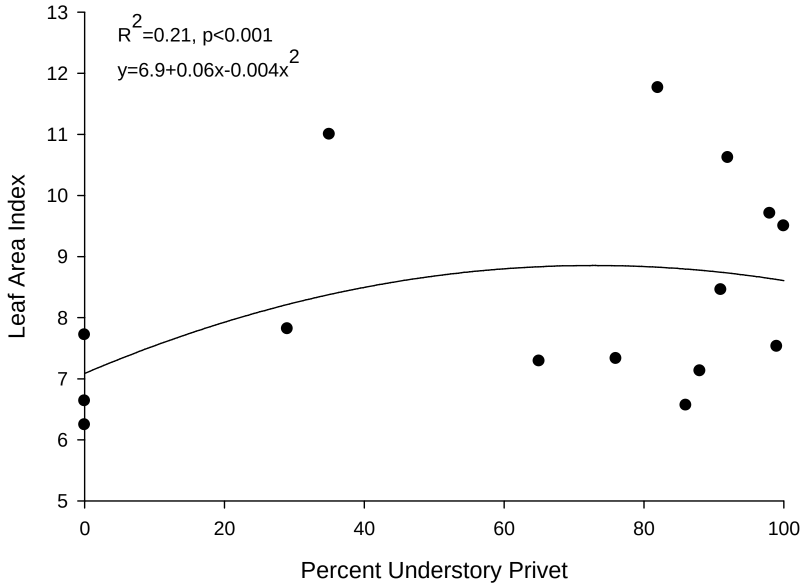

Figure 28. Significant quadratic regression relationship between percent understory Chinese privet and leaf area index in research plots.

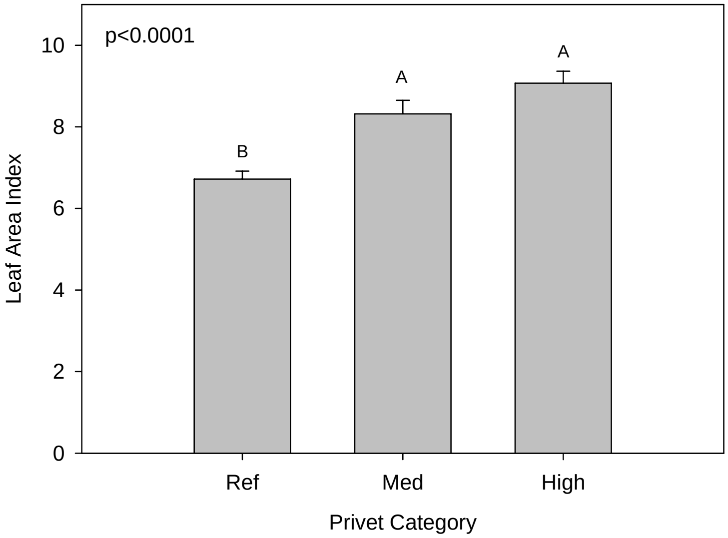

Figure 29. Comparison of leaf area index by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

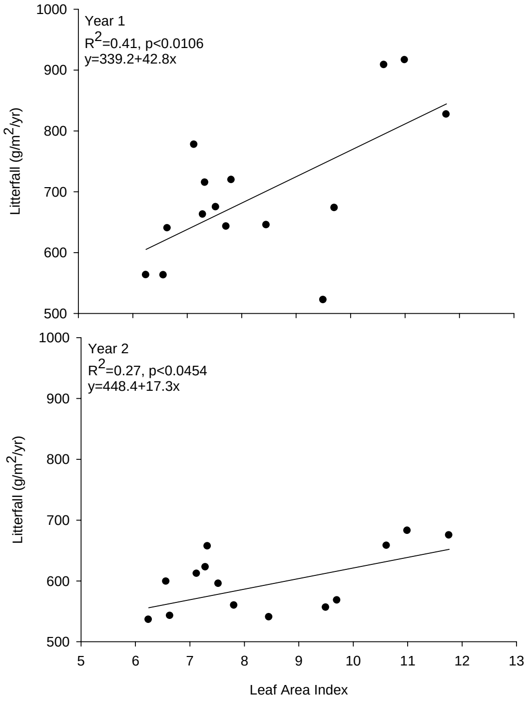

Figure 30. Linear regression relationship between total litterfall and leaf area index.

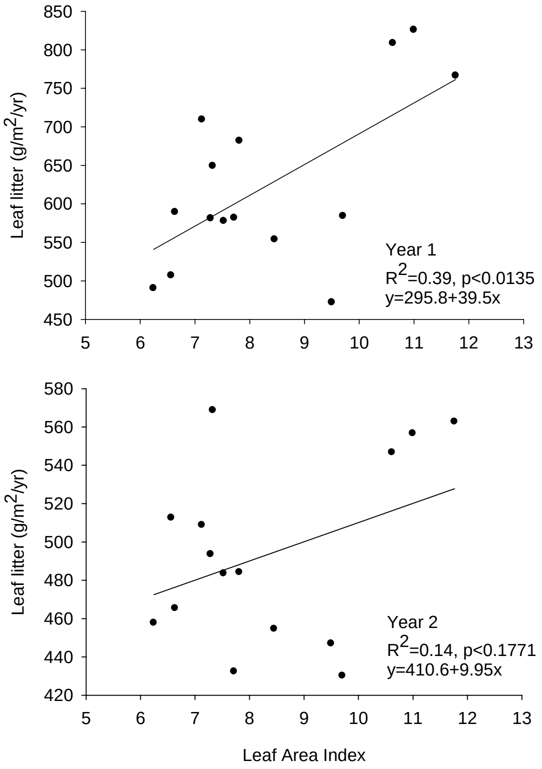

Figure 31. Linear regression relationship between leaf litter and leaf area index.

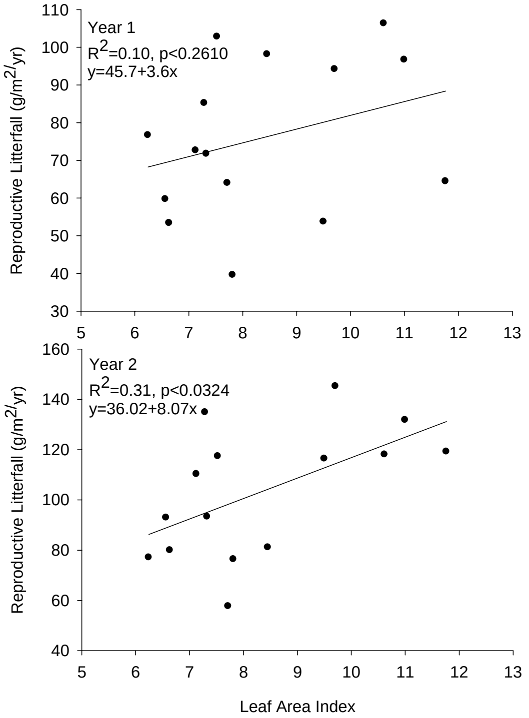

Figure 32. Linear regression relationship between reproductive litterfall and leaf area index.

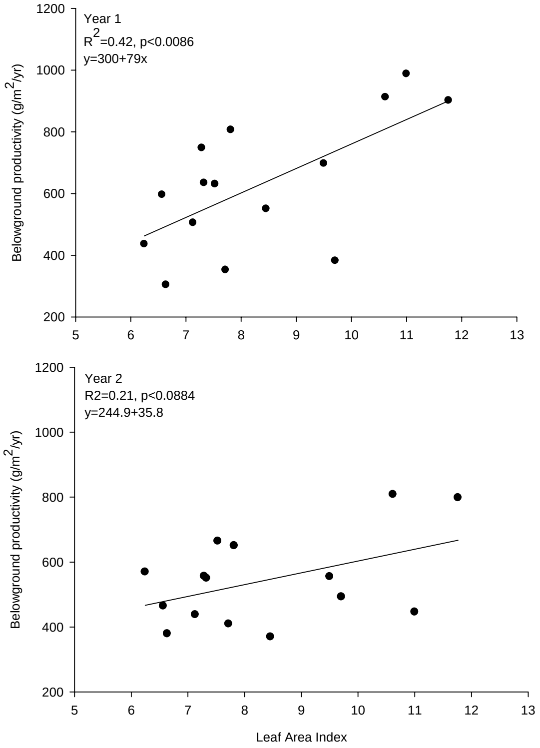

Figure 33. Linear regression relationship between belowground productivity and LAI.

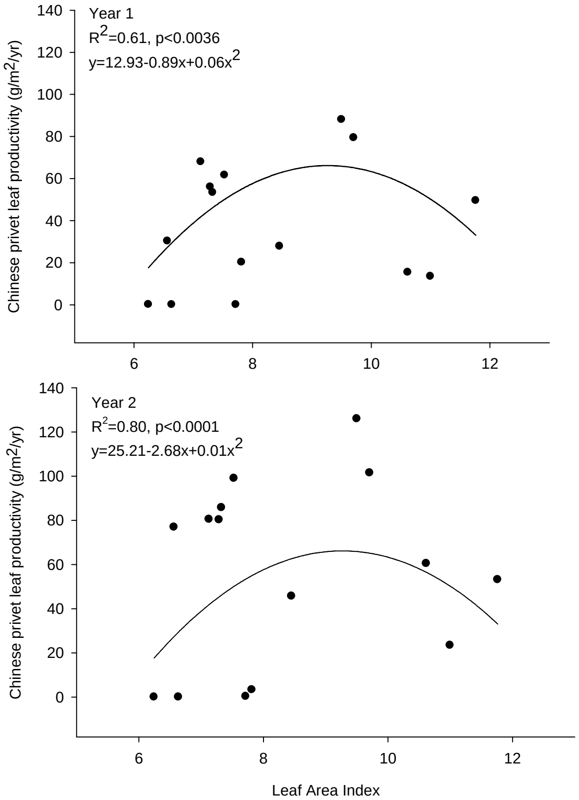

Figure 34. Significant quadratic regression relationship between Chinese privet leaf productivity and leaf area index.

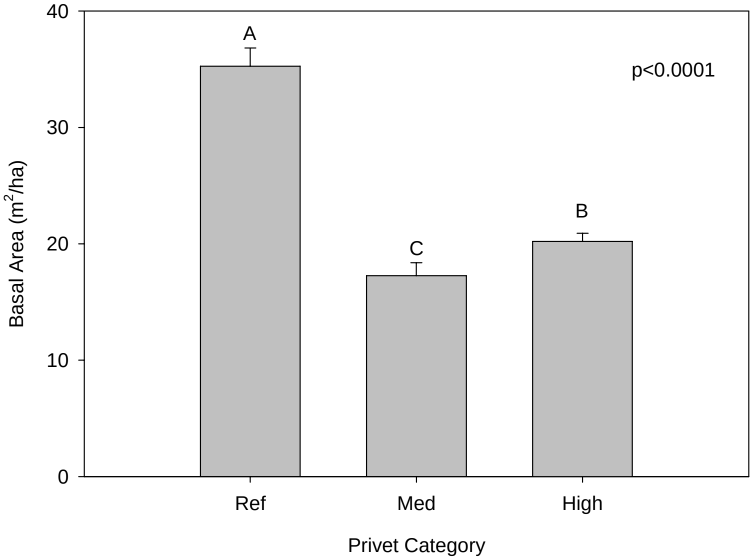

Figure 35. Comparison of basal area by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

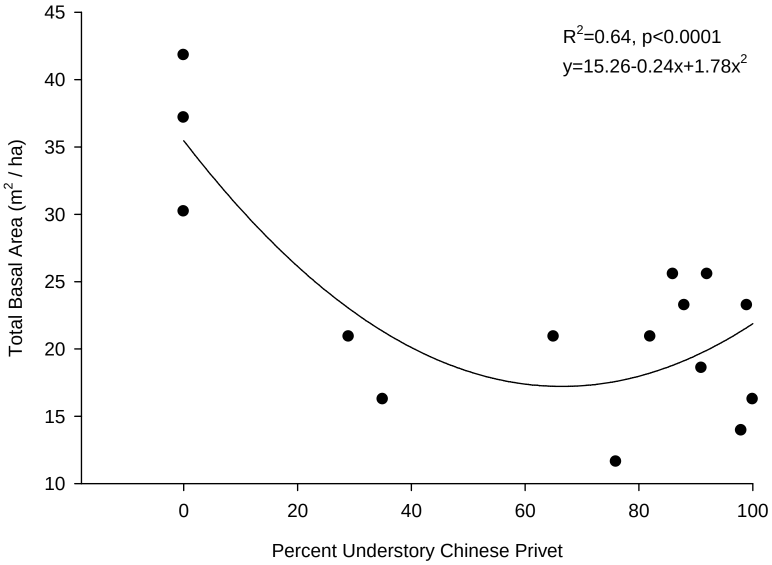

Figure 36. Significant regression relationship between percent understory Chinese privet and basal area.

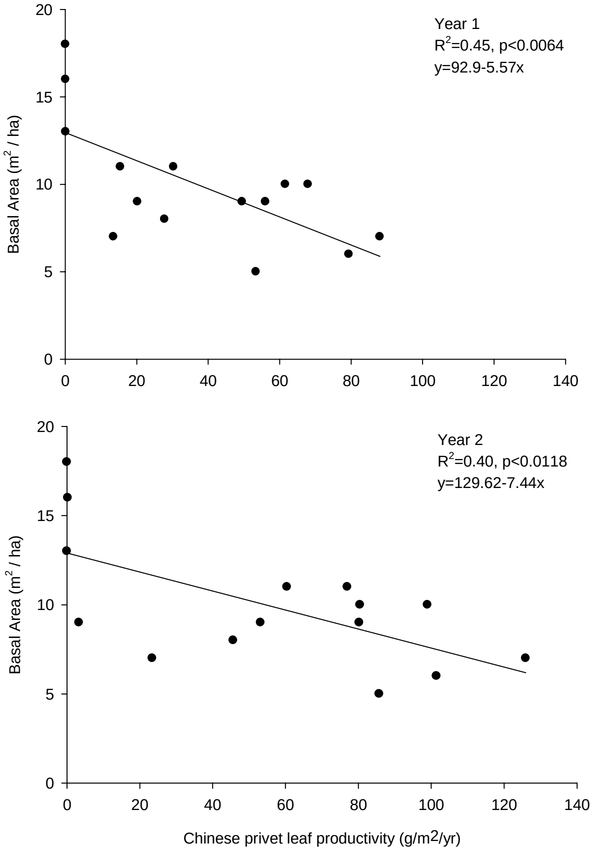

Figure 37. Significant linear regression relationship between Chinese privet leaf productivity and basal area.

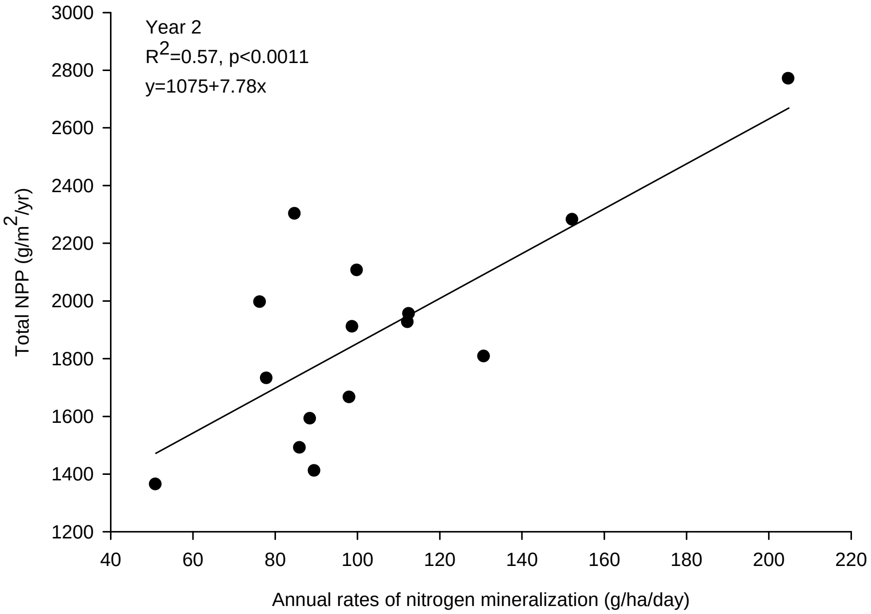

Figure 38. Significant linear regression relationship between total net primary productivity and annual rates of nitrogen mineralization, Period 2.

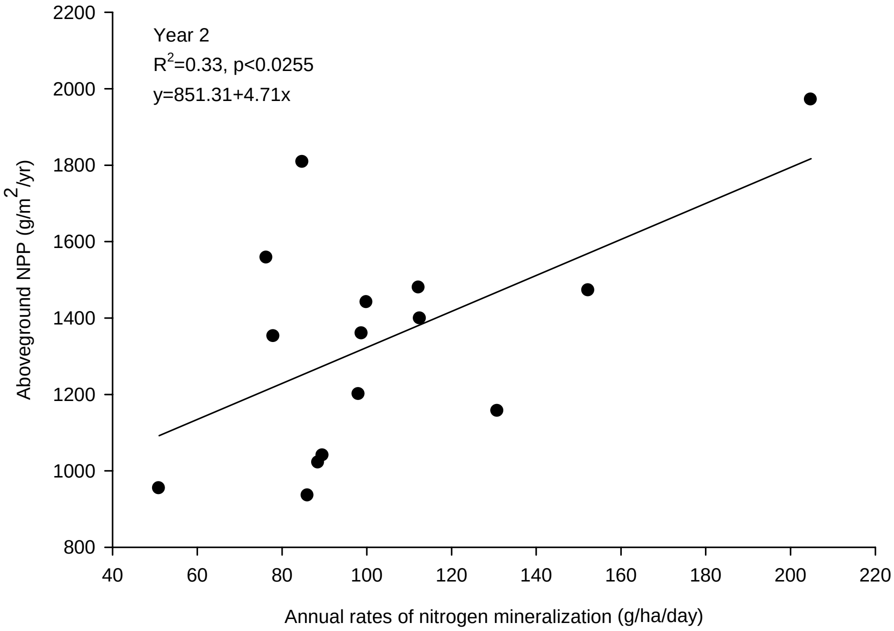

Figure 39. Significant regression relationship between aboveground net primary productivity and annual rates of nitrogen mineralization, Period 2.

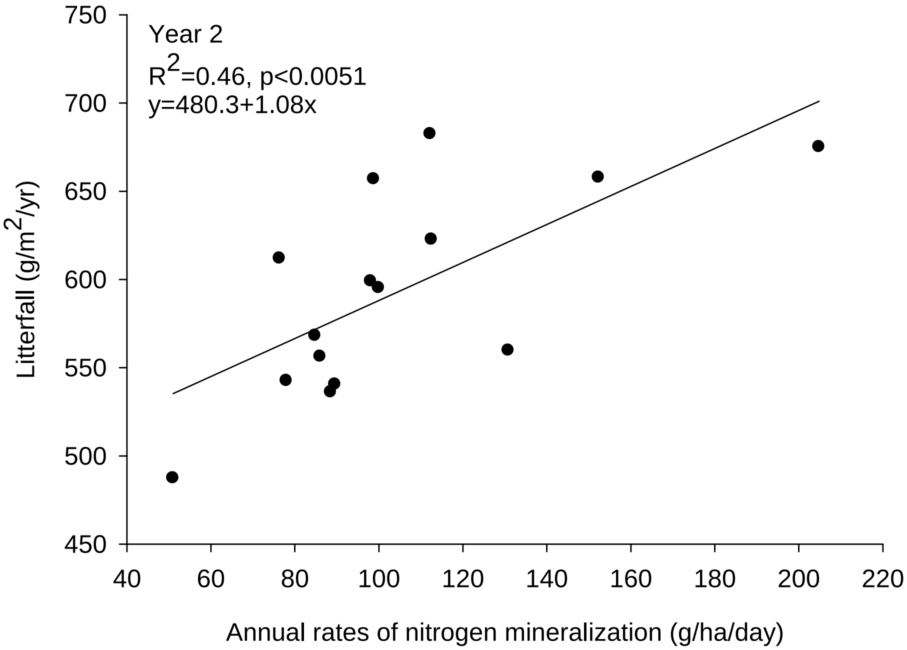

Figure 40. Significant linear regression relationship between total litterfall and annual rates of nitrogen mineralization, Period 2.

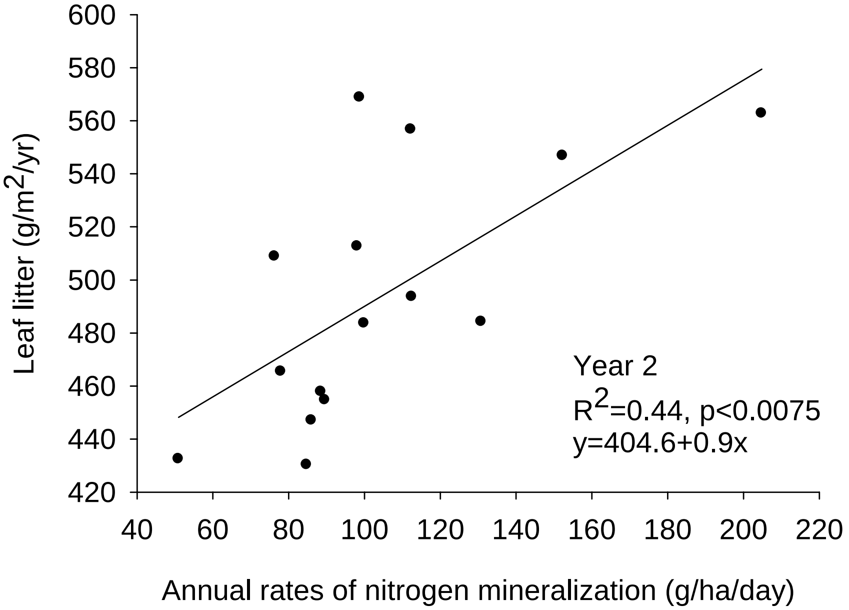

Figure 41. Significant linear regression relationship between leaf litter and annual rates of nitrogen mineralization, Period 2.

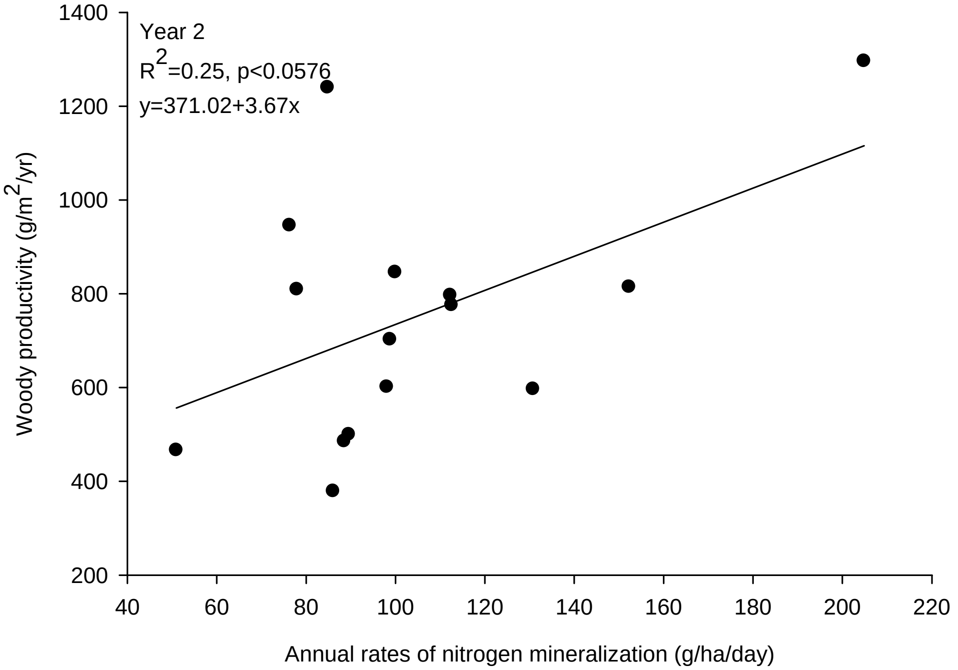

Figure 42. Significant linear regression relationship between woody productivity and annual rates of nitrogen mineralization, Period 2.

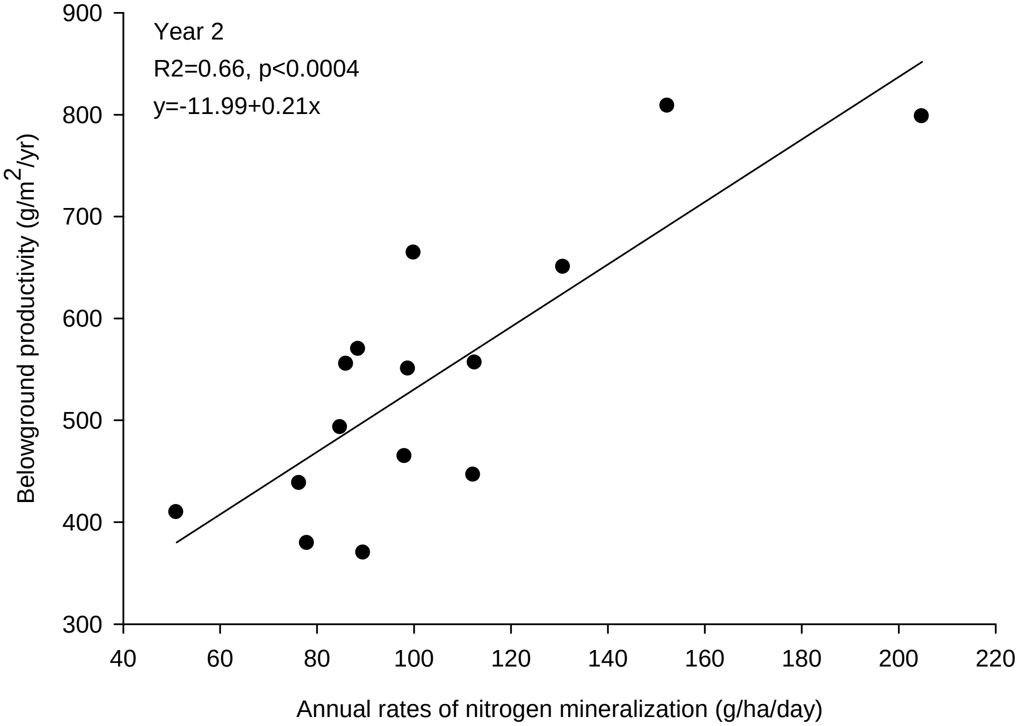

Figure 43. Significant linear regression relationship between belowground productivity and annual rates of nitrogen mineralization, Period 2.

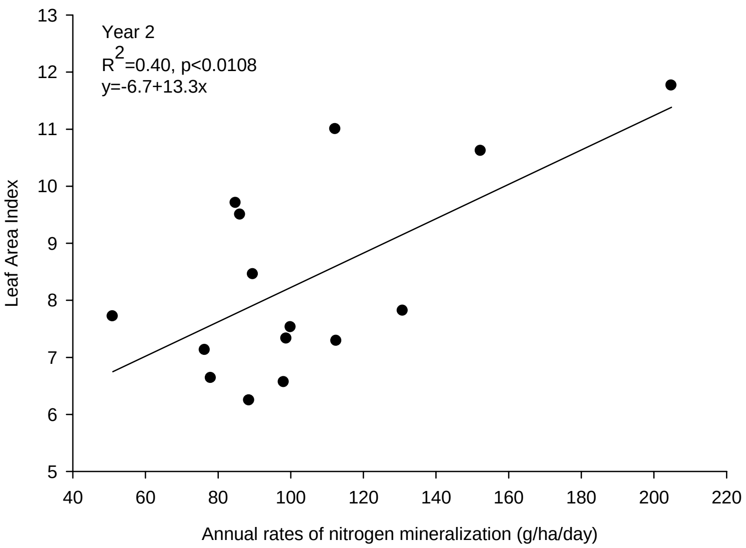

Figure 44. Significant linear regression relationship between leaf area index and annual rates of nitrogen mineralization, Period 2.

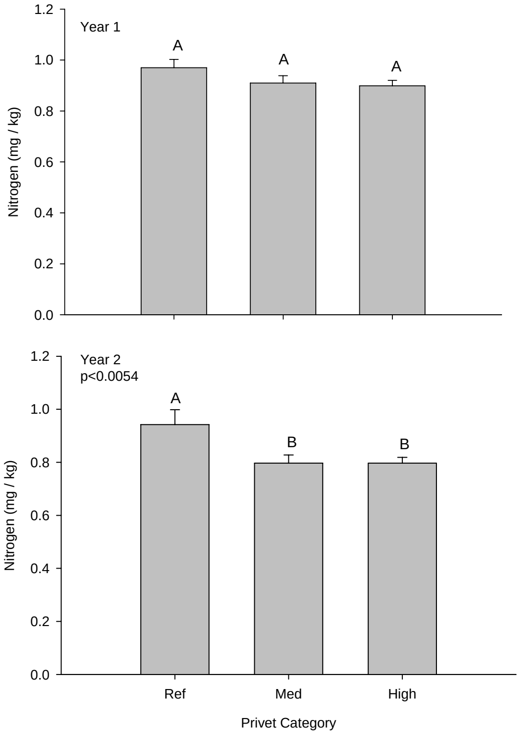

Figure 45. Comparison of live root nitrogen concentration by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

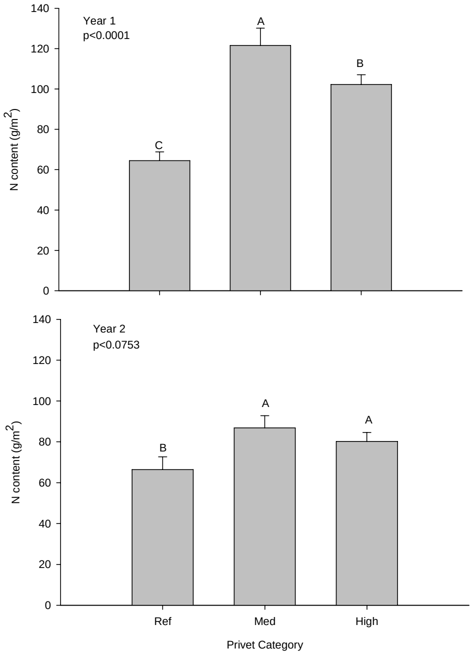

Figure 46. Comparison of live root nitrogen content by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

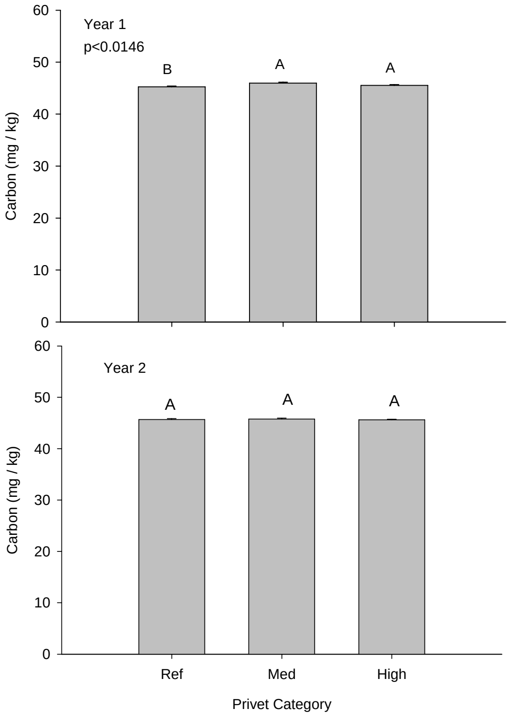

Figure 47. Comparison of live root carbon concentration by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

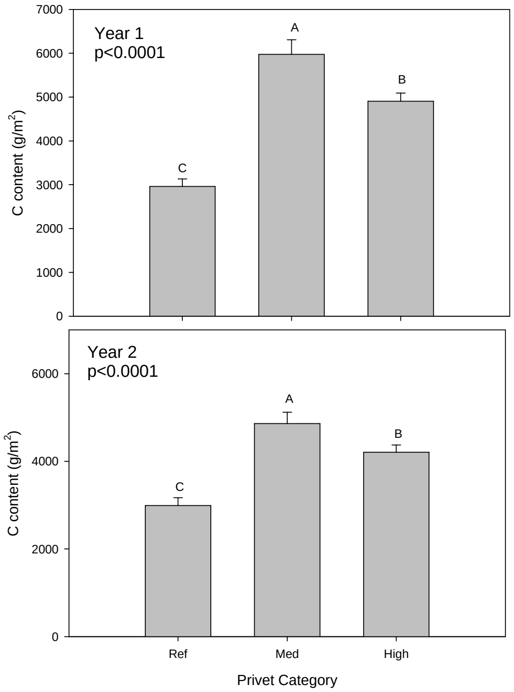

Figure 48. Comparison of live root carbon content by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

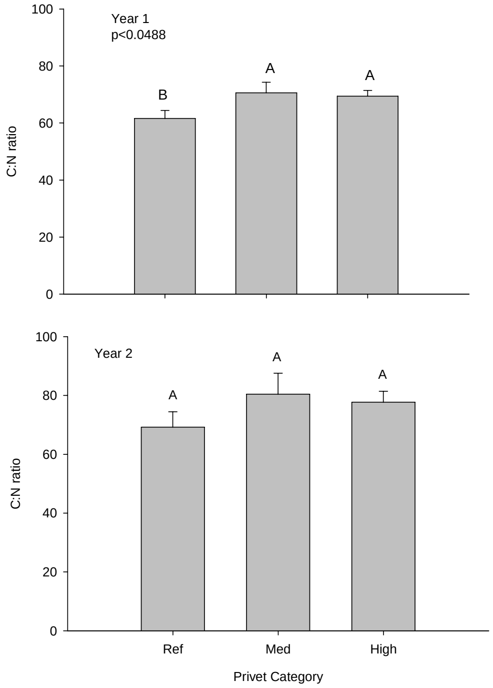

Figure 49. Comparison of live root carbon:nitrogen ratio by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

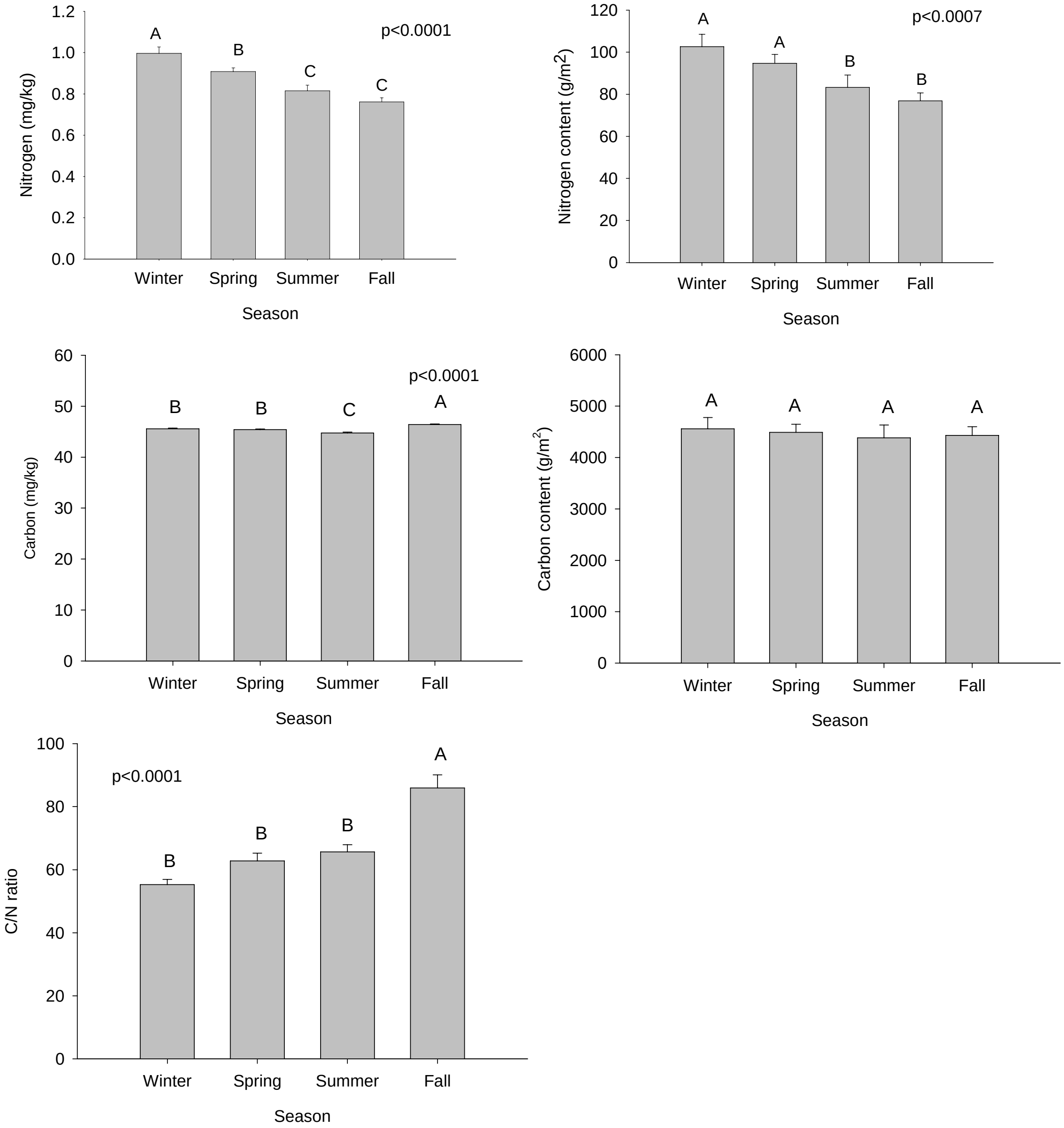

Figure 50. Comparison of live root nutrient measurements by season category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

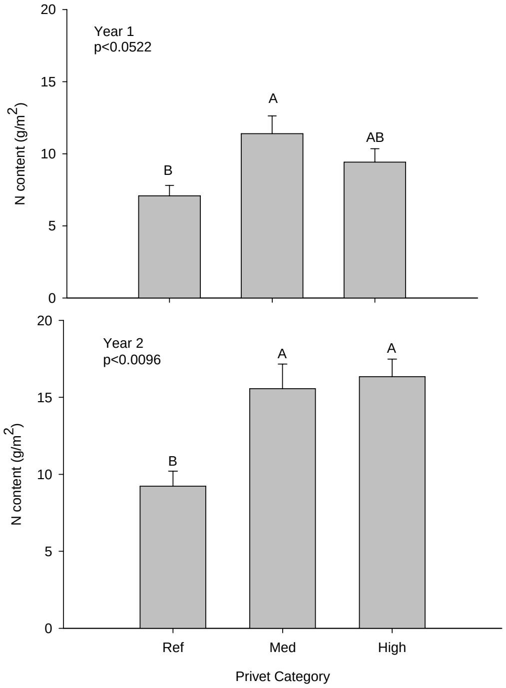

Figure 51. Comparison of dead root nitrogen content by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

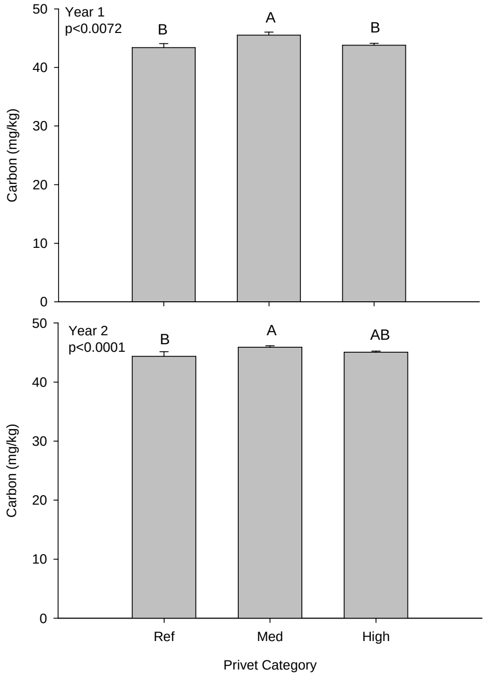

Figure 52. Comparison of dead root carbon concentration by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

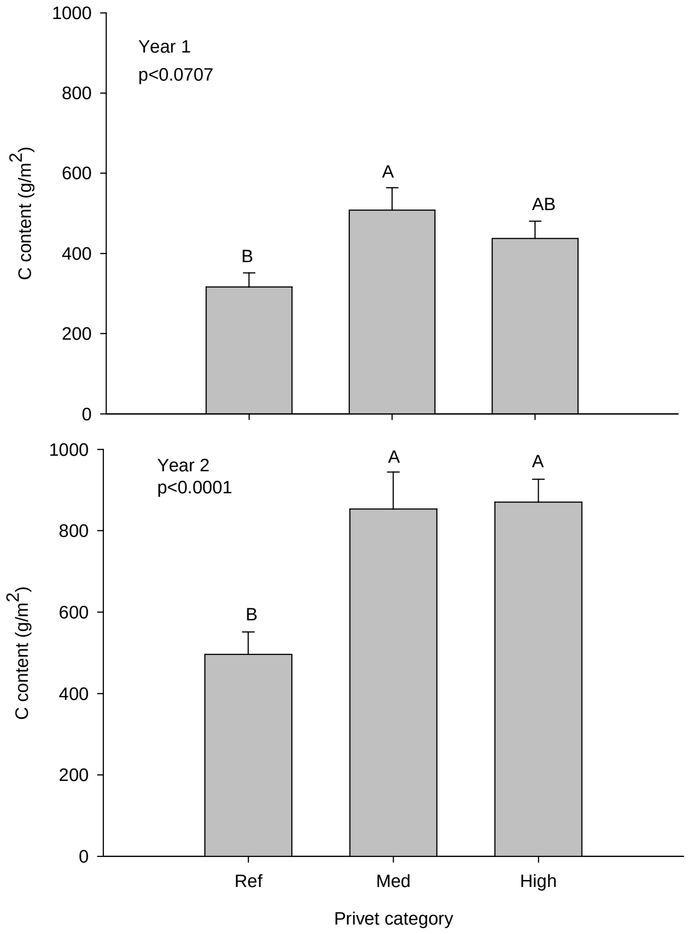

Figure 53. Comparison of dead root carbon content by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

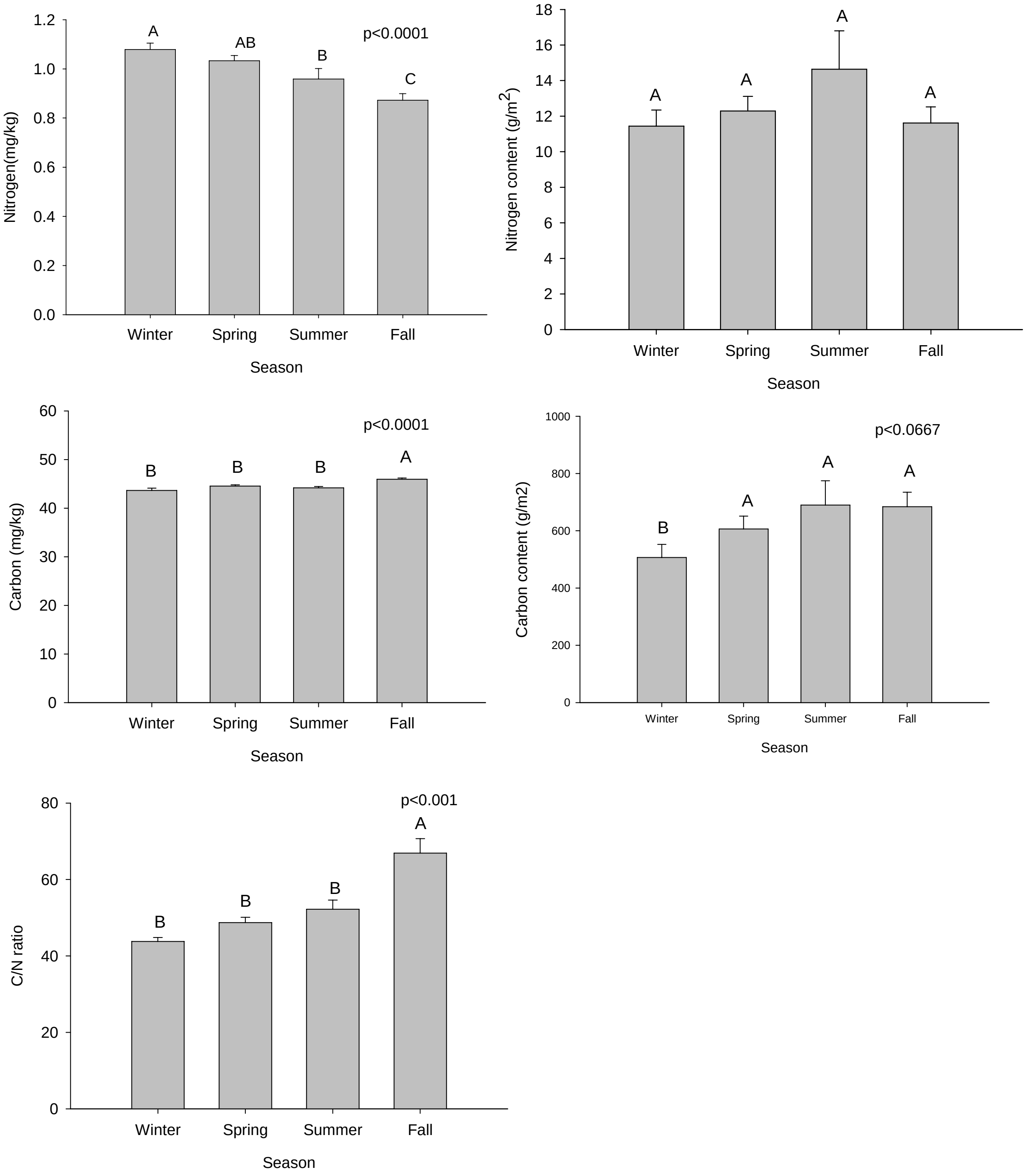

Figure 54. Comparison of dead root nutrient measurements by season category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

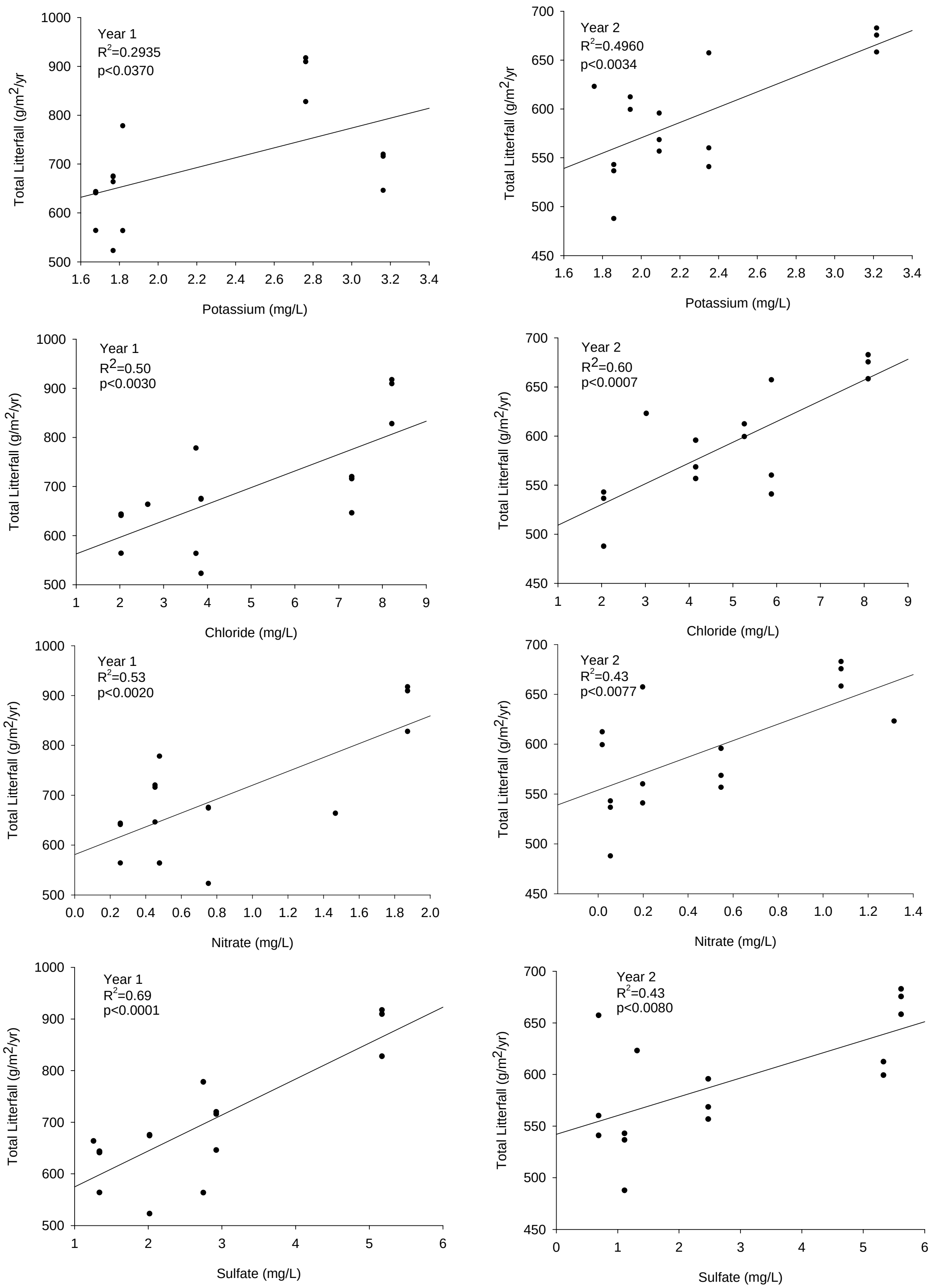

Figure 55. Aboveground litterfall productivity linear regression relationships with annual median water nutrient concentrations (mg/L).

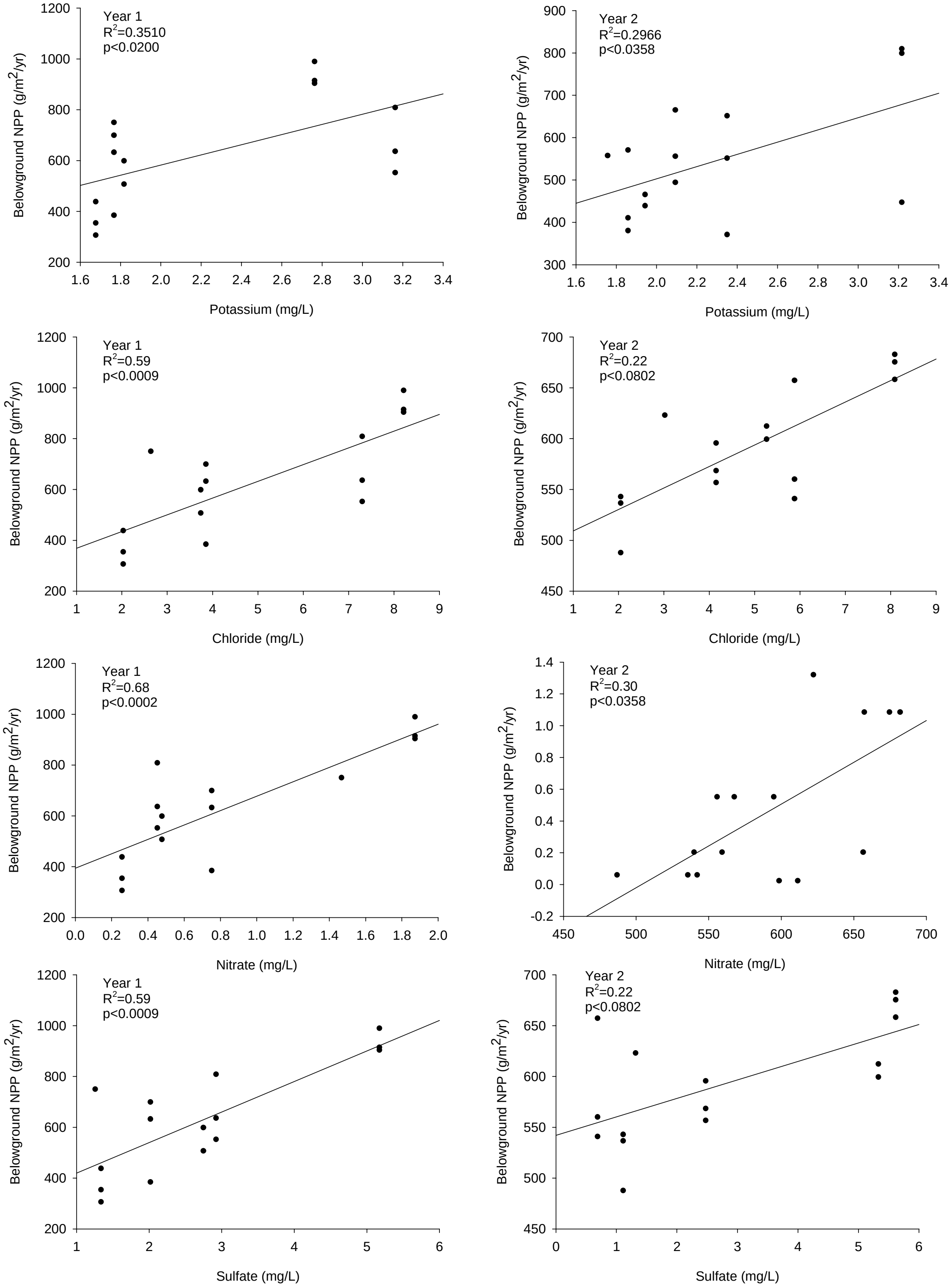

Figure 56. Belowground productivity linear relationships with annual median water nutrient concentrations (mg/L).

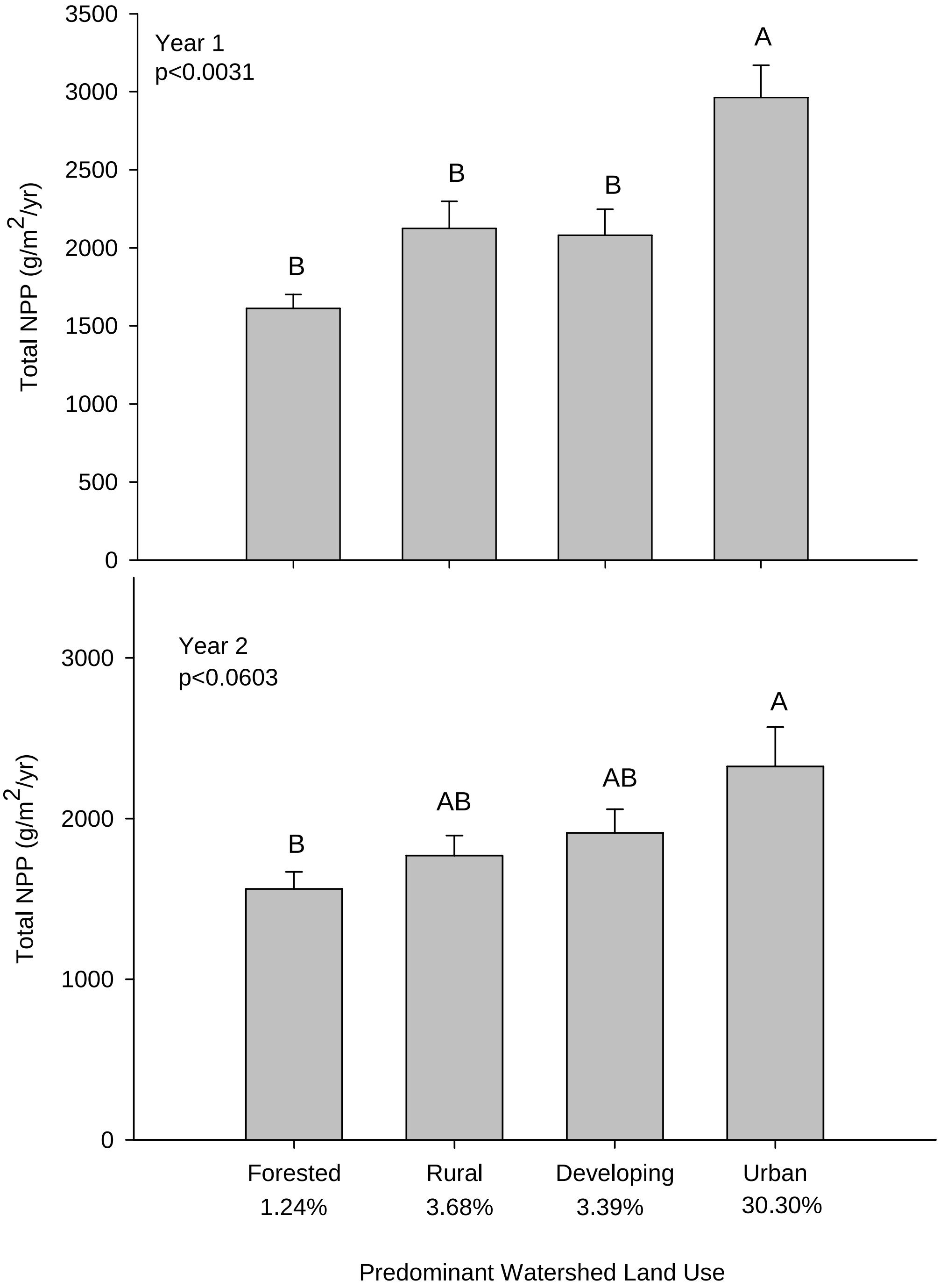

Figure 57. Comparison of total NPP by watershed land use. Mean watershed percent impervious surface noted below land use types. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

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CHAPTER III

INFLUENCE OF AN INVASIVE, NONNATIVE TREE SPECIES ON CARBON ALLOCATION AND SEQUESTRATION IN RIPARIAN FORESTS OF THE SOUTHERN PIEDMONT

INTRODUCTION

Invasive, Nonnative Vegetation

The introduction and proliferation of invasive, nonnative plant species in forests and fields is an increasing concern among scientists, land managers, and others. Morse et al. (1995) estimated that 5,000 nonnative plant species have become invasive, displacing native species in natural ecosystems found in the U.S. These nonnative vegetation invasions are detrimental to native biodiversity (Wilcove et al. 1998), have negative economic impacts (Miller 2003, Pimentel et al. 2005), and may cause significant alterations to the structure and functioning of ecosystems (MacDonald et al. 1989, Gordon 1998, Richardson et al. 2000, Katz and Shaforth 2003). Questions exist on how forest processes and functions are altered by successful invasions, especially regarding shifts in composition and structure that may be reflected in productivity and biogeochemistry (Katz and Shaforth 2003, Valery et al. 2004).

Many invasive, nonnative plant species in the southeast were introduced from far eastern and subtropical Asia (Stapanian et al. 1998). For example, Chinese privet (*Ligustrum sinense* Lour.) was introduced from China and Europe in the early to mid-1800s as an ornamental plant and has become naturalized throughout the Southeast as well as along the east coast to New England (USDA www.invasivespeciesinfo.gov). The species is an aggressive, invasive, shrub that forms dense thickets in riparian forests and along fencerows (Miller 2003). It is a semi-evergreen to evergreen member of the Olive family (Oleaceae) that may grow to 9 m in height. Although it becomes established easily in disturbed areas, Chinese privet also invades understories of undisturbed forests because of its reproductive and competitive features that include seed dispersal by birds and root suckering, shade tolerance, and wide-ranging soil-nutrient requirements (Langeland and Burkes 1998, Merriam and Feil 2002).

Southern floodplain forests that have experienced minimal disturbance are typically composed of regional oak-hickory (*Quercus – Carya*) species (Hodges 1998). Other woody vegetation found in minimally disturbed, Southern Piedmont floodplain forests typically include river birch (*Betula nigra* L.), sycamore (*Platanus occidentalis* L.), sweetgum (*Liquidambar styraciflua* L.), winged elm (*Ulmus alata* Michx.), and green ash (*Fraxinus pennsylvanica* Bush.). However, forests invaded by Chinese privet detour from the usual pattern of species succession and are characterized by dense stands of Chinese privet with minimal hardwood regeneration (Merriam and Feil 2002). The alteration of native vegetation species may result in large-scale ecosystem modifications (Merriam and Feil 2002, USDA 2008). For instance, Chinese privet may cause major reductions in production of merchantable timber products, may impact carbon sequestration and export, and may severely diminish floodplain biodiversity and associated habitat diversity. Alterations of floodplain ecosystem functions and processes potentially decrease the value of floodplains to society.

Carbon Allocation and Sequestration

The carbon cycle may be described as the movement of carbon between the biosphere, atmosphere, oceans, and geosphere. Carbon is stored in sinks, processed, and released back into the cycle. Net primary productivity of vegetation acts as a sink of carbon with plants absorbing carbon dioxide from the atmosphere during photosynthesis and releasing it to the atmosphere during respiration. Forests, especially in the temperate zone, have been identified as the potential missing sink in the global climate carbon balance (Sedjo 1990). Other sources of carbon include decomposition of soil organic matter (leaf litter, coarse woody debris) in the forest floor. Carbon allocation by plants regulates forest ecosystem carbon cycling through the shifting of photosynthesis products between respiration and biomass production, short-lived and long-lived tissues, and aboveground and belowground components (Litton et al. 2006). Carbon sequestration is the process through which carbon dioxide (CO_2) from the atmosphere is absorbed by plants through photosynthesis, and stored as carbon in biomass (tree trunks, branches, foliage and roots) and soils (US EPA 2008).

Carbon cycling in floodplains and wetlands is of interest not only because it is responsible for the main energy inputs into small order streams (Fisher and Likens 1973), but also because of the growing body of knowledge on the ability of wetlands, including riparian corridors, to sequester carbon due to their high productivity and large below-ground stocks of organic carbon (US Climate Change Technology Program 2003).

Carbon is stored both above- and belowground in living and dead plant and animal materials. Carbon modelers categorize soil organic carbon into three pools: (1) an active pool, including fresh plant material and root exudates with residence times of about a year, (2) a slow pool that includes microbes and decomposes with residence times of 1 – 100 years, and (3) a passive pool that includes microbes and decomposes with residence times of 100 – 1000 years (Parton et al. 1987).

A change in species composition may result in changes to root distribution patterns and aboveground community structure (Reynolds et al. 1997, Sala et al. 1997, Jackson 1999). These biomass allocation changes may influence carbon, nutrient, and water cycling. Consequently, study of both above- and belowground biomass and production is necessary in order to fully describe ecosystem changes. At the watershed level, shifts in species composition in a floodplain may also impact associated stream ecosystems in regard to carbon input and export. Ziegler and Brisco (2004) compared carbon dynamics in forested and agricultural watersheds. They determined that both organic matter source and nutrient concentrations significantly impact bioavailable carbon in small streams.

Molinero and Pozo (2004) studied litterfall inputs, benthic storage, and transport of coarse particulate organic matter of two headwater streams in northern Spain. One stream flowed through a mixed deciduous forest with native vegetation and the other stream flowed through a plantation of Blue gum (*Eucalyptus globulus* Labill). Timing, quality, and quantity of inputs and benthic storage of coarse particulate matter in streams changed when the natural forest was replaced with Blue gum. Coarse particulate organic matter, nitrogen, and phosphorus inputs were reduced in the stream flowing through the Blue gum plantation. However, benthic storage of coarse particulate organic matter was increased.

There is limited information on amounts of carbon sequestered by wetlands, including riparian areas (US Climate Change Technology Program 2003). Ecosystem function and diversity can be better estimated with increased knowledge of biomass, net primary productivity, and soil carbon storage, especially amid global climate change concerns (Clark et al. 2001).

Objective and Hypotheses

The objective of this research was to determine how increasing densities of Chinese privet influence above- and belowground carbon allocation and sequestration. It is hypothesized that, as Chinese privet understory stem densities increase, aboveground carbon allocation and sequestration will decline due to changes in stand structure (fewer large overstory trees). However, belowground carbon allocation and sequestration in the upper 11 cm of soil will increase as a result of higher fine root densities associated with dense stands of Chinese privet.

METHODS

Standing Crop Biomass

Aboveground. Litterfall was collected monthly from November 2004 until April 2007 in three 0.25 m^2 littertraps that were located systematically within each 0.04 ha study plot (Schilling and Lockaby 2005). The litterfall traps were made of treated lumber and lined with 2-mm nylon mesh. After collection, the litterfall was dried at 70° C for at least 48 hours or until constant mass was achieved. Biomass for total litterfall, reproduction, and miscellaneous pieces was recorded for each trap, samples were ground in a Wiley Mill to pass a 20 mesh sieve, and analyzed for carbon and nitrogen by thermal combustion (Perkin-Elmer 2400 series II CHNS/O analyzer; Perkin-Elmer Corp., Norwalk, CT) (Nelson and Sommers 1996). Annual litterfall production was estimated by summing average monthly litterfall biomass. Twigs were not included in the calculations as they are accounted for by the dry weight equations for standing crop biomass.

Annual woody productivity data were collected annually in December 2005, 2006, and 2007. Stem increment was estimated by recording diameter at breast height (DBH) of trees greater than 10 cm DBH on each 0.04 ha research plot. The aboveground woody dry mass was estimated for hardwood species using regression equations of Clark et al. (1985). Woody productivity was then calculated by subtracting standing crops of woody dry weight between sampling seasons to obtain annual increment. Basal area was estimated using a wedge prism with a basal area factor of 10. All trees in the plots were observed from plot center. Stand age was estimated by taking 3-7 incremental cores from canopy and mid-story trees on each plot.

Belowground. Two fine root samples were collected from the 3 m x 3 m belowground dynamics subplot every 6-8 weeks from February 2005 to April 2007 using the soil coring method described by Vogt and Persson (1991), Anderson and Ingram (1993), and summarized by Bledsoe et al. (1999). It has been noted that sequential coring does not capture root growth and mortality between sampling periods and is therefore likely to be a conservative estimate (Fahey et al. 1999). However, frequent sequential coring with replications at each plot provides an acceptable representation of fine root production and turnover (Baker et al. 2001, Calvacanti and Lockaby 2005). More than 50% of fine roots are found in the top 10 cm of soils (Baker et al. 2001), so soil cores 5-7 cm in diameter were collected to a depth of 11 cm. These soil samples were transported in a cooler and stored at 4º C to preserve live roots. Fine root samples were sorted within one month of collection in order to differentiate between live and dead roots.

Fine roots were separated from soil, debris, and organic matter. Roots were further separated into live and dead fractions. Root dry weight was determined by diameter class: very fine (0.1-1 mm), intermediate (1.1 – 2.0 mm), and coarse (2.1 – 3.0 mm). Live and dead roots were dried at 55-70º C until constant mass was achieved and weighed to report g m^{-2} of each diameter class. Fine root production was estimated by summing positive differences in mean fine root biomass between sample dates (Fogel 1983). Fine roots were ground in a Wiley Mill to pass a 20 mesh sieve and analyzed for C and N by thermal combustion (Perkin-Elmer 2400 series II CHNS/O analyzer; Perkin-Elmer Corp., Norwalk, CT) (Nelson and Sommers 1996). Fine root turnover was estimated as the annual belowground net primary productivity (see Chapter 2, Influence of Chinese Privet on Productivity of Riparian Forests of the Southern Piedmont) divided by the annual mean standing crop biomass (Aber et al. 1985).

Carbon Allocation and Sequestration

Carbon allocation was estimated as standing crop biomass of litterfall, woody stems, and fine roots multiplied by their respective annual carbon concentration (mg kg^{-1}). Carbon sequestration was estimated as the annual NPP of litterfall, woody stems, and fine roots multiplied by their respective annual carbon concentration (mg kg^{-1}) (see Chapter 2, Influence of Chinese Privet on Productivity of Riparian Forests of the Southern Piedmont).

Belowground carbon allocation was estimated using spring Period 1 and Period 2 fine root standing crop biomass**.** These collections tended to have the greatest mass among Chinese privet categories and so best represented the largest sampled belowground biomass.

Statistical Analysis

SAS software version 9.1 (SAS-Institute 2002-2003) was used for all statistical analyses. Regression analysis was used to assess relationships between independent variables such as percent understory Chinese privet and dependent variables such as standing crop biomass (PROC REG, SAS Institute 2002-2003). Mean comparisons were performed using analysis of variance (ANOVA) (PROC GLM, SAS Institute 2002-2003). Tukey’s HSD means comparison test was used as a posthoc test and all differences significant above the 90 percent confidence level were reported. Data sets were analyzed to ensure they met normality assumptions and log transformed when necessary.

RESULTS

Precipitation Patterns

Precipitation was variable during the 30 month study period (Fig. 6). Monthly measured rainfall ranged from 16.9 cm above the 30-year average to 8 cm below the 30-year average. More precipitation was measured from September 2004 – September 2005 than from September 2005 – May 2007. The Palmer Drought Index indicated drought conditions started in April 2006 and persisted throughout the remainder of the study (Fig. 7).

Temperature and Light

There were no differences between mean air and soil temperatures among Chinese privet categories (Fig. 8). Likewise, there were no differences among light intensity maxima and means among Chinese privet categories (Fig. 9).

Standing Crop Biomass, Carbon Allocation, and Sequestration

Totals for Period 1 and 2 standing crop biomass, carbon allocation, and carbon sequestration are presented by Chinese privet category in Tables 6, 7, 8, 9, 10, and 11 and discussed below. There was no significant difference in stand age among the categories (Fig. 5).

Period 1 Total Standing Crop Biomass, Carbon Allocation and Sequestration. Total standing crop biomass, carbon allocation and carbon sequestration included above- and belowground constituents. The range for total standing crop biomass was 137 to 276 Mg ha^{-1}. Carbon allocation varied from 65.7 to 130.7 Mg ha^{-1} and carbon sequestration had a range of 7 to 14.9 Mg ha^{-1} yr^{-1}. Significant differences were detected for total carbon sequestration in Period 1 (Fig. 58). Medium Chinese privet sites had numerically greater carbon sequestration than both the Reference and High sites, although this difference was only significant between the Reference sites and Medium sites ($p<0.08$, $F=3.14$). However, there was no significant difference among Chinese privet categories for total standing crop biomass or carbon allocation in Period 1 (Figs. 59 and 60). Additionally, total carbon sequestration was significantly related to percent understory Chinese privet in Period 1 ($R^2=0.49$, $p<0.02$) (Fig. 61). The shoot:fine root ratio (aboveground standing crop biomass / belowground fine root standing crop biomass) ranged from 81.1 to 140.0 in Period 1. There was no significant difference between shoot:root ratios among Chinese privet categories in Period 1 (Fig. 62).

Period 1 Aboveground Standing Crop Biomass, Carbon Allocation and Carbon Sequestration. Total aboveground standing crop biomass varied between 139.2-278.3 Mg ha^{-1}. Additionally, total aboveground carbon allocation ranged from 65 to 129 Mg ha^{-1} and carbon sequestration ranged from 4.2 to 10.6 Mg ha^{-1}. No significant difference in total aboveground standing biomass was detected among Chinese privet categories in Period 1 (Fig. 63). There were no significant differences among Chinese privet categories for total aboveground carbon allocation or carbon sequestration in Period 1 (Figs. 64 and 65).

Total litterfall standing crop biomass was estimated as the total mass of leaf litter + reproductive litter collected annually. Period 1 total litterfall standing crop biomass ranged from 5.2-9.2 Mg ha^{-1} in Period 1. Litterfall standing crop biomass was numerically greatest in the Medium Chinese privet category. However, this difference was not significant in Period 1 (Fig. 66).

Because standing crop biomass of litterfall (used to estimate carbon allocation) was also used as the estimate of annual NPP (used to estimate carbon sequestration), only litterfall carbon sequestration (Mg ha^{-1} yr^{-1}) is reported to reduce redundancy. Litterfall carbon allocation is reported as a percent of total in Tables 3 and 4. The range of litterfall carbon allocation varied from 3-4% of total carbon in Period 1. Litterfall carbon sequestration ranged from 2.4 to 4.3 Mg ha^{-1} yr^{-1}. Period 1 mean litterfall carbon concentrations were 47 mg kg^{-1} for all Chinese privet categories. Similar to litterfall standing crop biomass trends, total litterfall carbon sequestration was numerically greater in the Medium category for Period 1, but the difference was not significant (Fig. 67). Moreover, no significant relationship between percent understory Chinese privet and litterfall carbon sequestration was detected in Period 1 (Fig. 68).

Woody biomass composed the majority of the aboveground standing crop and varied from 128.8 to 267.9 Mg ha^{-1} in Period 1. Stem carbon allocation had a range of 61.9 to 125.9 Mg ha^{-1} and carbon sequestration rates were between 1.8 to 7.7 Mg ha^{-1} yr^{-1}. There were no significant differences in woody standing crop biomass, carbon allocation, or sequestration among Chinese privet categories that year (Figs. 69, 70, and 71). Also, there were no significant differences in mean stem carbon concentration across Chinese privet categories. Reference, Medium and High stem carbon concentration means were 47 (±0) mg kg^{-1}, 47 (±0.003) mg kg^{-1}, and 48 (±0.006) mg kg^{-1} respectively.

Period 1 Belowground Standing Crop Biomass, Carbon Allocation, and Carbon Sequestration. Live root annual mean standing crop biomass ranged between 2 to 5 Mg ha^{-1} in Period 1. Significant differences were detected for total live root standing crop biomass (all diameter size classes combined) among all Chinese privet categories (Medium>High>Reference) (Fig. 72) ($p<0.0001$, $F=21.41$). However, these belowground significant differences were not of sufficient magnitude to influence a difference in total standing crop biomass. Overall annual mean standing crop biomass of dead roots varied from 0.09 to 0.46 Mg ha^{-1}. When compared by Chinese privet category, total dead root standing crop biomass in the Reference category was significantly less than the Medium category in Period 1 ($p<0.0999$, $F=2.33$) (Fig. 73).

The Medium Chinese privet category had significantly more live standing crop biomass than the Reference category for each root diameter size class (Figs. 74, 75, and 76). Very fine roots (0.1-1.0 mm) made up most of the standing crop biomass for live roots and were more variable than either intermediate or coarse diameter size classes for standing crop biomass in Period 1. Significant differences among all Chinese privet categories were detected for live very fine roots (Medium>High>Reference) ($p<0.0001$, $F=23.93$) (Fig. 77). Live intermediate roots (1.1-2.0 mm) also displayed significant differences among all Chinese privet categories (Medium>High>Reference) ($p<0.0001$, $F=10.48$) (Fig. 78). Additionally, live coarse fine roots (2.1-3.0 mm) had greater standing crop biomass in the Medium Chinese privet category (Medium>High>Reference). However, this difference was only significant between the Reference category and the Medium and High Chinese privet categories ($p<0.0188$, $F=4.06$) (Fig. 79). No significant difference among Chinese privet categories was detected for dead root standing crop biomass in any of the diameter size classes in Period 1 (Figs. 80, 81, and 82).

Period 1 belowground live root carbon allocation ranged from 0.8 to 2.8 Mg ha^{-1} and carbon sequestration ranged from 1.4 to 4.5 Mg ha^{-1} yr^{-1}. Belowground carbon allocation was significantly less in the Reference Chinese privet category than the Medium Chinese privet category in ($F=3.43$, $p<0.0664$). However, the High Chinese privet category was not different from either the Reference or Medium Chinese privet category (Fig. 83). Additionally, the Reference Chinese privet category had significantly less live root carbon sequestration than both the Medium and High Chinese privet categories in Period 1 ($F=5.92$, $p<0.0163$) (Fig. 84). Moreover, there was no significant difference among Chinese privet categories in carbon concentration of live roots (mg kg^{-1}). Live root carbon concentration means were 0.45 mg kg^{-1} in the Reference category and 0.46 mg kg^{-1} in the Medium and High categories.

There was no significant regression relationship between percent understory Chinese privet and belowground carbon allocation (Fig. 85). However, there was a significant regression relationship between percent understory Chinese privet and fine root carbon sequestration ($R^2=0.54$, $p<0.0103$) (Fig. 86).

Fine root turnover ranged from 1.4-3.7 yr^{-1}and was not significantly different among Chinese privet categories for Period 1 (Fig. 87). Additionally, no significant regression relationship was detected between bulk density and fine root turnover (Fig. 88). Furthermore, the ratio of live to dead root standing crop biomass (live:dead) was not significantly different among Chinese privet categories (Fig. 89). Likewise, there was no significant linear regression relationship between percent Chinese privet in the understory and the live:dead root ratio (Fig. 90).

Period 2 Total Standing Crop Biomass, Carbon Allocation and Sequestration. In Period 2, total standing crop biomass varied from 141.5 to 287.7 Mg ha-^{1}. The range of total carbon allocation was from 65.7 to 130.7 Mg ha-^{1} and total carbon sequestration was from 7.0 to 14.9 Mg ha-^{1} yr^{-1}. There was no significant difference among Chinese privet categories for total standing crop biomass, carbon allocation, or carbon sequestration in Period 2 (Figs. 58, 59, and 60). No significant difference between aboveground standing crop biomass / belowground fine root standing crop biomass (shoot:fine root) was identified among Chinese privet categories. Lastly, the shoot:root ratio ranged from 81.4 to 112.1 (Fig. 62).

Period 2 Aboveground Standing Crop Biomass, Carbon Allocation, and Carbon Sequestration. Total aboveground standing crop biomass had a range of 147.0 to 287.7 Mg ha^{-1}. Additionally, total aboveground carbon allocation varied between 67.5 to 133.9 Mg ha^{-1} and total aboveground carbon sequestration ranged from 4.4 to 8.5 Mg ha-^{1} yr^{-1}. There was no significant difference in total aboveground standing biomass, total aboveground carbon allocation, and total aboveground carbon sequestration among Chinese privet categories in Period 2 (Figs. 63, 64, and 65).

Total litterfall standing crop biomass was significantly greater in the Medium Chinese privet category than in the Reference category in Period 2 ($F=4.44$, $p<0.0361$) (Fig. 66). However, this difference was not great enough to drive significant differences in total aboveground standing crop, carbon allocation, or carbon sequestration. A range of 5.0 to 6.9 Mg ha^{-1} of total litterfall standing crop biomass was collected.

Similar to litterfall standing crop biomass trends, total litterfall carbon sequestration was significantly greater in the Medium category compared with the Reference category for Period 2 ($F=5.20$, $p<0.0237$) (Fig. 67). Unlike Period 1, there was a significant regression relationship between percent understory Chinese privet and litterfall carbon sequestration ($R^2=0.60$, $p<0.0044$) (Fig. 68). The amount of litterfall carbon sequestration estimated was from 2 to 3 Mg ha^{-1}. Period 2 litterfall carbon concentration was the same as that of Period 1, 47 mg kg^{-1}, in all Chinese privet categories. Lastly, the range of litterfall carbon allocation was from 2-3% of total in Period 2.

Woody standing crop biomass ranged from 133.8 – 279.3 Mg ha^{-1}. Similar to Period 1, woody standing crop made up a majority of aboveground biomass and no significant differences among Chinese privet categories were found (Tables 6 and 7, Fig. 69). Furthermore, there were no significant differences in mean stem carbon concentration among Chinese privet categories: Reference 47 (±0) mg kg^{-1}, Medium 47 (±0.003) mg kg^{-1}, and High 48 (±0.006) mg kg^{-1}. Stem carbon allocation was estimated between 64.7 to 131.2 Mg ha-^{1} and carbon sequestration between 1.8 to 6.1 Mg ha-^{1} yr^{-1}. Moreover, no significant differences were detected among Chinese privet categories for stem carbon allocation or sequestration (Figs. 70 and 71).

Period 2 Belowground Standing Crop Biomass, Carbon Allocation and Carbon Sequestration. The Reference category (1.9 Mg ha^{-1}) had significantly less total live standing crop biomass (all diameter size classes combined) than either the Medium (2.9 Mg ha^{-1}) or High (2.5 Mg ha^{-1}) categories ($p<.0001$, $F=10.44$) (Fig. 71). However, these significant differences were not strong enough to influence total standing crop biomass. Standing crop biomass annual means for live roots varied between 1.5 and 4.1 Mg ha^{-1}.

A majority of the standing crop biomass in Period 2 live roots was composed of very fine roots (0.1-1.0 mm). Medium category live root standing crop biomass was greatest for each root diameter size class. However, this was not always significant. Very fine roots were more dynamic than either intermediate (1.1-2.0 mm) or coarse (2.1-3.0) root diameter size classes for standing crop biomass. Significant differences among Chinese privet categories were detected for live very fine root standing crop biomass (Medium=High>Reference) ($p<0.0001$, $F=13.64$) (Fig. 77). Live intermediate roots (1.1-2.0 mm) had significantly less standing crop biomass in the Reference category than the Medium and High categories which were similar to Period 1 (Medium=High>Reference) ($p<0.0001$, $F=10.56$) (Fig. 78). Finally, there was no significant difference among Chinese privet categories in live coarse root (2.1-3.0 mm) standing crop biomass (Fig. 79).

Dead root annual mean standing crop biomass ranged between 0.08 and 0.6 Mg ha^{-1} in Period 2. When separated by Chinese privet category, there was significantly less total dead root standing crop biomass in the Reference category as compared with the Medium and High categories in Period 2 ($p<0.0006$, $F=7.61$) (Fig. 73). Unlike Period 1, significant differences were detected for dead root standing crop biomass among Chinese privet categories. The Reference category had significantly less dead root standing crop biomass for each size class: very fine root ($p<0.0128$, $F=4.45$, mean=0.13 Mg ha^{-1}); intermediate ($p<0.0428$, $F=3.2$, mean=0.04 Mg ha^{-1}); and coarse ($p<0.0067$, $F=5.12$, mean =0.03 Mg ha^{-1}) (Figs. 80, 81, and 82).

Belowground carbon allocation was estimated between 0.6 and 2.7 Mg ha^{-1} and carbon sequestration varied from 1.7 to 3.8 Mg ha^{-1} yr^{-1}. There was no significant difference among Chinese privet categories for belowground carbon allocation (Fig. 83). Similarly, there was no significant difference in live root carbon sequestration (Fig. 84). Carbon concentrations (mg kg^{-1}) were not significantly different among Chinese privet categories (e.g., all 0.5 mg $kg^{-1}$for each category).

Percent understory Chinese privet and belowground carbon allocation were not significantly related (Fig. 85). In contrast to Period 1, no significant regression relationship was found between percent understory Chinese privet and live root carbon sequestration (Fig. 86). Fine root turnover for all plots ranged from 1.3 to 3.3 yr^{-1} and was not significantly different among Chinese privet categories (Fig. 38). However, there was a positive significant relationship between bulk density and fine root turnover ($R^2=0.32$, $p<0.0282$) (Fig. 88). Although the live:dead root ratio was not significantly different among Chinese privet categories (Fig. 89), there was a significant negative regression relationship between percent Chinese privet in the understory and that ratio ($R^2=0.22$, $p<0.0764$) (Fig. 90).

Comparison Between Periods. Student’s t-tests revealed no significant difference between periods in total standing crop biomass, total aboveground carbon allocation, or total aboveground carbon sequestration, for any Chinese privet category or shoot:root standing crop biomass ratio.

Significantly more leaf litter standing crop biomass was found in Period 1 (Reference = 6.2, Medium = 7.5, High = 7.0 Mg ha^{-1}) compared to Period 2 (Reference = 5.2, Medium = 6.3, High = 6.1 Mg ha^{-1}) among all Chinese privet categories (Reference $p<0.0413$; Medium $p<0.0941$; High $p<0.0658$) (Tables 6 and 7, Fig. 91). Similarly, Period 1 total litterfall carbon allocation and carbon sequestration (Reference 2.9, Medium 3.5, High 3.3 Mg ha^{-1} yr^{-1}) was significantly greater than Period 2 (Reference 2.4, Medium 3.0, High 2.8 Mg ha^{-1} yr^{-1}) among all Chinese privet categories (Reference $p<0.0313$, Medium $p<0.0850$, High $p<0.0619$) (Fig. 92). Lastly, no significant difference between years in stem carbon allocation or carbon sequestration was detected for any Chinese privet category.

There was no significant difference in belowground standing crop biomass or carbon allocation between years although Period 1 was numerically greater within all Chinese privet categories (Figs. 93 and 94). The belowground standing crop biomass for Period 1 was 1.9, 3.7, and 3.1 Mg ha^{-1} for the Reference, Medium, and High categories, respectively. In Period 2, belowground standing crop biomass for each category was Reference 1.9, Medium 2.9, and High 2.5 Mg ha^{-1}. Furthermore, Period 1 carbon allocation for the Reference, Medium, and High categories was 1.1, 1.9, and 1.8 Mg ha^{-1}, respectively. Carbon allocation in Period 2 was Reference 0.7, Medium 1.3, and High 1.5 Mg ha^{-1}. Belowground carbon sequestration was significantly greater in the first year in the Medium category ($p<0.0266$), but not in the Reference or High category (Fig. 95).

Chinese Privet Carbon Allocation and Sequestration

The aboveground contribution of Chinese privet to standing crop biomass, carbon allocation, and carbon sequestration is found in Tables 12 and 13. Period 1 Chinese privet total aboveground standing crop biomass was 0.001, 5.8, and 30.3 Mg ha^{-1} for the Reference, Medium, and High categories, respectively. Period 2 Chinese privet standing crop biomass was estimated for each category as 0.001 Mg ha^{-1} Reference, 6.4 Mg ha^{-1} Medium, and 32.5 Mg ha^{-1} High. Additionally, total aboveground carbon allocated by Chinese privet in Period 1 was Reference 0.0, Medium 2.8, and High 14.3 Mg ha^{-1}. The Period 2 Chinese privet total aboveground carbon allocation was estimated as 0.0, 3.0, and 15.3 Mg ha^{-1} for the Reference, Medium, and High categories. Chinese privet carbon sequestration in woody biomass for Period 1 was estimated in the Reference, Medium, and High categories as 0.0, 0.2, and 1.4 Mg ha^{-1} yr $^{-1}$. The Period 2 estimates for carbon sequestration by woody biomass were Reference 0.0, Medium, 0.3, and High 0.8 Mg ha^{-1} yr $^{-1}$. As would be expected, the High category had the greatest contribution of Chinese privet stem and Chinese privet leaf litter biomass, carbon allocation, and carbon sequestration followed by the Medium category and lastly, the Reference category (Tables 12 and 13). The specific belowground contribution of Chinese privet is not presented because separation of roots by species would be very difficult.

DISCUSSION

Standing Crop Biomass

The total and aboveground standing crop biomass estimates in this study (Tables 1 and 2) were within ranges noted by others for riparian forests. Lugo et al. (1990)

reported forested wetland total standing crop biomass estimates of 81-620 Mg ha^{-1} and aboveground standing crop biomass of 79-608 Mg ha^{-1}. Brinson (1990) described a range of aboveground standing crop for riverine forests of 25.5-608 Mg ha^{-1}. Belowground standing crop biomass estimates in the current study were lower than ranges reported for forested wetlands by Lugo et al. (1990) of 12-84 Mg ha^{-1}. Similarly, our estimates were lower than riverine forest belowground biomass ranges of 12-69 Mg ha^{-1} as summarized by Brinson (1990) because our data reflect only fine roots < 3 mm diameter. However, data from the present study were within ranges for sites reported by Cavalcanti and Lockaby (2005) of 2.6-8.2 Mg ha^{-1}, by Jolley (2008) of 0.06-5.6 Mg ha^{-1} for coastal plain riparian forests in west Georgia, by Helmisaari et al. (2007) of 1.49 and 3.86 Mg ha^{-1} for Norway spruce and Scots pine in Finland, and by Santantonio and Hermann (1985) of 4.8-6.5 Mg ha^{-1} for Douglas-fir in western Oregon.

The lack of significant differences in total or aboveground standing crop biomass among Chinese privet categories was likely due to the homogeneity of stem standing crop biomass among categories (Figs. 58 and 63). Specifically, stem standing crop biomass made up a large proportion of the total (95-97%) and aboveground (97-98%) standing crop biomass and was not significantly different among categories. This masked any significant differences detected among Chinese privet categories for litterfall and fine root standing crop biomass. Litterfall biomass made up between 2-3% of total aboveground and 2-3% total standing crop biomass. Brinson (1990) also reported that leaves represented between 1% and 10% of total aboveground standing crop biomass in riverine forests.

Belowground standing crop biomass in the current study composed 0.8%-2% of the total (Tables 6 and 7). Brinson (1990) reported much higher estimates of belowground standing crop to total biomass. However, his estimates included total belowground biomass and this study's estimates encompassed only the fine roots in the uppermost soil. Furthermore, belowground standing crop estimates tend to vary due to differences in sampling methods, but generally are less than aboveground biomass estimates (Brinson 1990).

Brinson (1990) noted that up until a stand reaches the age of 20 years, most of the accumulation in biomass and volume in riverine forests is due to recruitment into the >2.5 cm DBH size class (understory) and that a steady state is achieved after 70 years. The average age of stands in this study ranged between 38 and 42 years which is less than the general age of steady state, but is greater than the period of time when recruitment of understory stems typically impacts standing crop biomass. The ability of Chinese privet to invade established stands with closed canopies may have extended the period of time that understory stems >2.5 cm contribute to standing crop biomass. That is, Chinese privet appeared to exert a strong influence on standing crop biomass in the Medium and High Chinese privet sites for litterfall and fine roots (Figs. 66 and 72). The apparent increase in both litterfall and belowground biomass in Medium and High Chinese privet sites is counter to some reports that indicated decreases in aboveground biomass with a concomitant shift to belowground resources along decreasing water and resource availability gradients (Cuevas 2001, Kimmins 2004).

The contrast of higher litterfall and fine root standing crop biomass in the Medium sites and decreasing biomass in the High Chinese privet sites may be attributed to the high number of understory Chinese privet stems in the former. Similarly, Ishii et al. (2004) noted that understory tree species may play a significant role in enhancing stand productivity. Sunlight may be captured and used more efficiently when a diversity of vertical structures exists, leading to increased stand productivity (Kira et al. 1969, Hartley 2002). This increase in productivity would be reflected in an increase in biomass.

Young et al. (1995) found a similar pattern related to invasion of a barrier island by wax myrtle (*Morella cerifera*). Sites early in the invasion process exhibited high recruitment and shrub growth. However, sites considered 'older' in the wax myrtle shrub invasion process exhibited reduced shrub growth. Furthermore, overall productivity and standing crop biomass may also be influenced by a loss in species richness with the increase of Chinese privet understory stems. Several studies have suggested that a reduction in species richness may lead to less efficient acquisition of resources which lowers production of biomass and sequestration of CO_2 (Naeem et al. 1994, Hector et al. 1999, Costanza et al. 2007).

Both litterfall and fine root standing crop biomass were greater in Period 1 as compared with Period 2 in the Medium and High Chinese privet category; however, this difference was only significant for litterfall (Figs. 91 and 93) The drought may have contributed to a decrease in standing crop biomass of litterfall and fine roots in Period 2.

Although the Reference sites had numerically greater shoot:fine root ratios than the Medium or High Chinese privet sites, no significant differences were detected among Chinese privet categories in either sampling year (Fig. 62). This suggests the increase in understory stem numbers and density do not strongly influence belowground or aboveground biomass partitioning. Casper et al. (1998) also noted consistent root:shoot ratios of velvetleaf (*Abutilon theophrasti*) across a broad range of plant sizes in varying amounts of competition.

Nutrient-demanding species have been noted to have a greater belowground response to environmental stresses than non-nutrient demanding species (Kimmins 2004). It is possible Chinese privet is a non-nutrient demanding species that is able to tolerate shifts in environmental conditions such as drought. Chinese privet foliage was found to have a very wide range of nitrogen concentrations (0.91-2.24 mg kg^{-1}) in west Georgia riparian forests (Lockaby, unpublished data) which suggests that the species may be somewhat plastic in terms of nutrient requirements.

Carbon Allocation and Sequestration

Carbon allocation is an important regulator of forest ecosystem carbon cycling (Litton et al. 2006). Additionally, carbon sequestration and its link to global climate change is a heavily studied topic. Riparian corridors and wetlands are of special interest in carbon sequestration because of their high productivity and large below-ground stocks that sequester carbon (US Climate Change Technology Program 2003). In this study, sites with Medium densities of the nonnative Chinese privet have greater litterfall and fine root carbon sequestration than Reference sites (Figs. 67 and 84). The data suggest that the dense understory of Chinese privet in the Medium and High sites contributed to increased litterfall and belowground carbon sequestration rates. Perhaps the addition of understory Chinese privet beneath the canopy of overstory native trees on these sites resulted in greater biomass production than Reference sites. This is supported by Ehrenfeld (2003) who noted that invasive, nonnative species frequently increase standing crop biomass and NPP due to their different morphology and phenology compared to native species.

The Chinese privet influence on standing crop biomass and NPP (Chapter 2) may have translated into changes in carbon allocation and carbon sequestration. The lack of a difference in total or aboveground carbon allocation among Chinese privet categories was likely attributed to the masking effect of stem carbon allocation mentioned previously. However, there was significantly more litterfall carbon allocation and carbon sequestration in the Medium and High sites compared with the Reference sites for Period 2 (Fig. 67). Again, the presence of a dense understory of Chinese privet at the Medium and High sites along with the canopy of larger native trees may have contributed to the greater amounts of litterfall carbon allocation and carbon sequestration. Understory tree species tend to allocate greater biomass to leaves than support tissues (King 1991, Bongers and Sterck 1998) and maximize leaf area (Ellsworth and Reich 1992) to increase efficiency of light interception. These adaptations to low-light conditions contribute to overall stand productivity (Ishii et al. 2004) which strongly influences carbon allocation and sequestration.

Changing forest structure and consequential alteration in carbon sequestration potential were observed in comparisons of the Reference, Medium, and High Chinese privet categories (Figs. 96 and 97). All sites had full canopy closure, but had different understory characteristics. For example, Reference sites had a sparse, but diverse understory with native vegetation present as regeneration, understory, and mid-story layers. Overall, the Medium Chinese privet category sites tended to retain some structure associated with the Reference sites while concurrently displaying accelerated rates of

Chinese privet invasion in the regeneration, understory, and mid-story layers. This translated into increased litterfall and belowground carbon sequestration capacity. Finally, High Chinese privet sites tended to have a fully developed mid-story of larger Chinese privet, fewer understory stems, and regeneration layers that were largely composed of Chinese privet. Merriam and Feil (2002) also noted that Chinese privet severely reduced herbaceous species in mixed-hardwood forest in western North Carolina.

Changes in forest structure have been linked to carbon sequestration (Ellison et al. 2005, Litton et al. 2006, Hoover and Stout 2007). Ellison et al. (2005) found that the decline of foundation species due to exotic pests, pathogens, selective removal, and over-harvesting disrupts fundamental processes such as carbon sequestration. Additionally, Hoover and Stout (2007) noted that changes in stand structure with different thinning techniques had altered carbon sequestration in a northwestern Pennsylvania Allegheny hardwood stand. For example, carbon sequestration was increased when small diameter stems were harvested. However, carbon sequestration decreased when middle or larger diameter stems were harvested. Chinese privet may have served as a ‘biological thinning agent’ in the High Chinese privet sites, suppressing native species regeneration, especially hardwoods, that would have occupied the larger diameter understory and mid-story forest layer (Merriam and Feil 2002, Chapter 4)

Belowground carbon allocation was significantly different among Chinese privet categories in Period 1, but not Period 2 (Fig. 83). In both years, Medium and High Chinese privet sites had greater belowground carbon allocation than Reference sites. That is, sites with a dense understory of Chinese privet stems had greater belowground carbon allocation than Reference sites with little or no understory Chinese privet stems. Belowground response of plants to increased aboveground competition is variable and depends on many factors including available resources (Casper et al. 1998, Cahill 2002). In other studies, there does not appear to be a clear pattern of belowground or aboveground productivity in response to competition. Cahill (2002) noted that while some studies found no correlation between the intensity of competition and productivity (Wilson and Tilman 1995, Belcher et al. 1995, Cahill 1999), positive correlations (Reader and Best 1989, Kadmon 1995, Sammul et al. 2000), as well as negative correlations, had also been noted (Davis et al. 1998). In this study, the density of understory Chinese privet stems strongly increased belowground carbon allocation during a period of plentiful rainfall. Furthermore, a positive relationship was detected between aboveground productivity and competition that agrees with the studies of Reader and Best (1989), Kadmon (1995), and Sammul et al. (2000).

Period 1 belowground carbon allocation was numerically greater than Period 2, but this difference was not significant (Fig. 94). It has been noted that fine root biomass is generally increased when moisture and nutrients are limited in order to satisfy aboveground demands (Keyes and Grier 1981). However, the present study showed a numerical, but not significant, decrease in fine root carbon allocation during a period of low soil moisture for all Chinese privet categories.

Similar to belowground carbon allocation, the Medium and High Chinese privet sites sequestered greater amounts of carbon than the Reference sites (Fig. 95). However, differences were only significant in Period 1. Although understory tree species generally allocate more biomass to leaves than support tissue (King 1991, Bongers and Sterck

1998) the dense numbers of understory Chinese privet stems likely contributed to the increase in fine root productivity and carbon sequestration found in the Medium and High sites. Shan et al. (2001) demonstrated the importance of understory vegetation on fine root productivity in a slash pine plantation and noted that fine root productivity and soil carbon storage were reduced when understory vegetation was eliminated.

Reference sites sequestered slightly more carbon as fine roots in Period 2 due to greater fine root production in response to the drought year or the ability of more deeply rooted native vegetation to access water (Kimmins 2004). Thomas (1984) noted that a more deeply rooted grass had a competitive advantage over a more shallow rooted grass in drought conditions. In contrast, there were significant decreases in carbon sequestration in the Medium sites in Period 2. This may be explained by the shallow root system of Chinese privet which was not able to access deeper soil moisture and resulted in decreased belowground productivity and carbon sequestration.

Root Dynamics

Fine root turnover influences the biogeochemical cycle of carbon in terrestrial systems and is a major contributor to the formation of soil organic matter (Matamala et al. 2003). Fine root turnover ranges reported in this study are consistent with those of Gill and Jackson (2000) and Trumbore and Gaudinski (2003). There was no significant difference among Chinese privet categories in fine root turnover in Period 1 or 2 (Fig. 87). Changes in fine root turnover may have been undetected as a result of sampling periodicity (time between samplings). However, it is possible that Chinese privet fine roots may share similar turnover characteristics as native plant fine roots, and thus, differences among sites are minimized. The significant negative regression relationship between fine root turnover and bulk density in Period 2 may be attributed to the shedding and re-growth of roots in inhospitable environments (Eissenstat and Van Rees 1994), such as might be associated with higher soil bulk density.

There was no significant difference among Chinese privet categories for the live:dead root ratio in either sampling year (Fig. 90). However, there was a significant negative regression relationship between live:dead root ratio and percent Chinese privet in the understory in Period 2. Indeed, in periods of low rainfall such as in Period 2, there were significantly more dead roots in sites heavily dominated by a Chinese privet understory. This contributed to the significant decrease in live:dead root ratio along the Chinese privet continuum and may further support Kimmins' (2004) suggestion that native trees with well developed root systems are able to withstand low soil moisture while shallow rooted plants such as Chinese privet may show greater root mortality. However, the use of live:dead root ratios as ecosystem indicators has been noted to be uncertain due to the variability associated with soils, plants, lab methods, fine root longevity, and decay rates of dead roots (Ehrenfeld et al. 1997, Borken et al. 2007).

CONCLUSION

Chinese privet influenced above- and belowground carbon dynamics in southern Piedmont riparian forests. The alterations observed in the current study may be harbingers for shifts in forest structure and corresponding impacts to carbon sequestration rates in these ecosystems. It was hypothesized that, as Chinese privet understory stem densities increased, aboveground carbon allocation and sequestration would decline and that carbon allocation and sequestration associated with roots would increase. Contrary to the stated hypothesis, there was an increase in total aboveground carbon sequestration under moderate levels of Chinese privet invasion in riparian community understories (25-79% of total understory) during the first year of the current study. However, when the proportion of understory Chinese privet was greater than 80%, there were indications of a decrease in aboveground carbon sequestration levels. These differences were not significant. Belowground carbon sequestration was significantly less in the Reference category than in the Medium Chinese privet category which supported the hypothesis. However, when the proportion of understory Chinese privet was greater than 80%, belowground carbon sequestration levels were numerically , but not significantly, less than in the 25-79% category.

Total aboveground carbon sequestration patterns for Period 2 were also different from the stated hypothesis. As the proportion of Chinese privet in the understory increased, so did the rate of total aboveground carbon sequestration, though these increases were not statistically significant. However, belowground carbon sequestration trends in Period 2 supported the hypothesis that as understory Chinese privet increased, so would the belowground carbon component. Increases in belowground carbon sequestration were also not significant in Period 2.

Variation in carbon sequestration patterns between the study years was likely due to several factors, including a disparity in precipitation. Rainfall amounts were near 30 year averages in Period 1 and drought conditions were observed in Period 2. It is likely the shallow root system of Chinese privet was negatively impacted by the drought leading to a decrease in belowground carbon sequestration in the Medium and High categories that eliminated significant differences from the Reference category in Period 2.

Additionally, the lack of significant differences observed for total aboveground carbon sequestration among Chinese privet categories was influenced by the presence of large, native overstory trees found on all research plots. Most of the vegetative carbon in the research plots was allocated to woody stems (Fig. 98) and woody carbon sequestration rates were not significantly different among Chinese privet categories (Fig. 71) due to the overriding influence of large, native trees. As an example, woody carbon sequestration masked significant differences observed in total litterfall carbon sequestration for Period 2. Reference total litterfall carbon sequestration was significantly less than in the Medium and High Chinese privet categories in Period 2. This was influenced by the high amount of reproductive litterfall observed in the Medium and High categories as reported in Chapter 2 (Influence of Chinese Privet on Productivity of Riparian Forests of the Southern Piedmont).

Future changes in southern Piedmont riparian forests' structure by Chinese privet may be strongly linked to decreased carbon sequestration. At medium levels of understory Chinese privet invasion (25-79%) there was a noticeable shift to increased Chinese privet understory stems, less native species in the mid-story, and decreased native species regeneration (Chapter 4, Influence of Chinese Privet On Native Plant Regeneration in Riparian Forests of the Southern Piedmont). Furthermore, it was observed that at high levels of Chinese privet invasion in the understory (>80%) were characterized by a shift in stand structure to a dense mid-story of Chinese privet, fewer understory Chinese privet stems, and limited native species understory and regeneration.

Merriam and Feil (2002) also noted that Chinese privet severely reduced herbaceous species and suppressed native hardwood species regeneration in a mixed-hardwood forest in western North Carolina. The current study observed similar or increased rates of carbon sequestration in riparian sites invaded by Chinese privet as compared to reference sites. This trend will not persist as the large native canopy trees are lost and not replaced due to suppression of native species regeneration (Chapter 4, Influence of Chinese Privet on Native Plant Regeneration in Riparian Forests of the Southern Piedmont).

Table 6. Period 1 standing crop biomass for Chinese privet categories Reference, Medium, and High and overall range for data. Means followed by different letters across classes are significantly different by Tukey's HSD (α=0.10). Standard errors in parentheses.

Period 1		Privet Category		
Standing Crop biomass (Mg ha^{-1})	Reference	Medium	High	Range
Litterfall Total	6.2 (0.26)^{a}	7.5 (0.56)^{a}	7.0 (0.46)^{a}	5.2-9.2
Woody biomass	217.0 (23.6)^{a}	200.1 (20.8)^{a}	198.8 (20.2)^{a}	128.8-267.9
Total Aboveground	223.1 (23.7)^{a}	207.6 (20.7)^{a}	205.8 (20.3)^{a}	139.2-278.3
Belowground	1.9 (0.12)^{c}	3.7 (0.24)^{a}	3.1 (0.13)^{b}	1.8-5.1
Total	224.8 (23.5)^{a}	210.6 (20.3)^{a}	208.8 (20.2)^{a}	137-276
Shoot-Root Ratio	139.6 (34.1)^{a}	88.1 (33.2)^{a}	81.1 (14.4)^{a}	81.1-140

Table 7. Period 2 standing crop biomass for Chinese privet categories Reference, Medium, and High plots and overall range for data. Means followed by different letters across classes are significantly different by Tukey's HSD (α=0.10). Standard errors in parentheses.

Period 2		Privet Category		
Standing Crop biomass (Mg ha^{-1})	Reference	Medium	High	Range
Litterfall Total	5.2 (0.17)^{b}	6.3 (0.28)^{a}	6.1 (0.18)^{a}	5.0-6.9
Woody biomass	222.8 (24.7)^{a}	206.5 (21.3)^{a}	207.0 (20.9)^{a}	133.8-279.3
Total Aboveground	228.1 (24.8)^{a}	212.8 (21.3)^{a}	213.0 (20.9)^{a}	147.0-287.7
Belowground	1.9 (0.10)^{b}	2.9 (0.16)^{a}	2.5 (0.11)^{a}	1.5-4.1
Total	230.2 (24.6)^{a}	215.7 (21.0)^{a}	215.4 (21.0)^{a}	141.5-287.7
Shoot-Root Ratio	112.1 (24.9)^{a}	81.4 (20.6)^{a}	99.1 (14.0)^{a}	81.4-112.1

Table 8. Period 1 carbon allocation for Chinese privet categories Reference, Medium, and High and overall range. Percent of total presented. Means followed by different letters across classes are significantly different by Tukey's HSD (α=0.10). Standard errors in parentheses.

Period 1			Privet Category				
Carbon Allocation	Reference		Medium		High		Range
	% of total	Mg ha^{-1}	% of total	Mg ha^{-1}	% of total	Mg ha^{-1}	Mg ha^{-1}
Litterfall Total	3%	2.9 (0.11)^{a}	4%	3.5 (0.25)^{a}	3%	3.3 (0.22)^{a}	5.22-9.16
Woody biomass	96%	102.0 (11.1)^{a}	95%	94.7 (10.4)^{a}	95%	94.3 (9.1)^{a}	61.9-125.9
Total Aboveground	99%	104.9 (11.1)^{a}	98%	97.9 (10.0)^{a}	98%	97.5 (9.2)^{a}	65-129
Belowground	1%	1.1 (0.22)^{a}	2%	1.9 (0.32)^{a}	2%	1.8 (0.11)^{a}	0.84-2.8
Total	100%	106.0 (10.98)^{a}	100%	99.8 (10.0)^{a}	100%	99.3 (9.2)^{a}	65.7-130.7

Table 9. Period 2 carbon allocation for Chinese privet categories Reference, Medium, and High plots and overall range. Percent of total presented. Means followed by different letters across classes are significantly different by Tukey's HSD (α=0.10). Standard errors in parentheses.

Period 2			Privet Category				
Carbon Allocation	Reference		Medium		High		Range
	% of total	Mg ha^{-1}	% of total	Mg ha^{-1}	% of total	Mg ha^{-1}	Mg ha^{-1}
Litterfall Total	2%	2.4 (0.09)^{b}	3%	3.0 (0.13)^{a}	3%	2.8 (0.08)^{a}	5.0-6.9
Woody biomass	97%	104.7 (11.6)^{a}	96%	97.7 (10.6)^{a}	96%	98.1 (9.4)^{a}	64.7-131.2
Total Aboveground	99%	107.2 (11.7)^{a}	99%	100.3 (10.3)^{a}	99%	100.9 (9.4)^{a}	67.5-133.9
Belowground	1%	0.73 (0.09)^{b}	1%	1.3 (0.22)^{ab}	1%	1.5 (0.19)^{a}	0.6-2.7
Total	100%	107.9 (11.6)^{a}	100%	101.6 (10.2)^{a}	100%	102.4 (9.5)^{a}	65.7-130.7

Table 10. Period 1 carbon sequestration for Chinese privet categories Reference, Medium, and High and overall range. Means followed by different letters across classes are significantly different by Tukey's HSD (α=0.10). Standard errors in parentheses.

Period 1		Privet Category		
Carbon Sequestration (Mg ha^{-1} yr^{-1})	Reference	Medium	High	Range
Litterfall Total	2.9 (0.11)^{a}	3.5 (0.25)^{a}	3.3 (0.22)^{a}	2.4-4.3
Woody biomass	2.98 (0.49)^{a}	4.5 (0.62)^{a}	4.2 (0.58)^{a}	1.8-6.7
Total Aboveground	5.89 (0.55)^{a}	8.0 (0.80)^{a}	7.4 (0.73)^{a}	4.2-10.6
Belowground	1.6 (0.16)^{b}	3.6 (0.34)^{a}	2.9 (0.29)^{a}	1.4-4.5
Total	7.5 (0.40)^{b}	11.6 (1.2)^{a}	10.3 (0.80)^{a}	7-14.9

Table 11. Period 2 carbon sequestration for Chinese privet categories Reference, Medium, and High plots and overall range. Means followed by different letters across classes are significantly different by Tukey's HSD (α=0.10). Standard errors in parentheses.

Period 2		Privet Category		
Carbon Sequestration (Mg ha^{-1} yr^{-1})	Reference	Medium	High	Range
Litterfall Total	2.8 (0.08)^{b}	2.97 (0.13)^{a}	2.4 (0.09)^{a}	2.3-3.2
Woody biomass	2.8 (0.52)^{a}	3.4 0.22)^{a}	3.9 (0.54)^{a}	1.8-6.1
Total Aboveground	5.2 (0.58)^{a}	6.4 (0.33)^{a}	6.7 (0.59)^{a}	4.4-8.5
Belowground	2.0 0.27)^{a}	2.5 (0.19)^{a}	2.6 (0.29)^{a}	1.7-3.8
Total	7.2 (0.50)^{a}	8.8 (0.15)^{a}	9.3 (0.76)^{a}	7.0-14.9

Table 12. Period 1 Chinese privet standing crop biomass, carbon allocation, and carbon sequestration for Chinese privet categories Reference, Medium, and High. Means followed by different letters across classes are significantly different by Tukey's HSD (α=0.10). Standard errors in parentheses.

Period 1		Chinese privet Category	
	Reference	Medium	High
Litterfall Total Standing Crop biomass (Mg ha^{-1})	0.001 (0.0)^{b}	0.36 (0.11)^{a}	0.53 (0.09)^{a}
Woody biomass Standing Crop biomass (Mg ha^{-1})	0.0^{a}	5.5 (1.8)^{a}	29.8 (9.98)^{a}
Total Aboveground Standing Crop biomass (Mg ha^{-1})	0.001 (0.00)^{a}	5.8 (1.9)^{a}	30.3 (10.0)^{a}
Litterfall Carbon Allocation (Mg ha^{-1})	0.0^{b}	0.2 (0.05)^{a}	0.2 (0.04)^{a}
Woody biomass Carbon Allocation (Mg ha^{-1})	0.0^{a}	2.6 (0.9)^{a}	14.0 (4.7)^{a}
Total Aboveground Carbon Allocation (Mg ha^{-1})	0.0^{a}	2.8 (0.9)^{a}	14.3 (4.7)^{a}
Litterfall Carbon Sequestration (Mg ha^{-1} yr^{-1})	0.0^{b}	0.2 (0.05)^{a}	0.2 (0.04)^{a}
Woody biomass Carbon Sequestration (Mg ha^{-1} yr^{-1})	0.0^{a}	2.0 (.05)^{a}	1.4 (.4)^{a}
Total Aboveground Carbon Sequestration (Mg ha^{-1} yr^{-1})	0.0^{b}	.22 (.05)^{a}	1.6 (.4)^{a}

Table 13. Period 2 Chinese privet standing crop biomass, carbon allocation, and carbon sequestration for Chinese privet categories Reference, Medium, and High. Means followed by different letters across classes are significantly different by Tukey's HSD (α=0.10). Standard errors in parentheses.

Period 2		Chinese privet Category	
	Reference	Medium	High
Litterfall Total Standing Crop biomass (Mg ha^{-1})	0.0 (0.0) ^{b}	0.48 (0.2) ^{a}	0.80 (0.1) ^{a}
Woody biomass Standing Crop biomass (Mg ha^{-1})	0.0 (0.0) ^{a}	5.9 (1.9) ^{a}	31.7 (10.7) ^{a}
Total Aboveground Standing Crop biomass (Mg ha^{-1})	0.0 ^{a}	6.4 (2.1) ^{a}	32.5 (10.7) ^{a}
Litterfall Carbon Allocation (Mg ha^{-1})	0.0 ^{b}	0.2 (0.05) ^{a}	0.2 (0.04) ^{a}
Woody biomass Carbon Allocation (Mg ha^{-1})	0.0 ^{a}	2.8 (0.9) ^{a}	14.9 (5.0) ^{a}
Total Aboveground Carbon Allocation (Mg ha^{-1})	0.0 ^{a}	3.0 (0.997) ^{a}	15.3 (5.1) ^{a}
Litterfall Carbon Sequestration (Mg ha^{-1} yr^{-1})	0.0 ^{b}	0.2 (0.05) ^{a}	0.2 (0.04) ^{a}
Woody biomass Carbon Sequestration (Mg ha^{-1} yr^{-1})	0.0 ^{a}	0.33 (0.22) ^{a}	0.82 (0.29) ^{a}
Total Aboveground Carbon Sequestration (Mg ha^{-1} yr^{-1})	0.0 ^{b}	0.33 (0.22) ^{a}	0.82 (0.29) ^{a}

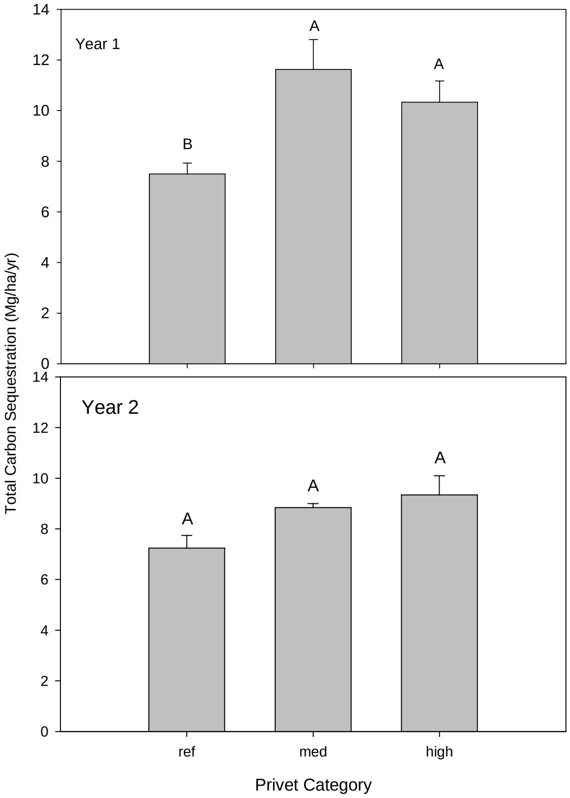

Figure 58. Comparison of Total Carbon Sequestration by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

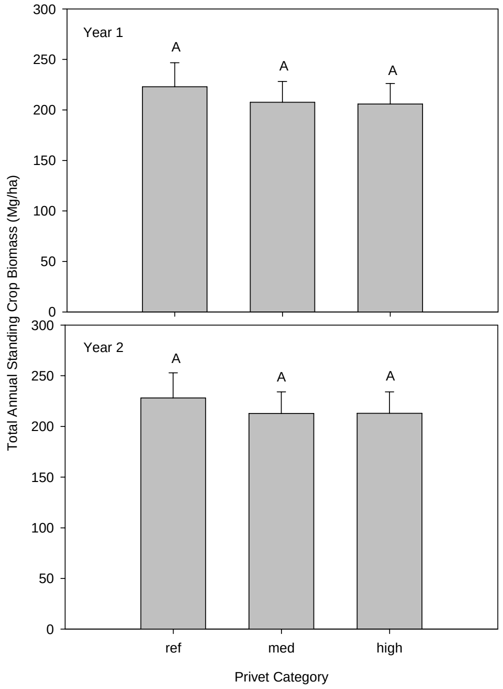

Figure 59. Comparison of Total Annual Standing Crop Biomass by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

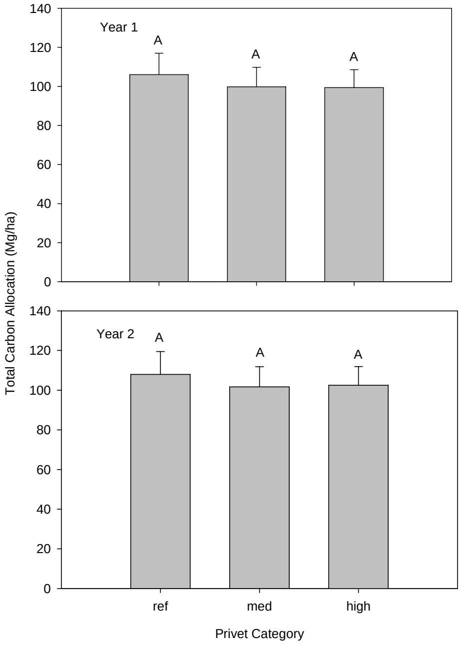

Figure 60. Comparison of Total Carbon Allocation by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

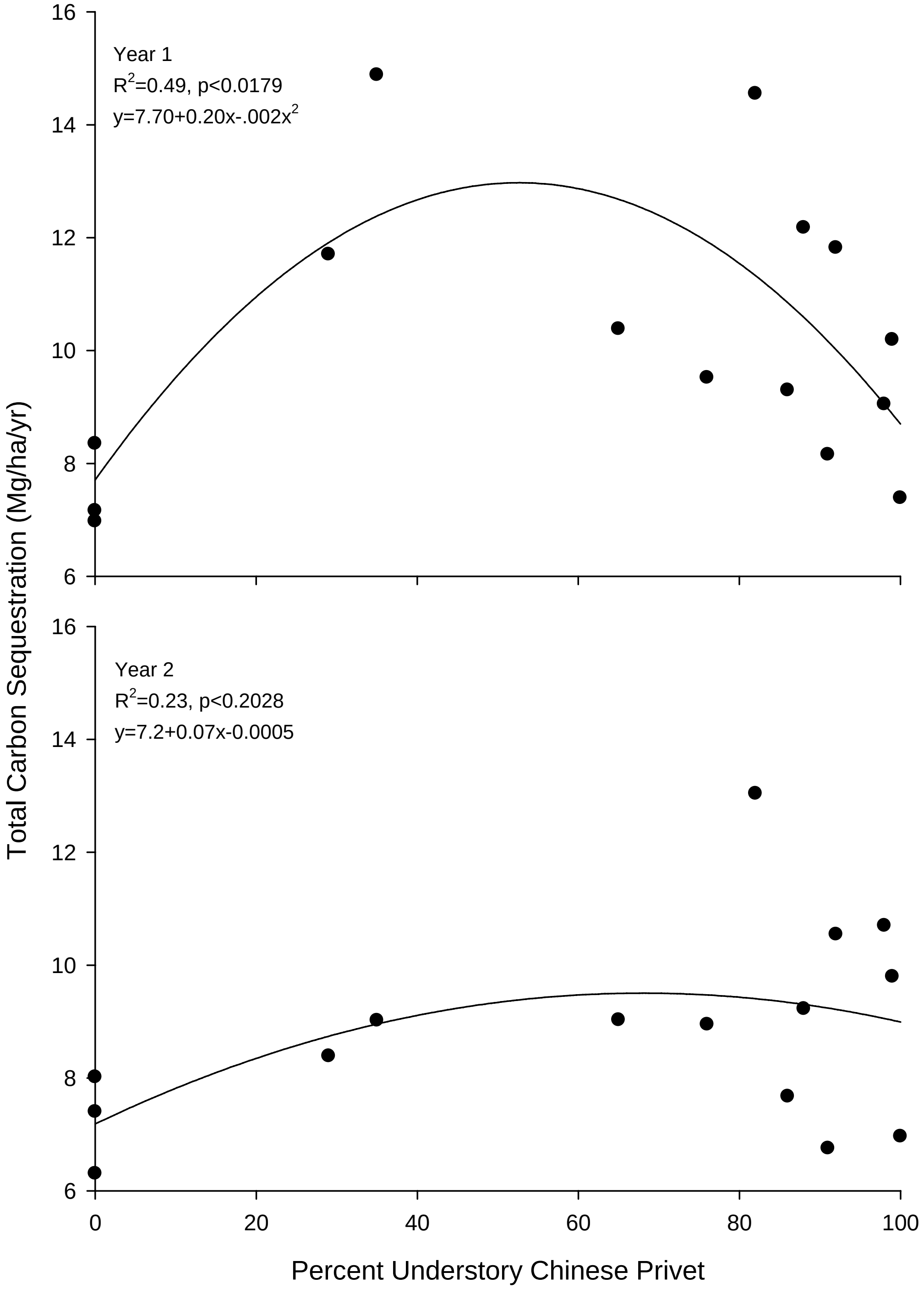

Figure 61. Significant regression relationships between total carbon sequestration and percent understory Chinese privet.

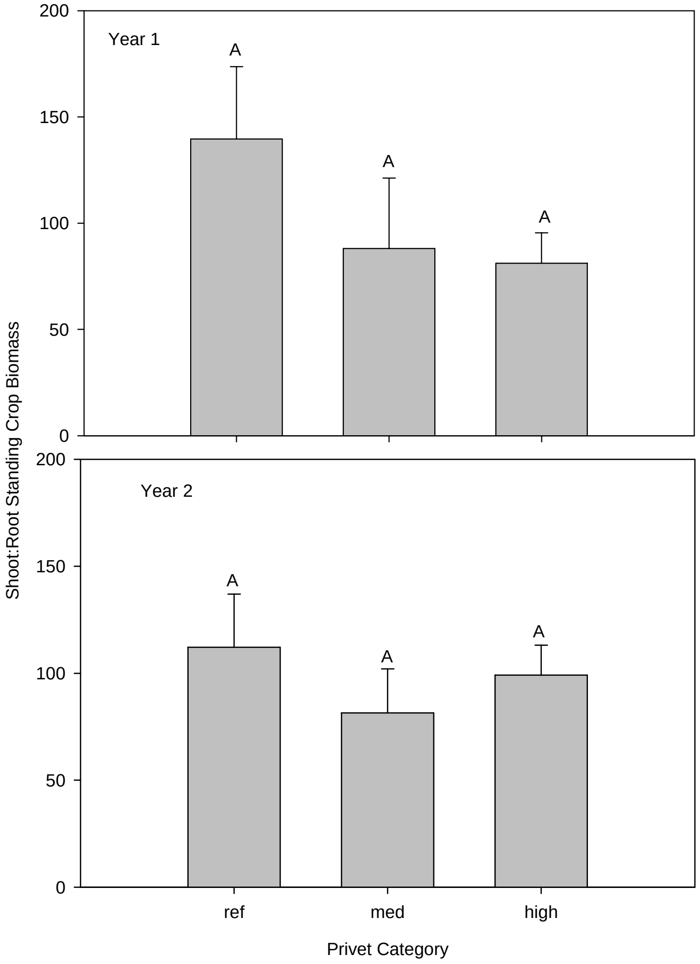

Figure 62. Comparison of Shoot:Fine Root Standing Crop Biomass ratio by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

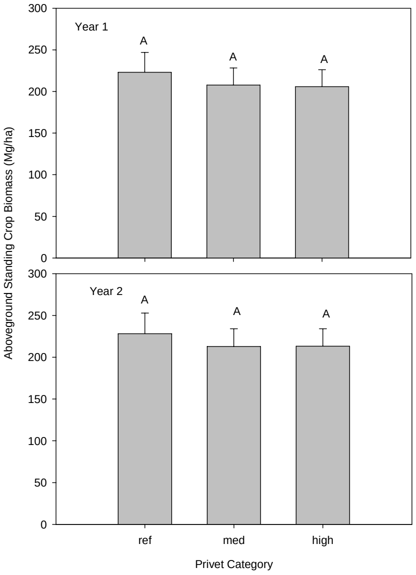

Figure 63. Comparison of total aboveground standing crop biomass by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

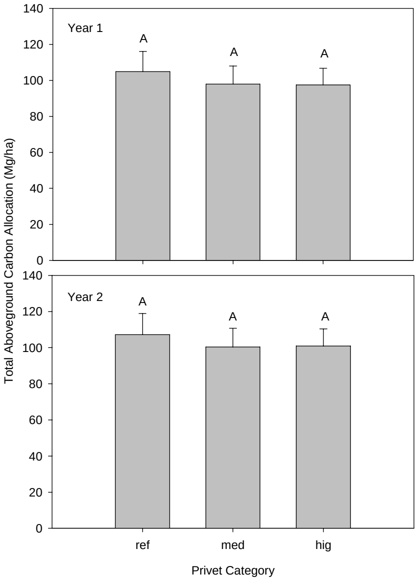

Figure 64. Comparison of total aboveground carbon allocation by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

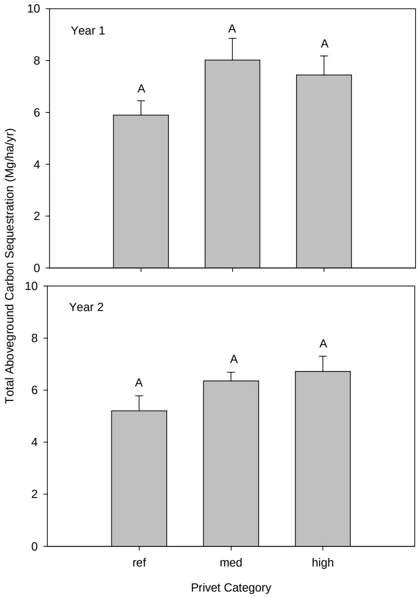

Figure 65. Comparison of total aboveground carbon sequestration by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

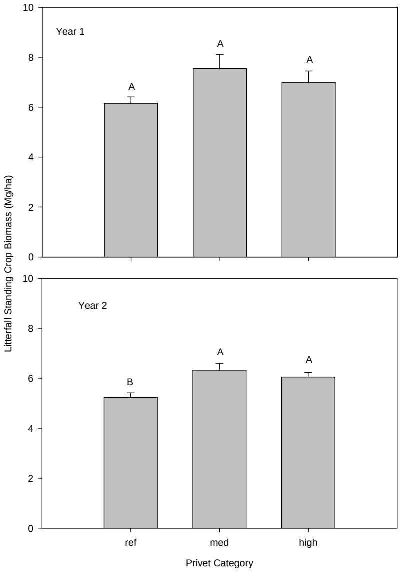

Figure 66. Comparison of litterfall standing crop biomass by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

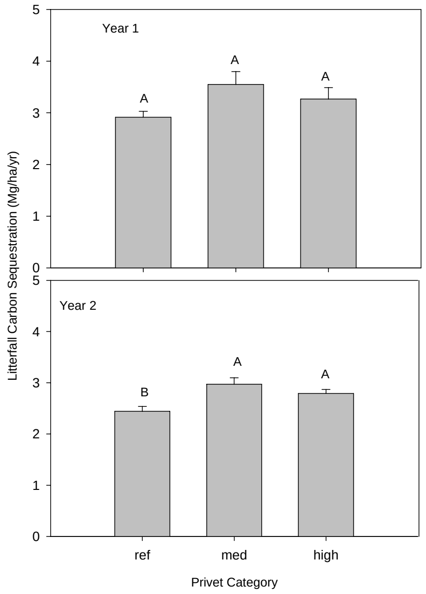

Figure 67. Comparison of litterfall carbon sequestration by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

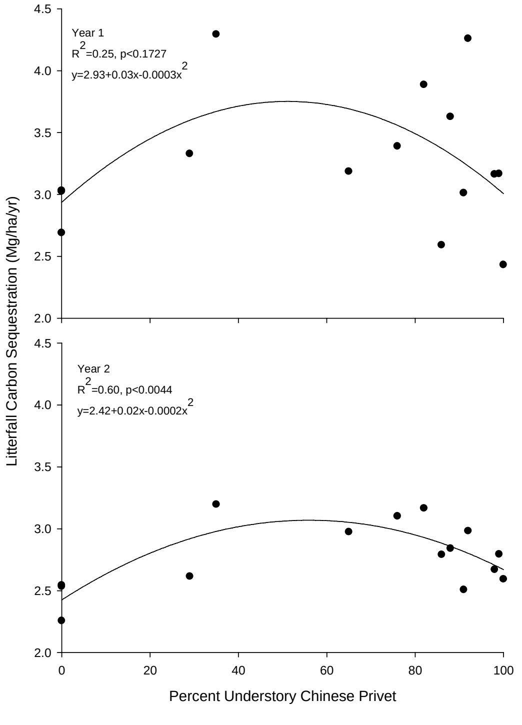

Figure 68. Quadratic regression relationship between percent understory Chinese privet and litterfall carbon sequestration.

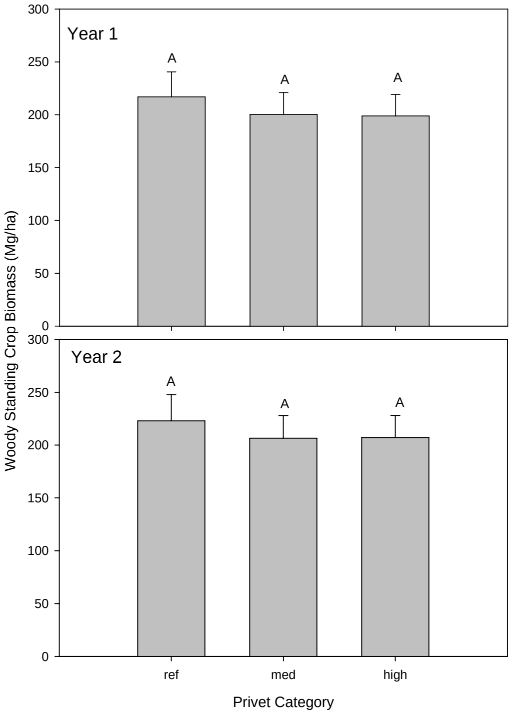

Figure 69. Comparison of woody standing crop biomass by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

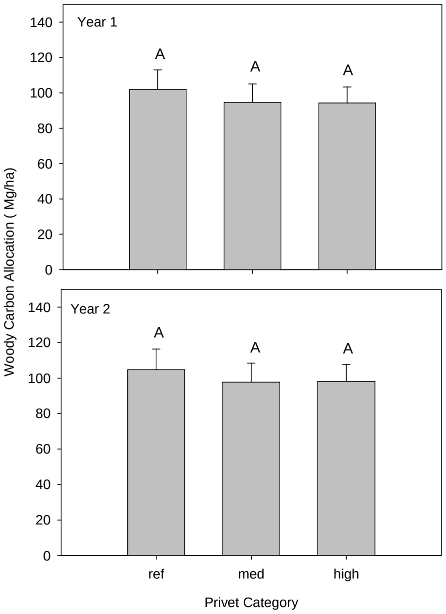

Figure 70. Comparison of woody carbon allocation by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

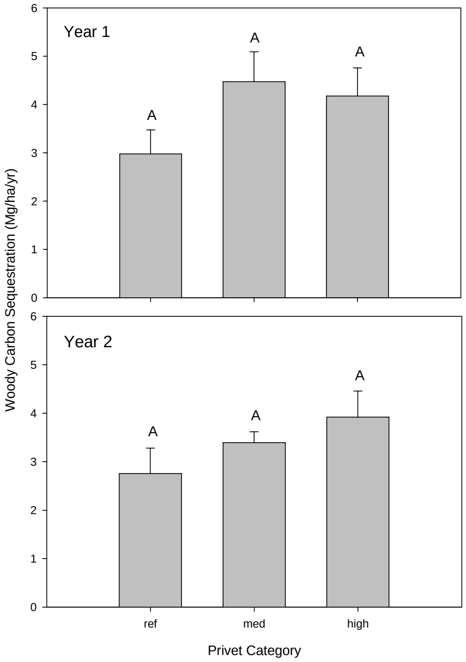

Figure 71. Comparison of woody carbon sequestration by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

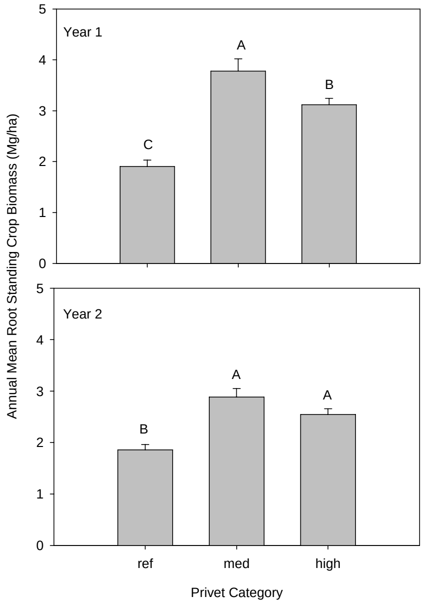

Figure 72. Comparison of live root annual standing crop biomass by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

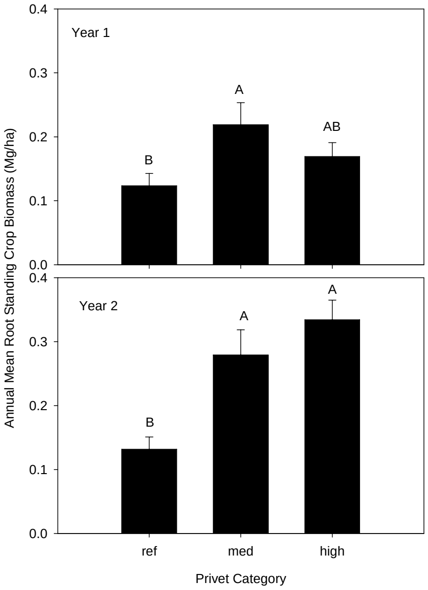

Figure 73. Comparison of dead root annual standing crop biomass by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

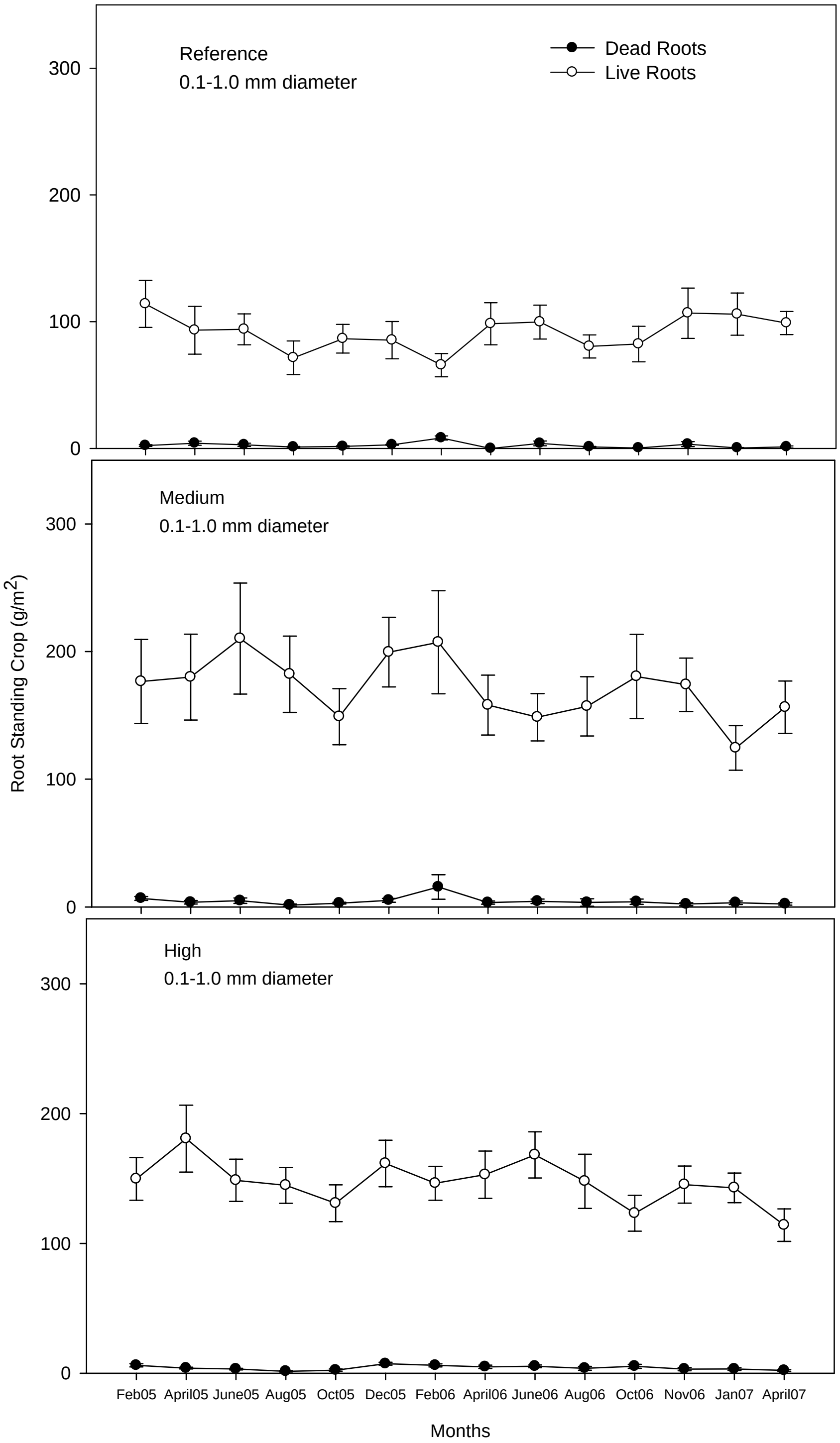

Figure 74. Fine root standing crop biomass by Chinese privet category for very fine root diameter class (0.1-1.0 mm). Vertical bars indicate standard errors.

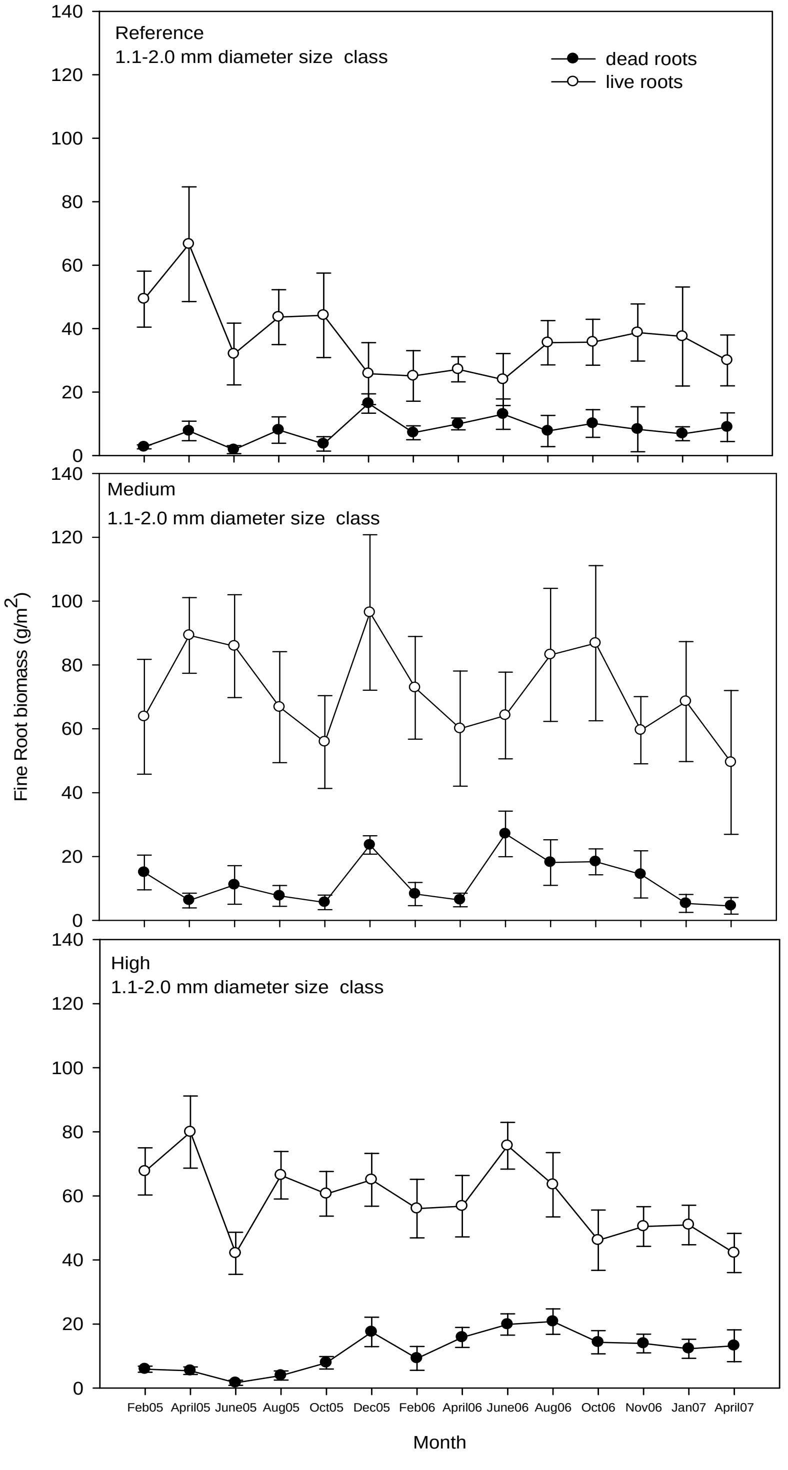

Figure 75. Fine root standing crop biomass by Chinese privet category for fine root diameter class (1.1-2.0 mm). Vertical bars indicate standard errors.

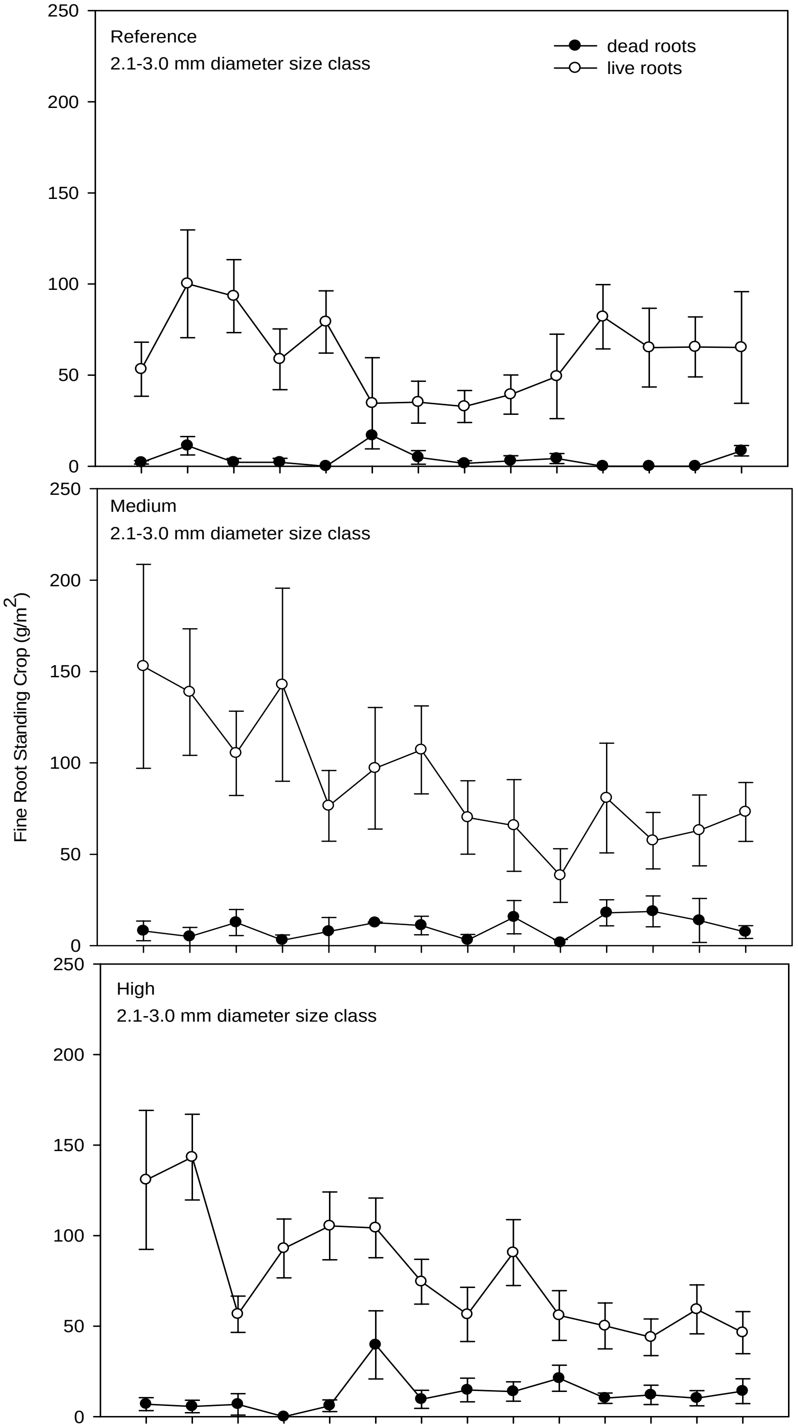

Figure 76. Fine root standing crop biomass by Chinese privet category for coarse fine root diameter class (2.1-3.0 mm). Vertical bars indicate standard errors.

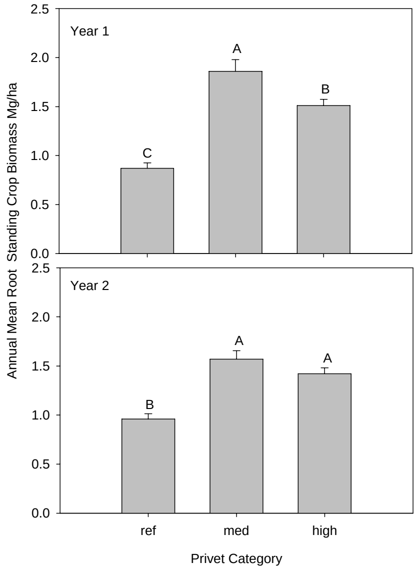

Figure 77. Comparison of Very Fine Root (0.1-1.0 mm) live root standing crop biomass by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

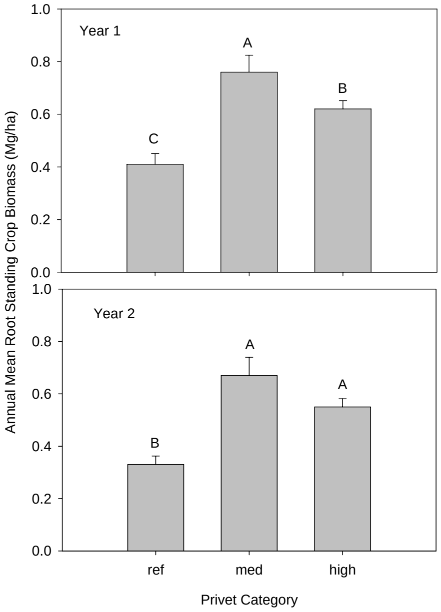

Figure 78. Comparison of Intermediate Fine Root (1.1-2.0 mm) live root standing crop biomass by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

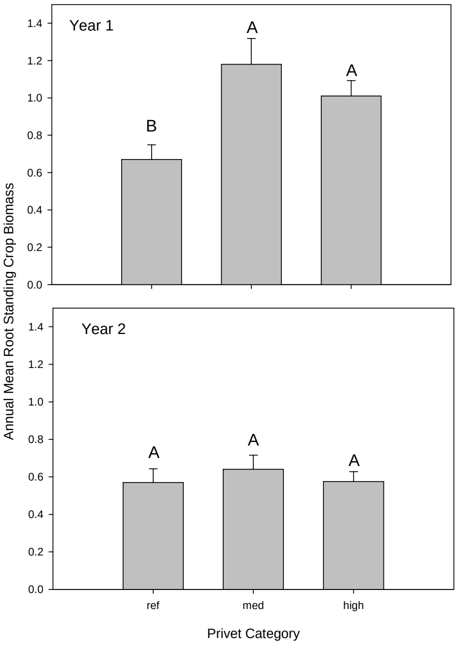

Figure 79. Comparison of Coarse Fine Root (2.1-3.0 mm) live root standing crop biomass by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

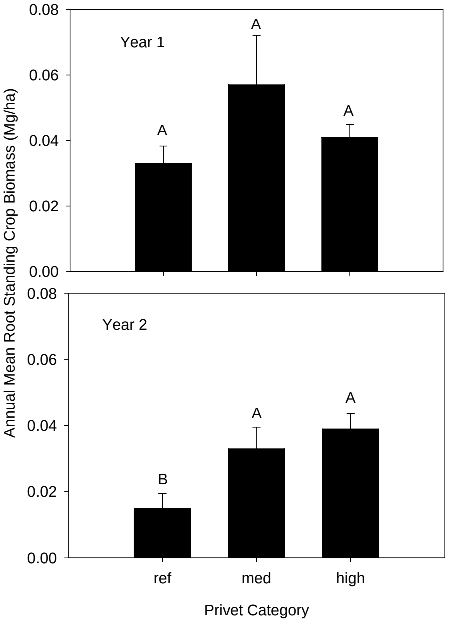

Figure 80. Comparison of Very Fine Root (0.1-1.0 mm) dead root standing crop biomass by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

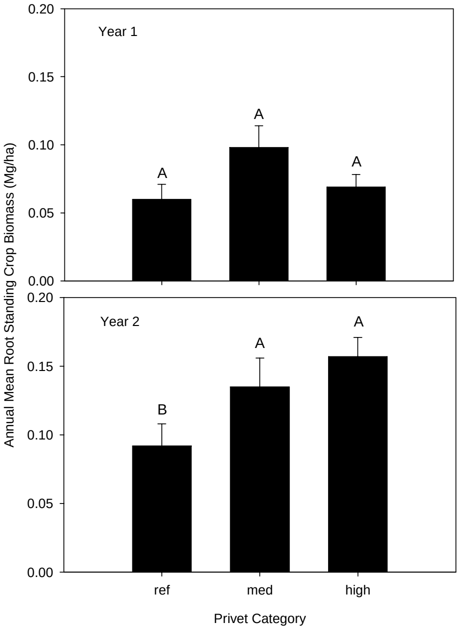

Figure 81. Comparison of Intermediate Fine Root (1.1-2.0 mm) dead root standing crop biomass by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

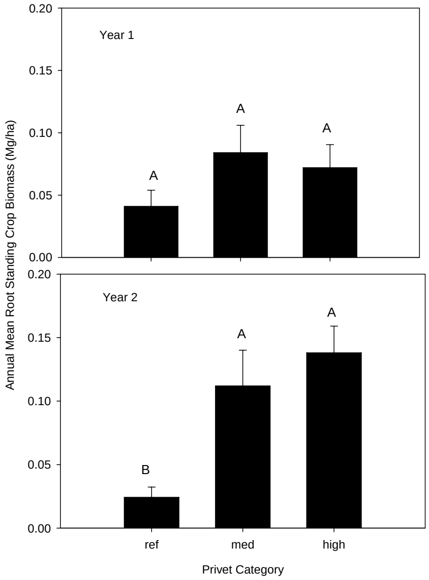

Figure 82. Comparison of Coarse Fine Root (2.1-3.0 mm) dead root standing crop biomass by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

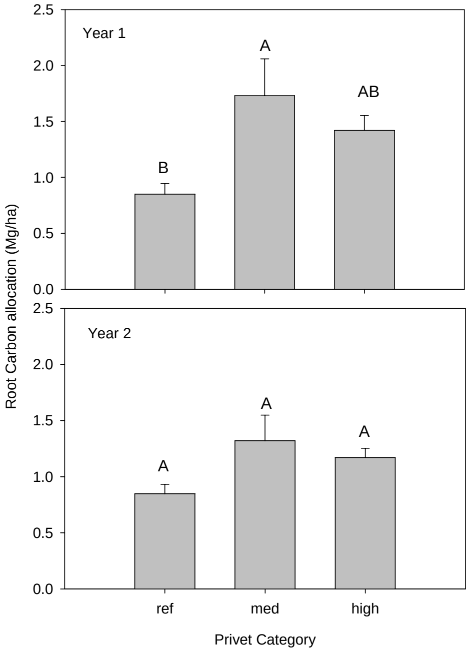

Figure 83. Comparison of live root carbon allocation by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

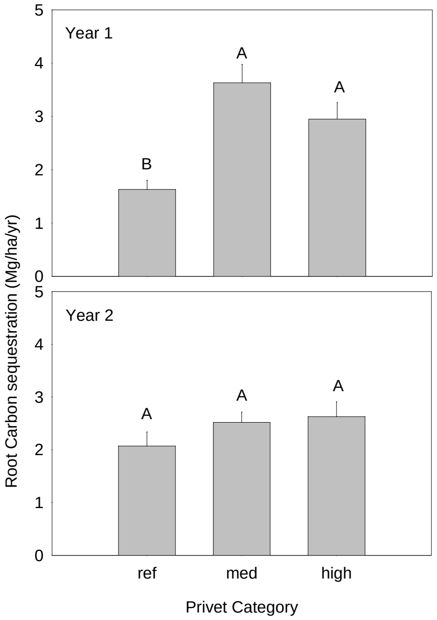

Figure 84. Comparison of live root carbon sequestration by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

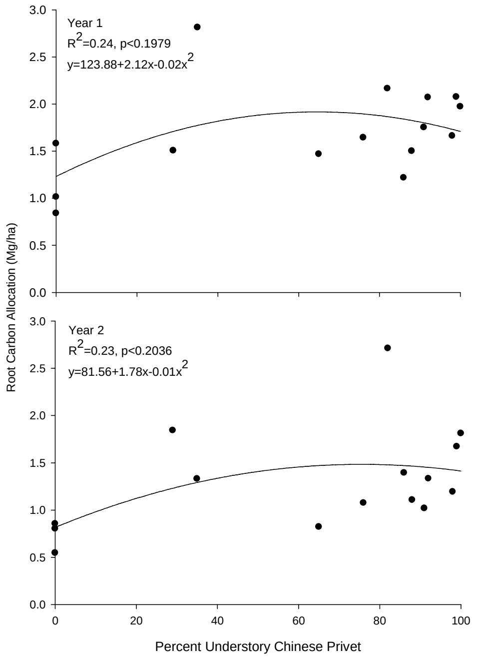

Figure 85. Quadratic regression relationship between percent understory Chinese privet and live root carbon allocation.

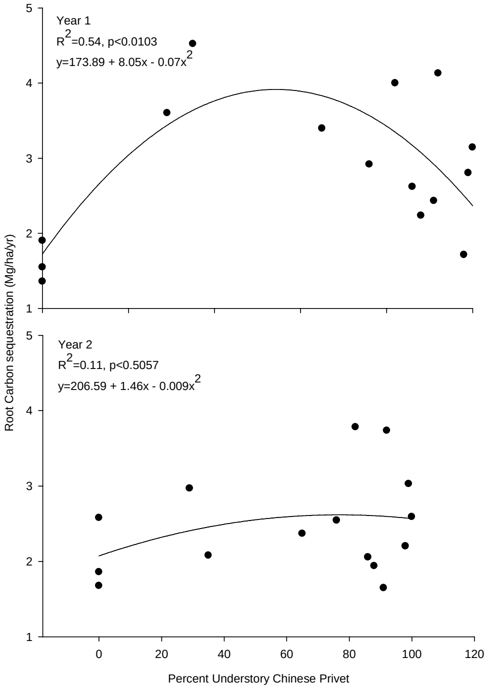

Figure 86. Quadratic regression relationship between percent understory Chinese privet and live root carbon sequestration.

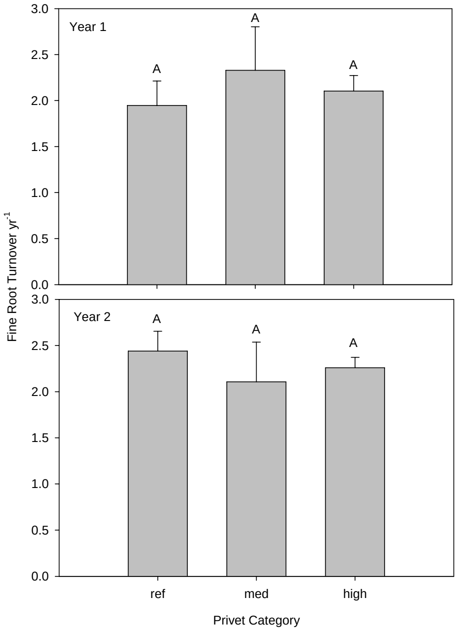

Figure 87. Comparison of fine root turnover by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

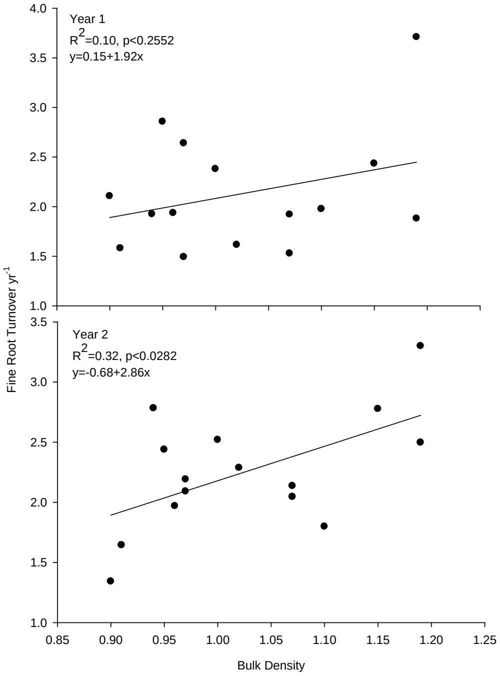

Figure 88. Regression relationship between bulk density and fine root turnover. Period 1 and Period 2 shown separately.

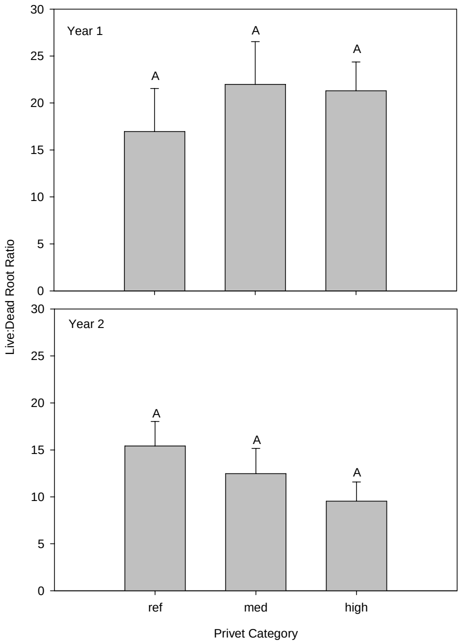

Figure 89. Comparison of live:dead root ratio by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

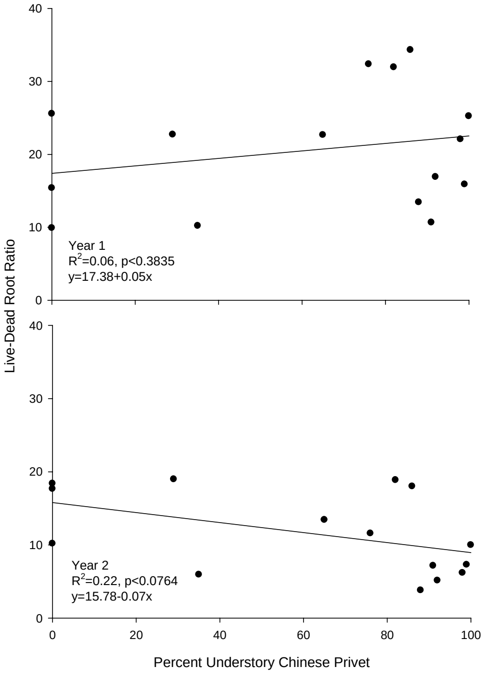

Figure 90. Linear regression relationship between Live:Dead root ratio and percent understory Chinese privet.

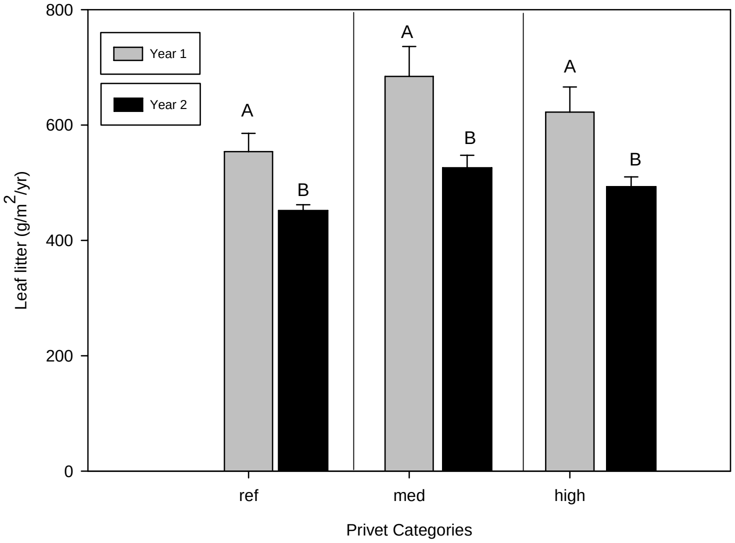

Figure 91. Comparison of leaf litter standing crop biomass by sampling year and Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

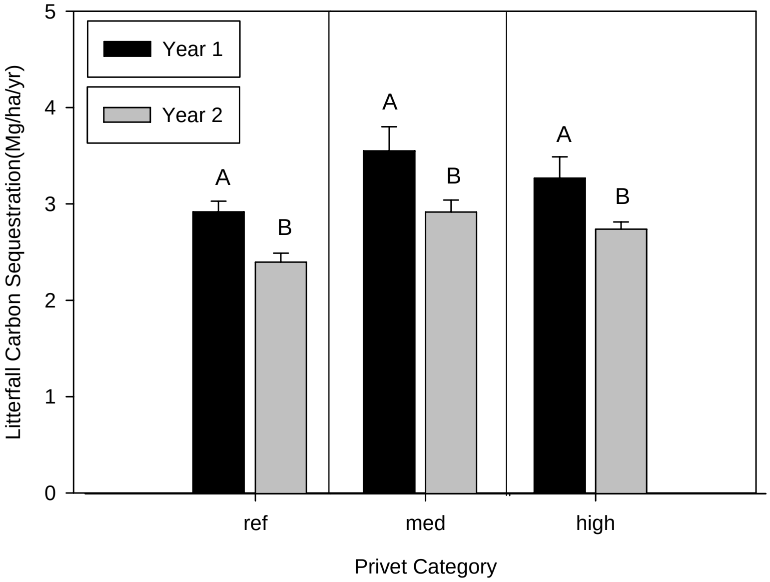

Figure 92. Comparison of litterfall carbon sequestration by Chinese privet category between years. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

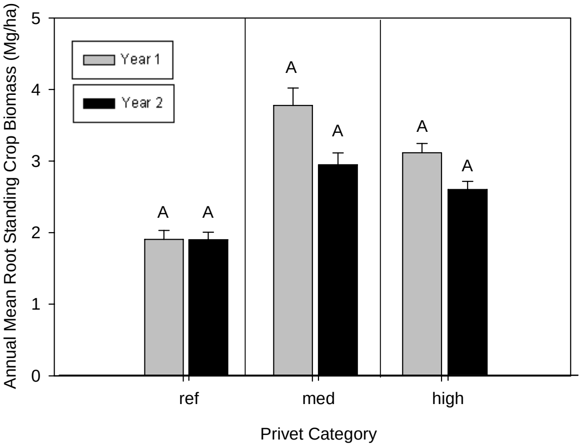

Figure 93. Comparison of annual mean root standing crop biomass by Chinese privet category between years. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

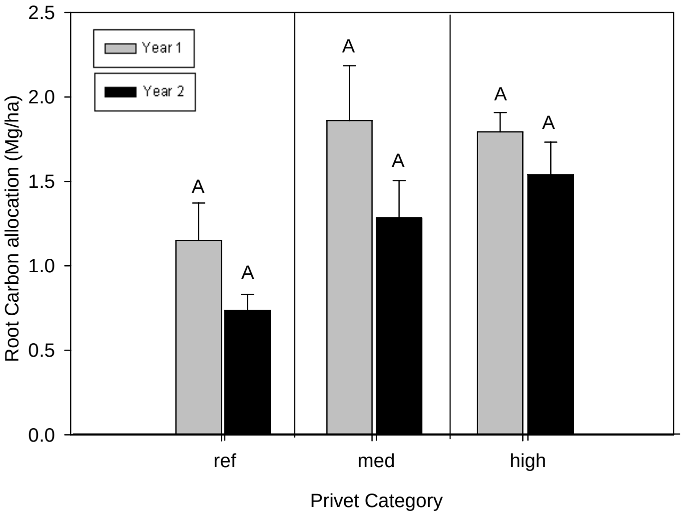

Figure 94. Comparison of root carbon allocation by Chinese privet category between years. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

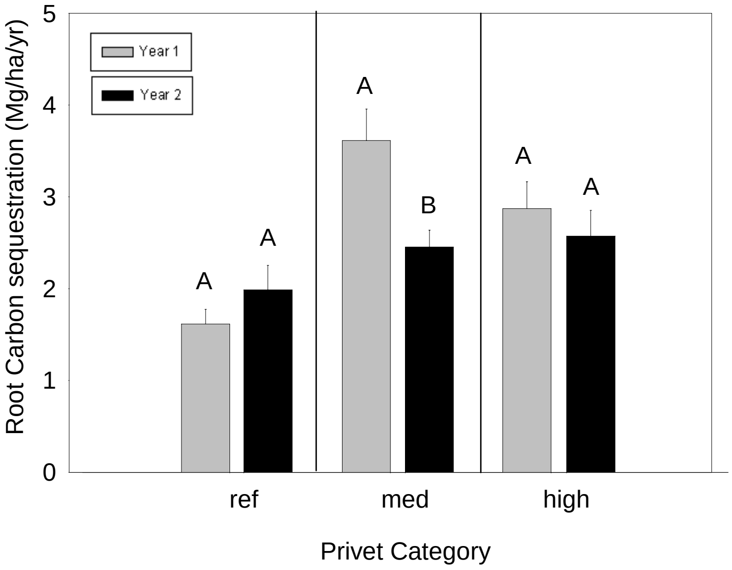

Figure 95. Comparison of root carbon sequestration by Chinese privet category between years. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

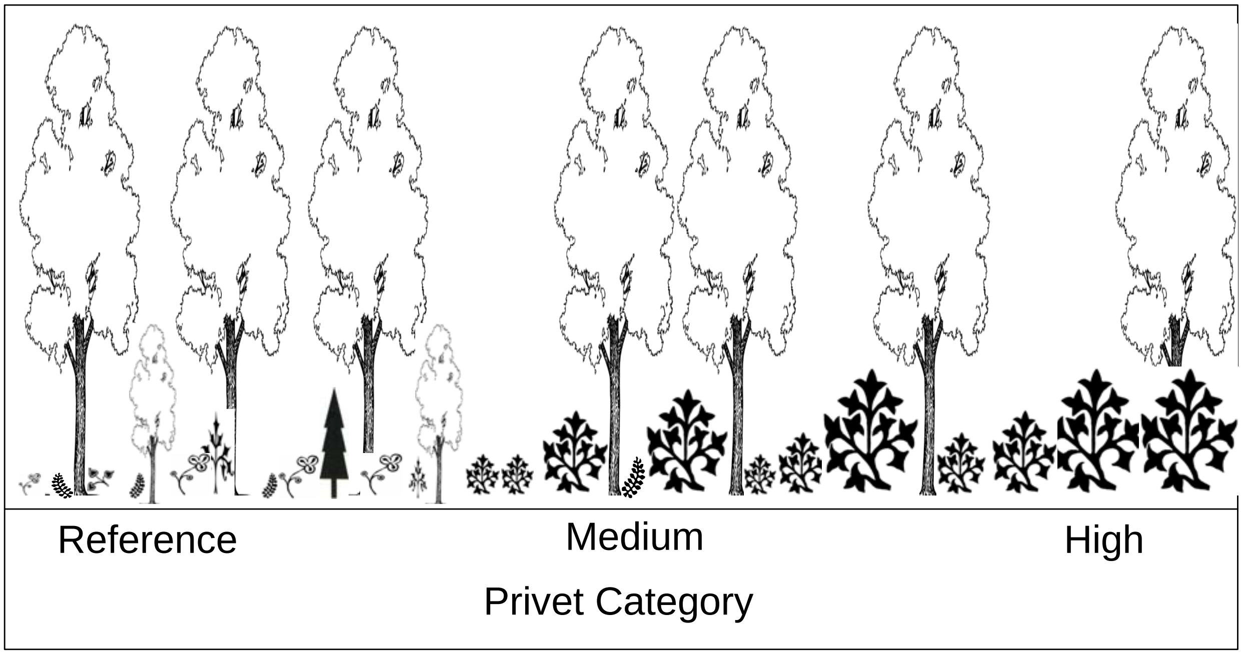

Figure 96. Idealized model of effects of understory Chinese privet invasion at increasing percentages (Reference=0%, Medium=25-79%, High=>80%) and observed changes in strata in a Southeastern Piedmont riparian forest.

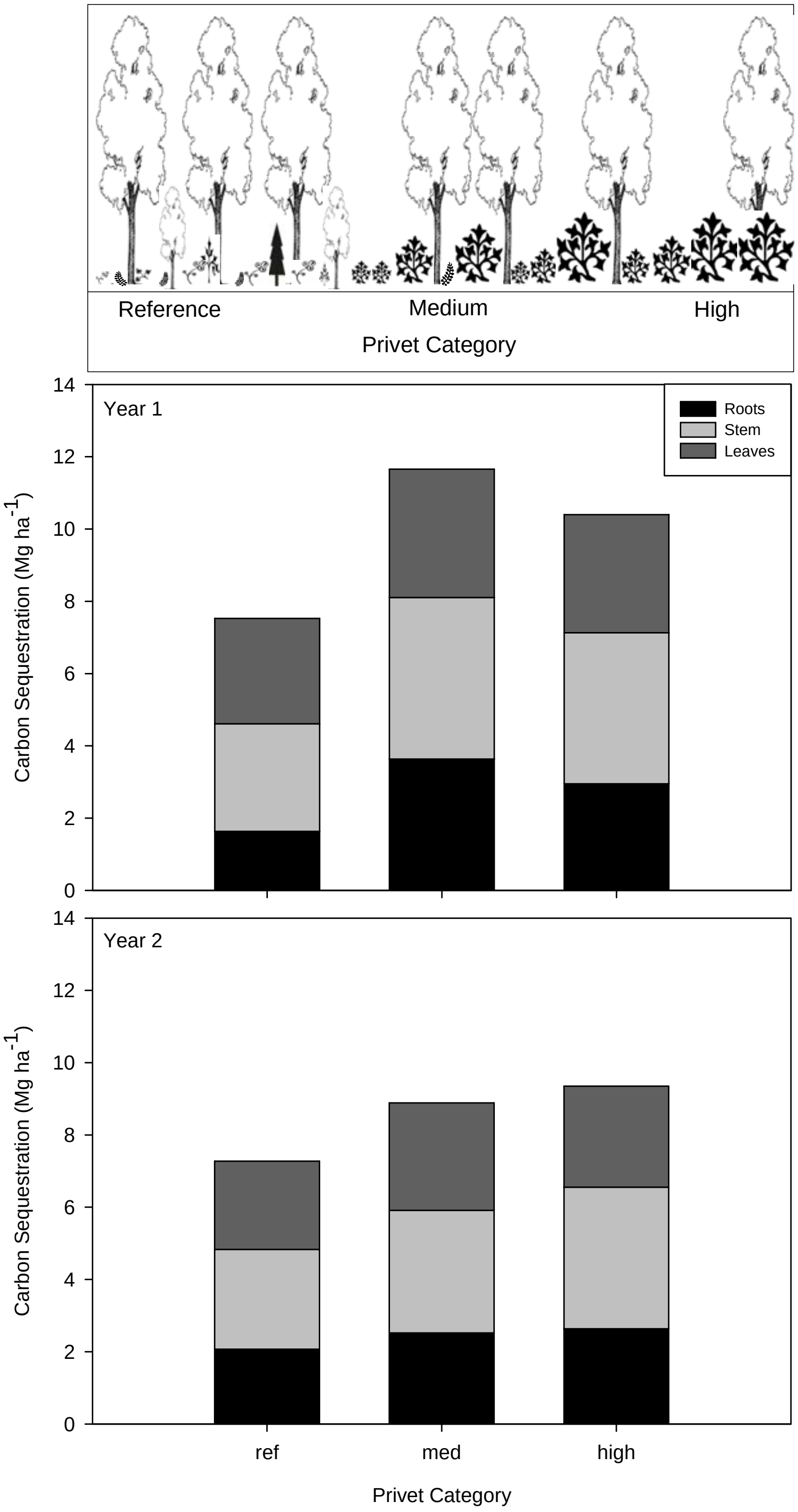

Figure 97. Total carbon sequestration separated into roots, stems, and leaves by Chinese privet category.

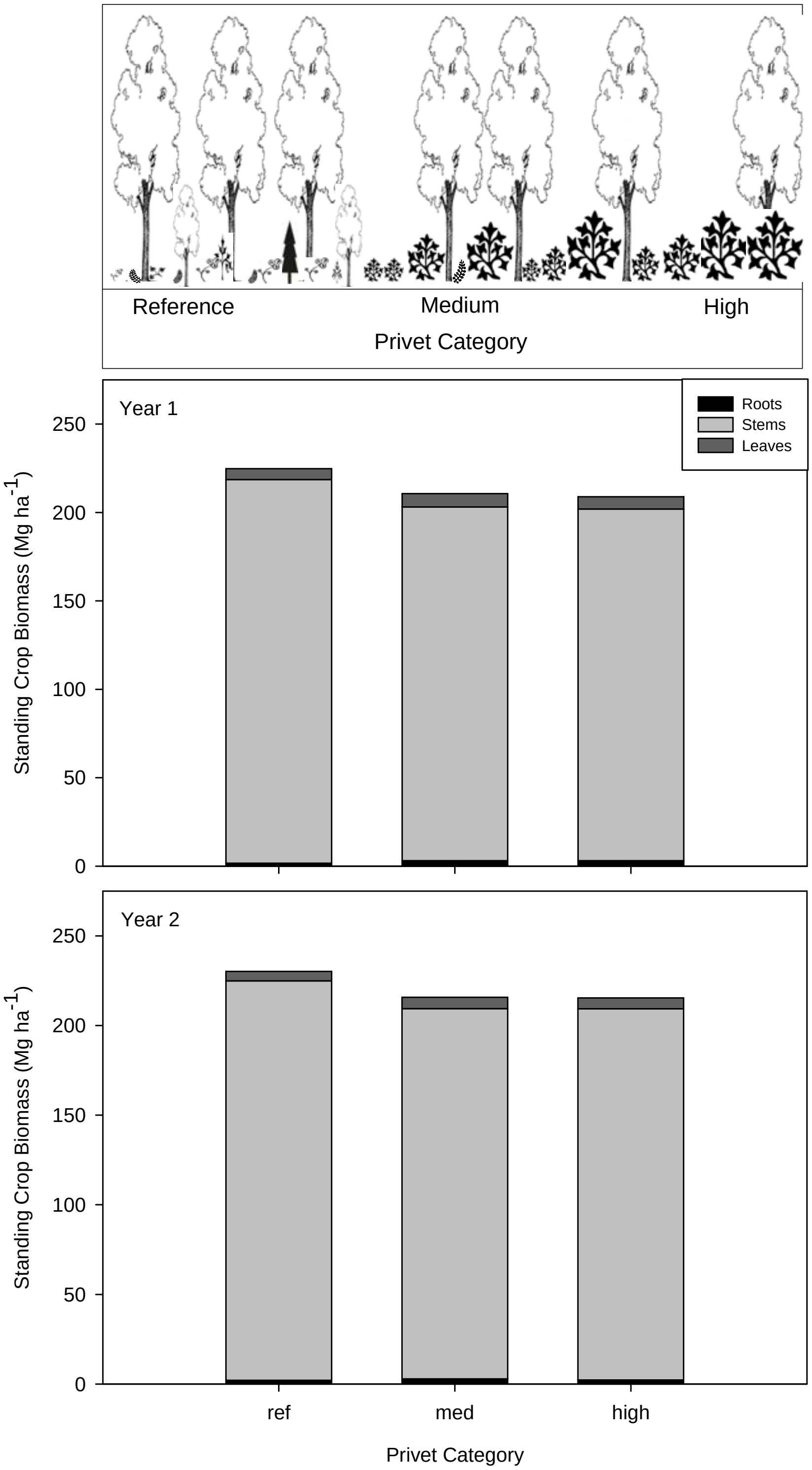

Figure 98. Standing crop biomass separated into roots, stems, and leaves by Chinese privet category.

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CHAPTER IV

INFLUENCE OF CHINESE PRIVET ON NATIVE PLANT REGENERATION IN RIPARIAN FORESTS OF THE SOUTHERN PIEDMONT

INTRODUCTION

Invasive, Nonnative Vegetation

Landscape alterations induced by invasive, nonnative plants are of growing concern to land managers, scientists, and concerned citizens. Because they have been introduced into areas outside of their natural range, nonnative plants lack natural enemies such as insects and diseases that tend to limit unchecked population growth (Miller 2003). The economic impacts of invasive, nonnative plants and animals may be as great as $120 billion per year in the United States (Pimentel et al. 2005). Moreover, Wilcove et al. (1998) noted that invasive, nonnative plant species are the second greatest threat to threatened and endangered species in the United States after habitat loss. Morse et al. (1995) estimated that 5,000 nonnative plant species have become invasive, displacing native vegetation in natural ecosystems found in the United States. In particular, nonnative woody plants may be of special concern in that they are not as common as herbaceous plants, but they have a greater potential to influence shifts in community structure (Marco and Paez 2000).

Research regarding impacts of invasives on regeneration of native plant species and general ramifications for succession, native biodiversity, and ecosystem structure has been reported (MacDonald et al. 1989, Gordon 1998, Katz and Shaforth 2003). However, there is a need for better understanding of how critical forest processes and functions are altered by successful invasions, especially given that shifts in composition and structure drive changes in productivity and biogeochemistry (Katz and Shaforth 2003, Valery et al. 2004).

Many of the invasive, nonnative plant species in the Southeast were introduced from far eastern and subtropical Asia (Stapanian et al. 1998). Chinese privet (*Ligustrum sinense* Lour.), a member of the Olive family (Oleaceae), was introduced from China and Europe in the early to mid-1800s as an ornamental plant and has become naturalized throughout the Southeast as well as along the east coast to New England (USDA 2008). It is an aggressive, invasive semi-evergreen to evergreen shrub that forms dense thickets in riparian forests and along fencerows (Miller 2003). In particular, Chinese privet invades floodplain forests because of its reproductive and competitive features that include seed dispersal by birds, root suckering, shade tolerance, and wide-ranging soil-nutrient requirements (Langeland and Burkes 1998). Although it becomes established easily in disturbed areas, Chinese privet also has the capability to invade understories of undisturbed forests (Langeland and Burkes 1998, Merriam and Feil 2002), explaining its rapid expansion across the Southeast.

Due to Chinese privet’s capacity to out-compete and displace native vegetation, large-scale ecosystem modifications may occur (Merriam and Feil 2002, USDA 2008). For example, in regions where Chinese privet invasions have occurred, the usual pattern of species succession is halted and dense stands of Chinese privet form in the place of native hardwood regeneration (Merriam and Feil 2002). Furthermore, Chinese privet may diminish timber production, may impact carbon sequestration and export, and may alter the nutrient transformation capacity of riparian forests.

Watershed Land Use Influences

The rate and extent of invasive, nonnative plant dispersal is strongly influenced by current landscape characteristics and past land uses, especially related to shifts in land use from agriculture to urban / suburban (Hutchinson and Vankat 1997, Ward 2002, Loewenstein and Loewenstein 2005, Burton and Samuelson 2007). For example, Loewenstein and Lowenstein (2005) found that urban plots in Columbus, Georgia were characterized by greater numbers of nonnative species, including Chinese privet. Although, developing and rural plots in west Georgia also had abundant Chinese privet that may be artifacts of past land use. Lundgren et al. (2004) reported that past land use was the strongest predictor of invasive, nonnative cover and richness and that current land development and physical soil characteristics were strongly correlated with invasive, nonnative cover and richness. Similarly, abandoned agricultural fields and home sites were closely tied with expansion of Chinese privet in the Oconee River basin in north Georgia (Ward 2002).

Native Plant Regeneration

When a nonnative plant is introduced into a community, its effects may range from competitive replacement of one or more species to the loss or reduction of entire vegetation strata (Lundgren et al. 2004). Invasive, nonnative plants that are successfully established in new ecosystems have demonstrated their ability to out-compete and replace native species (Merriam and Feil 2002, Reinhart et al. 2006, Galbraith-Kent and Handel 2008). There are many examples of nonnative species that have suppressed native species regeneration and these include Green Sri Lanka privet (*Ligustrum robustum walkeri* Decne.) in the forests of La Reunion Island (Lavergne et al. 1999), Nepalese browntop (*Microstegium vimineum* Trin. A. Camus) in southeastern forests of the USA (Loewenstein and Loewenstein 2005, Oswalt et al. 2007), Cinnamon (*Cinnamomum verum* J. Presl.) in tropical forests in the Seychelles (Kueffer et al. 2007), Amur honeysuckle (*Lonicera maackii* (Rupr.) Herder) in eastern North America (Gorchov and Trisel 2003), Norway maple (*Acer platanoides* L.) in northeastern forests of the USA (Galbraith-Kent and Handel 2008), and Chinese privet (*Ligustrum sinense* Lour.) in southern U.S. forests (Merriam and Feil, Loewenstein and Loewenstein 2005, Burton et al. 2005).

The loss of native species recruitment may have long-term impacts including a decrease in species diversity (Wilcove et al. 1998, McKinney and Lockwood 1999, Lundgren et al. 2004), a loss of habitat that may be detrimental to native flora and fauna (Wilcove et al. 1998), a reduction of forest structural complexity (Luken and Thieret 1996, Burton et al. 2005), and diminished net primary productivity (NPP) and carbon sequestration potential (Naeem et al. 1994, Hector et al. 1999, Costanza et al. 2007). Conversely, invasions by nonnative species may result in enhanced NPP, increased standing crop biomass, and increased nitrogen mineralization (Ehrenfeld 2003). The need to better understand impacts of Chinese privet on native plant regeneration in riparian forests is critical due to its rapid expansion across the Southeast, its likely impacts on habitat diversity, ecosystem processes, and merchantable timber regeneration, and the need for targeted management of Chinese privet invaded areas. Although some invasive, nonnative species appear to proliferate after small-scale and large-scale disturbances (Parker et al. 1993, Davis et al. 2000, Meekins and McCarthy 2001, Bartuszevige et al. 2007), Chinese privet has the potential to become readily established with or without disturbance due to its bird assisted seed dispersal (Langeland and Burks 1998). Brown and Pezeshki (2000) noted that invasive species such as Chinese privet that are able to tolerate environmental conditions such as dense shade and flooding pose a prominent threat to bottomland ecosystems by disrupting natural competition and succession.

Objective and Hypotheses

The objective of this research was to determine the extent to which varying levels of understory Chinese privet stems might alter riparian forest native species regeneration. It is hypothesized that as Chinese privet stem densities increase, regeneration of native vegetation will correspondingly decrease.

METHODS

Study Site and Design

During inventories, woody stems greater than 10 cm diameter at breast height (DBH) were considered components of the midstory or overstory (Fig. 99). Each tree greater than 10 cm DBH on the 0.04 plots was measured in December of 2004, 2005, and

2006. Additionally, subplots of 5 m x 5 m were used to study understory dynamics. On the latter plots, woody stems greater than 1.3 m in height and less than 5 cm DBH were counted as a component of the understory. Lastly, the regeneration layer was considered to be all woody stems less than 4 cm diameter at root collar. Twelve 1 m^2 subplots were designated on each main plot starting at plot center on compass directions North, South, East and West. Each compass direction had 3 subplots positioned at 3 m, 6 m, and 9 m from plot center. Regeneration vegetation was counted and identified by species after leaf out in May 2005 and May 2006.

Statistical Analysis

All statistical analyses utilized SAS software version 9.1 (SAS-Institute 2002-2003). Regression analysis was used to assess relationships between independent variables such as percent understory Chinese privet, number of Chinese privet stems per hectare, LAI, and basal area and dependent variables such as native plant regeneration, Chinese privet regeneration, and basal area (PROC REG, SAS Institute 2002-2003). Mean comparisons of productivity, leaf area index, and standing crop were performed using analysis of variance (ANOVA) (PROC GLM, SAS Institute 2002-2003). Tukey's HSD means comparison test was used as a posthoc test and all differences significant above the 90 percent confidence level were reported. Data sets were analyzed to ensure that normality assumptions were met and log transformed when necessary.

RESULTS

Precipitation Patterns

Precipitation was variable during the 30 month study period (Fig. 6) with less rainfall during the second year. In particular, September 2004 – September 2005 was a wetter period than September 2005 – May 2007. Monthly measured rainfall ranged from 16.9 cm above the 30-year average to 8 cm below the 30-year average. The Palmer Drought Index indicated drought conditions starting in April 2006 and drought persisted throughout the remainder of the study (Fig. 7).

Temperature and Light

There were no differences among Chinese privet categories in terms of mean air and soil temperatures (Fig. 8). Likewise, there were no differences among categories for light intensity maximums and means (Fig. 9).

Native Plant Regeneration

There was no significant difference in overstory stand age among the Chinese privet categories (Fig. 5). Native plant regeneration was significantly greatest in the Reference category compared to the Medium and High Chinese privet categories for 2005 ($F=54.84$, $p<0.0001$) and 2006 ($F=27.33$, $p<0.0001$) (Fig. 100). Also, the proportion of native plants in the regeneration layer was most strongly negatively related to the percent of Chinese privet in the understory in 2005 ($R^2=0.95$, $p<0.0001$) and 2006 ($R^2=0.86$, $p<0.0001$) (Fig. 101). Native vegetation regeneration was suppressed below

50% of total regeneration when the understory was composed of about 40% Chinese privet.

Regeneration of native species was influenced to a lesser degree by the number of Chinese privet stems per hectare greater than 5 cm DBH in 2005 (R^2=0.28, p<0.0359) and 2006 (R^2=0.31, p<0.0260) (Fig. 102). Additionally, a significant, but weak negative relationship was found between percent native vegetation in the regeneration layer and number of understory Chinese privet stems per hectare in 2005 (R^2=0.20, p<0.0825), but this relationship was not significant in 2006 (R^2=0.11, p<0.2197) (Fig. 103). No significant regression relationship was detected between percent of native species in the regeneration layer and total number of understory Chinese privet stems per hectare or total number of Chinese privet stems per hectare greater than 5 cm DBH.

Leaf area index (LAI) was not significantly related to percent of native species in the regeneration layer. However, a significant relationship was detected between percent native vegetation in the regeneration layer and total detectable basal area in 2005 (R^2=0.57, p<0.0042) and 2006 (R^2=0.51, p<0.0094) (Fig. 104). These data suggest that when the detectable basal area is above about 30 m^2 ha^{-1}, there was an increase in the percentage of native vegetation regeneration. This threshold reflects the ‘reverse j-shape’ relationship between percent understory Chinese privet and total basal area (R^2=0.64, p<0.0001) (Fig. 105). That is, plots with greater percentages of Chinese privet in the understory had reduced total basal area.

Chinese Privet Regeneration

The proportion of Chinese privet in the regeneration layer of High and Medium Chinese privet categories was significantly greater than in the Reference category (High>Medium>Reference) in 2005 ($F=57.05$, $p<0.0001$) and 2006 ($F=27.33$, $p<0.0001$) (Fig. 106). As would be expected, the percent of Chinese privet in the regeneration layer was strongly influenced by the percent of understory Chinese privet in 2005 ($R^2=0.95$, $p<0.0001$) and 2006 ($R^2=0.86$, $p<0.0001$) (Fig. 107). Similarly, weak, but significant, regression relationships also existed between percent of Chinese privet in the regeneration layer and number of Chinese privet stems > 5 cm DBH per hectare in 2005 ($R^2=0.28$, $p<0.0359$) and 2006 ($R^2=0.31$, $p<0.0260$) (Fig. 108). Additionally, the number of understory Chinese privet stems per hectare was weakly related to Chinese privet in the regeneration layer in 2005 ($R^2=0.20$, $p<0.0825$), but not in 2006 ($R^2=0.11$, $p<0.2197$) (Fig. 109). However, no significant relationship was detected between percent of Chinese privet in the regeneration layer and total numbers of understory stems per hectare or total number of stems per hectare greater than 5 cm DBH.

As was the case with native plant regeneration results, no significant relationship existed between percent of Chinese privet in the regeneration layer and LAI. However, there was a significant negative relationship between total basal area and percent of Chinese privet in the regeneration layer in 2005 ($R^2=0.57$, $p<0.0042$) and 2006 ($R^2=0.51$, $p<0.0094$) (Fig. 110). Similar to native plant regeneration, a detectable basal area of about 30 m^2 ha^{-1} was observed below which Chinese privet regeneration increased. As previously mentioned, this threshold is strongly influenced by the significant ‘reverse jshaped' regression relationship between percent understory Chinese privet and basal area (R^2=0.64, p<0.0001) (Fig. 105).

Regeneration Comparison Between Years

Student's t-tests detected no significant differences between years among Chinese privet categories (Reference, Medium, or High) for regeneration of native vegetation or Chinese privet. Changes from Period 1 to Period 2 in proportion of Chinese privet in the understory are displayed in Table 14. The greatest increase in Chinese privet regeneration from 2005 to 2006 was 33% and the greatest increase in native plant regeneration from 2005 to 2006 was 20%.

Influence of Watershed Land Use

Significant differences in the percent of native vegetation in the regeneration layer were detected among predominant watershed land use categories in 2005 (F=20.73, p<0.0001) and 2006 (F=23.68, p<0.0001) (Fig. 111). Reference watersheds had significantly greater percentages of native vegetation in the regeneration layer compared with all other watershed land uses (rural, developing, and urban) in 2005 and 2006. Conversely, the rural, developing, and urban watersheds had significantly greater percentages of Chinese privet in the regeneration layer than reference watersheds in 2005 (F=20.73, p<0.0001) and 2006 (F=23.68, p<0.0001) (Fig. 112).

DISCUSSION

Chinese privet had a significant negative correlation with regeneration of native plants in riparian areas where it had invaded the understory. The strongest predictor of Chinese privet influence on native plant regeneration was the proportion or percent of understory stems composed of Chinese privet. In fact, at about 40% understory Chinese privet stems, native species regeneration was suppressed to below 50% of total (Fig. 101). At 60% understory Chinese privet stems, the native plant regeneration decreased to less than 20% of total (Fig. 101). The number of Chinese privet stems per hectare in the understory was also a significant predictor of native species regeneration (Fig. 103). At 200 Chinese privet stems >5 cm DBH per hectare, the percent of native plant regeneration dropped below 40% of total. Native species regeneration was suppressed to less than 20% of total when there were 400 understory Chinese privet stems > 5 cm per hectare (Fig. 102). Interestingly, basal area was also a strong predictor of native species regeneration (Fig.104). Detectable basal area and native species regeneration was detected. At a basal area of about 30 m^2 ha^{-1} the percent of native species regeneration is suppressed below 40% of total. This relationship is tied closely to the strong negative regression relationship between basal area and percent understory Chinese privet stems. That is, increased understory Chinese privet was significantly correlated with decreased detectable basal area due to the heavy understory of Chinese privet stems and leaves.

Suppression of native species regeneration by an invasive, nonnative species has been reported in other studies. For example, Loewenstein and Loewenstein (2005) and Merriam and Feil (2002) each reported a 40% loss in species richness in forests with a dense understory of Chinese privet. Similarly, Burton et al. (2005) noted a decrease in species diversity in west Georgia riparian communities invaded by Chinese privet. Native tree sapling growth was inhibited in a suburban forest in New Jersey when the understory was composed of the invasive tree Norway maple (*Acer platanoides*) (Galbraith-Kent and Handel 2008). Hutchinson and Vankat (1997) noted a negative correlation between density of the invasive, nonnative shrub, Amur honeysuckle (*Lonicera maackii*), and the density and species richness of tree seedlings in southwest Ohio.

There were significantly greater percentages of Chinese privet in the regeneration layers of High and Medium Chinese privet categories than in the Reference category in 2005 and 2006 (Fig. 106). Additionally, a strong positive regression relationship existed between percent of Chinese privet in the regeneration layer and percent of Chinese privet in the understory. Brown and Pezeshki (2000) noted that Chinese privet has a distinct advantage over many native woody species and may out-compete seedlings of other woody vegetation found in the understory due to its tolerance of dense shade and flooding. The success of the invasive, nonnative tree Norway maple and the corresponding suppression of native vegetation have also been linked to its ability to tolerate dense shading (Reinhart et al. 2006).

Our data suggest native species regeneration is significantly suppressed when Chinese privet made up about 40% of the understory stems in a riparian forest and when 200 Chinese privet stems per hectare > 5 cm DBH were present. Similarly, Lowenstein and Loewenstein (2005) noted overstory regeneration potential was substantially impacted where dense populations of Chinese privet were present in West Georgia watersheds. Additionally, Chinese privet invasion has been linked to a loss of native vegetation regeneration and a corresponding increase in dense stands of Chinese privet in a mixed hardwood forest in Western North Carolina (Merriam and Feil 2002). Each of the plots in this study had full canopy cover during this research project and no evidence of overstory tree mortality was observed.

Without regeneration, forest stand dynamics will follow a course of growth to thinning to senescence (Horn 1981). Due to regeneration mortality, multiple native tree seedlings are required to insure replacement of individual older canopy trees as mortality occurs. That is, adequate stocking numbers are needed to ensure perpetuation of existing species (Horn 1981). Without this regeneration layer, it is likely that canopy trees will not be replaced and stand structure will follow a trajectory toward a shrub dominated system (Lowenstein and Loewenstein 2005, Oliver and Larson 1996). This loss of native plant regeneration has serious implications for a number of riparian forest functions and processes including maintenance of net primary productivity (NPP), carbon sequestration, and habitat diversity (Chapter 2, Influence of Chinese Privet on Productivity of Riparian Forests of the Southern Piedmont and Chapter 3, Influence of an Invasive, Nonnative Tree Species on Carbon Allocation and Sequestration in Riparian Forests of the Southern Piedmont).

High percentages of Chinese privet regeneration were found in all watershed land use categories except the Reference watersheds (Fig. 112). No Chinese privet was found in Reference watersheds' regeneration layers in 2005, but several stems were identified in 2006 suggesting the beginning of an invasion in the Reference watersheds.

The bird-assisted dispersal of Chinese privet seeds has been identified as a source of Chinese privet invasions in undisturbed forests (Langland and Burks 1998). Likewise, Merriam (2003) noted that streams and associated flood events are major corridors for dissemination of Chinese privet seed. Rural and developing watersheds have also been identified as areas of rapid Chinese privet invasion. Ward (2002) noted increased Chinese privet in the Upper Oconee River, GA watershed primarily due to the invasion of abandoned agricultural fields and pastures. Remnant forests in less disturbed areas were observed to have increased Chinese privet invasion, but not at as rapid a rate as the abandoned fields and pastures. Interestingly, Ward (2002) observed that Chinese privet often invaded along floodplains in an initial longitudinal pattern that shifted toward lateral expansion across bottomland surfaces such as abandoned fields and pastures. Observations confirmed a similar invasion pattern along riparian corridors in this study's research plots.

Other studies have linked human-induced disturbances and land use changes to increases in Chinese privet invasion (Ward 2002, Loewenstein and Loewenstein 2005, Burton et al. 2005, Burton and Samuelson 2007). Loewenstein and Loewenstein (2005) found Chinese privet across all land uses in an urban-rural watershed gradient in west Georgia. Additionally, Chinese privet was found to be highly abundant in rural, developing, and urban watersheds in west Georgia (Burton and Samuelson 2007).

CONCLUSION

It was hypothesized that, as Chinese privet stem densities increase, regeneration of native species will correspondingly decrease. This trend was detected and the percent of understory Chinese privet stems was the strongest negative predictor of native plant regeneration. Riparian forest understories composed of about 40% Chinese privet exhibited suppressed native vegetation regeneration < 50% of total. Likewise, increased levels of understory Chinese privet were strongly and positively correlated with levels of Chinese privet in the regeneration layer. Additionally, when the detectable total basal area was approximately 30 m^2 ha^{-1}, the proportion of Chinese privet regeneration increased. These data strongly suggest that a riparian understory occupied by as little as 40% Chinese privet may severely disrupt natural patterns of stand replacement. Additionally, native plant suppression below 40% of total was detected with about 200 Chinese privet stems per hectare > 5 cm DBH. These results foreshadow the potential loss of large native canopy trees in riparian corridors invaded by an understory of Chinese privet.

It is worthy to note that steps to control Chinese privet invasions may improve native vegetation regeneration. Merriam and Feil (2002) noted an increase in native herb and tree seedlings in areas where Chinese privet had been removed. The lack of a significant relationship between LAI and native plant regeneration suggests there may be a suite of factors beyond shading that influence regeneration including competition for nutrients, decreased soil moisture, and allelopathy. Ultimately, Southeastern Piedmont riparian forest functions and processes, such as net primary productivity and carbon sequestration may be diminished as large overstory native tree species are lost and not replaced due to suppression of native species regeneration by Chinese privet.

Table 14. Native plant and Chinese privet regeneration by research plot for 2005 and 2006.

% Under-story Chinese privet	% Chinese privet in regen layer 2005	% Chinese privet in regen layer 2006	% native vegetation in regen layer 2005	% native vegetation in regen layer 2006	Difference between Chinese privet regen (2006-2005)	Difference between native plant regen (2006-2005)
0	0	7	100	93	7	-7
0	0	0	100	100	0	0
0	0	0	100	100	0	0
29	35	47	65	53	12	-12
35	50	30	50	70	-20	20
48	59	92	41	8	33	-33
65	82	84	18	16	2	-2
76	83	92	17	8	9	-9
82	81	70	19	30	-11	11
86	98	99	2	1	1	-1
88	99	98	1	2	-1	1
91	98	96	2	4	-2	2
92	86	80	14	20	-6	6
98	98	98	2	2	0	0
99	83	92	17	8	9	-9
100	96	97	4	3	1	-1

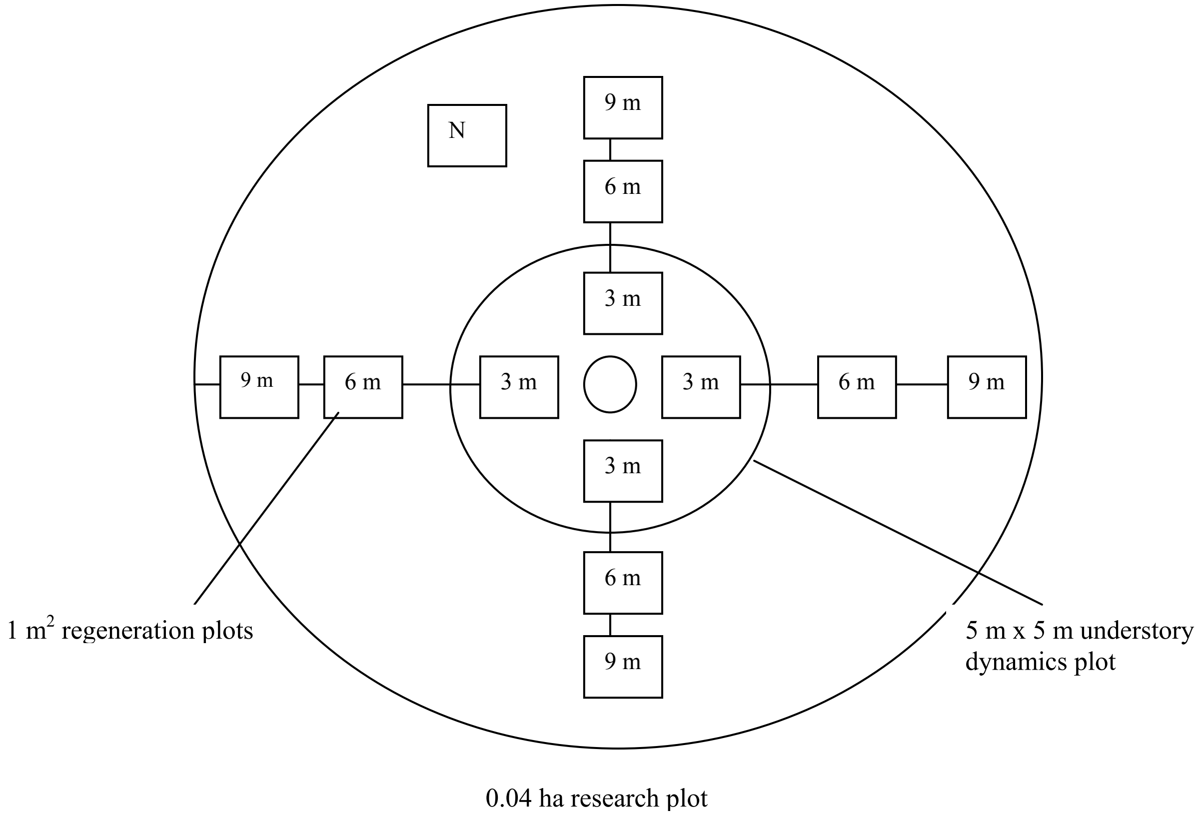

Figure 99. Regeneration plot layout.

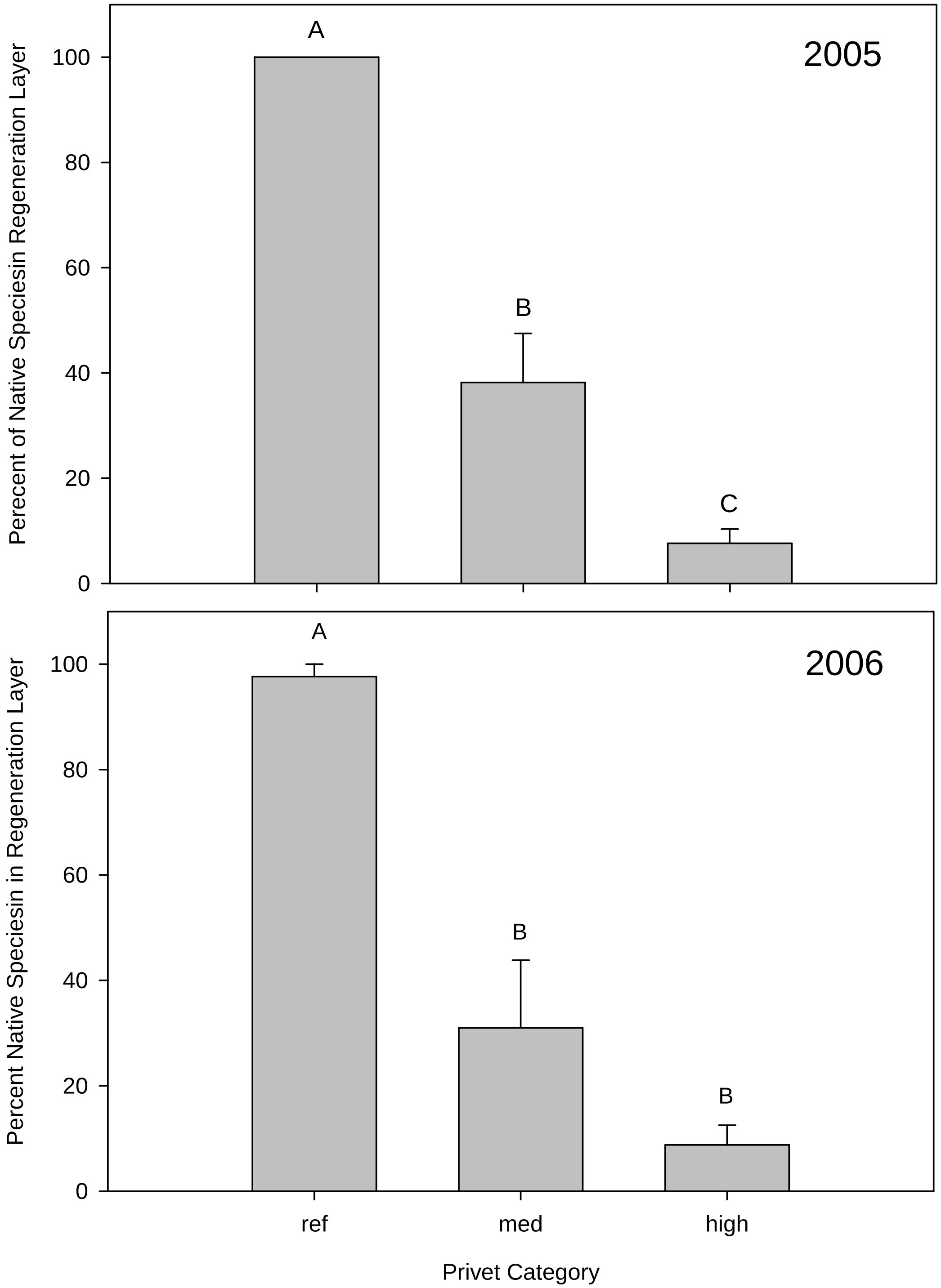

Figure 100. Percent of native species in the regeneration layer by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

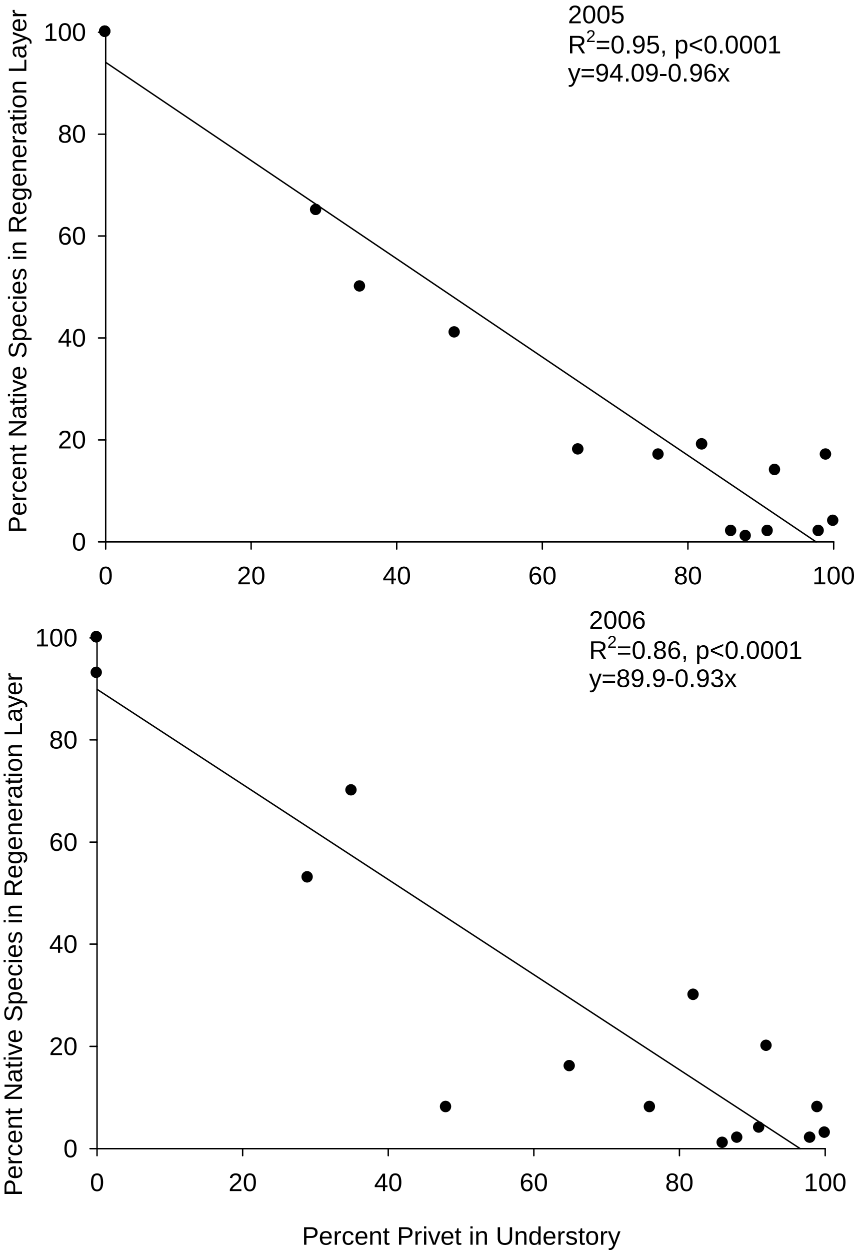

Figure. 101. Significant linear regression relationships between percent of native species in the regeneration layer and percent of Chinese privet in the understory.

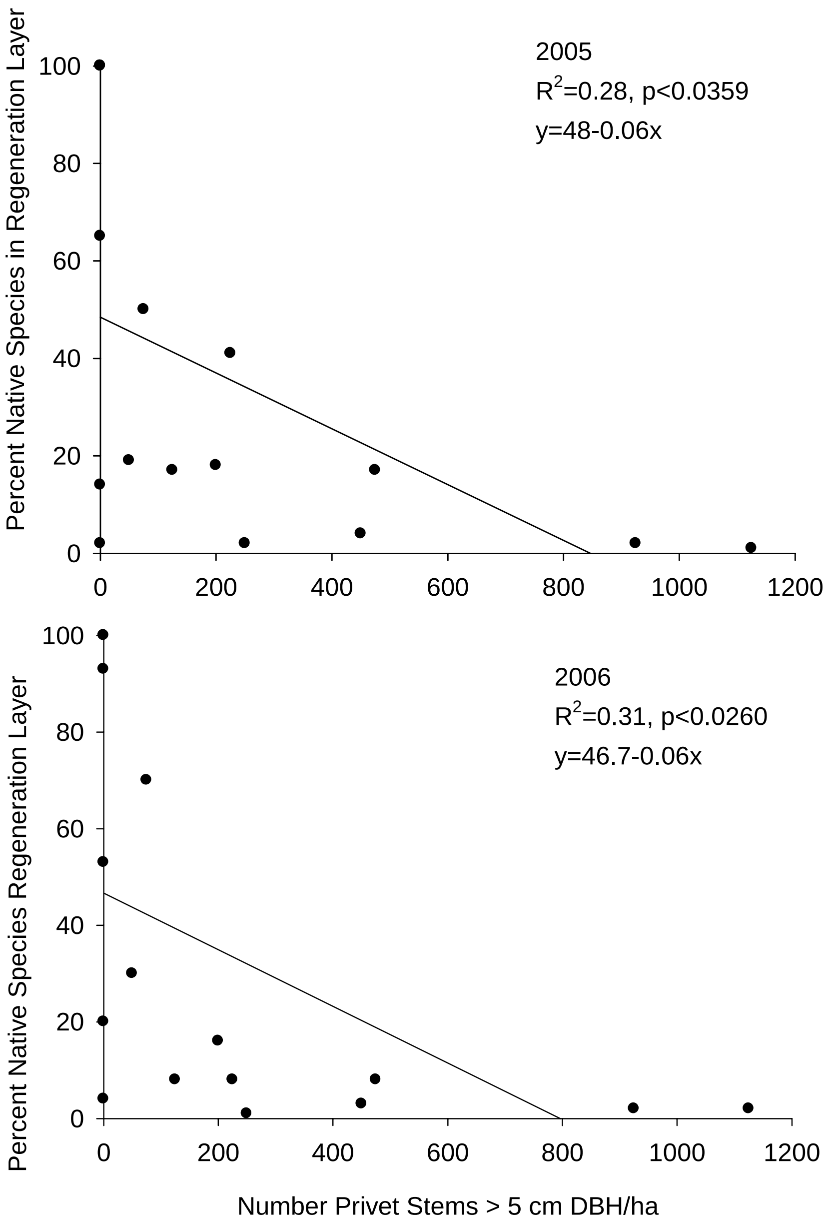

Figure 102. Significant regression relationships between percent of native species in the regeneration layer and density of Chinese privet stems greater than 5 cm DBH per hectare.

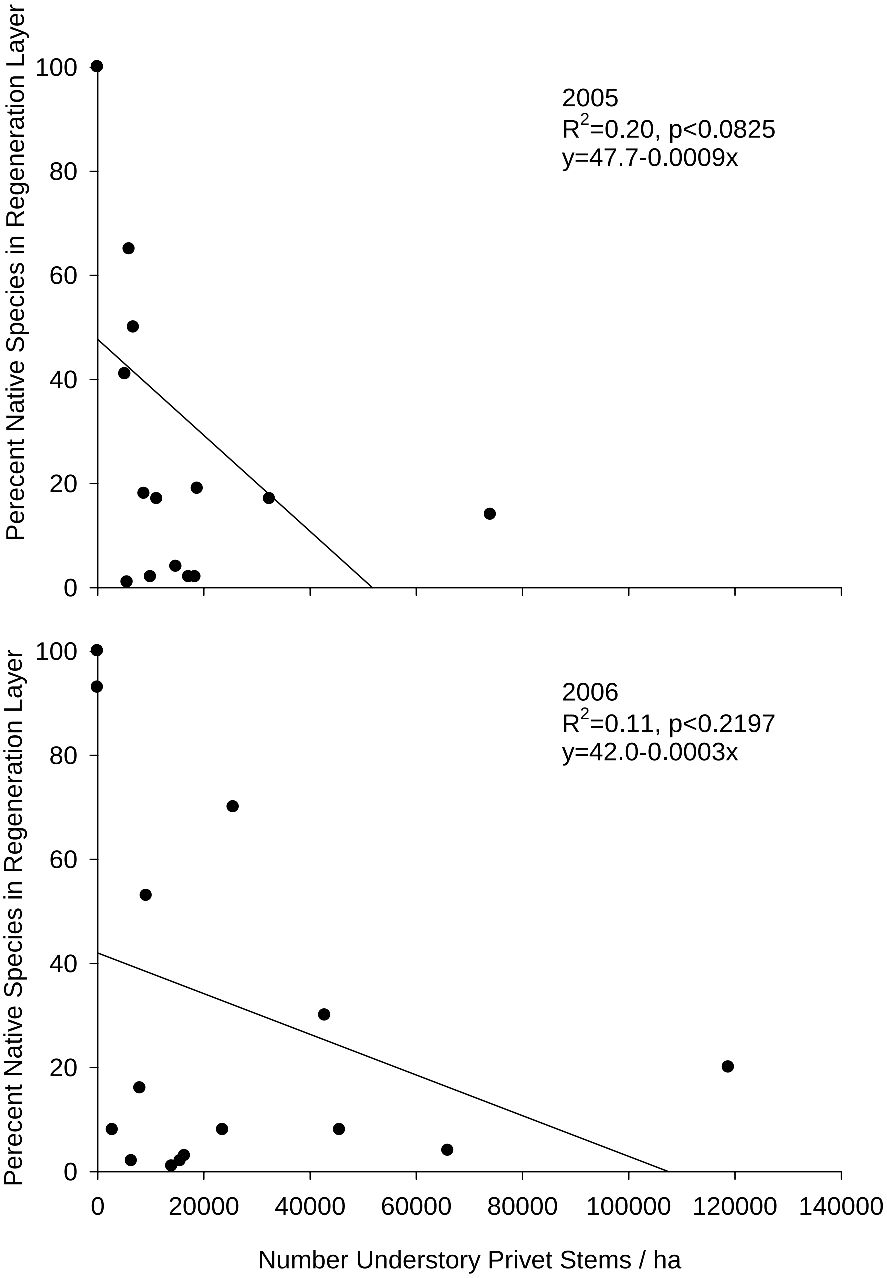

Figure 103. Regression relationships between percent of native vegetation in the regeneration layer and density of Chinese privet stems in the understory.

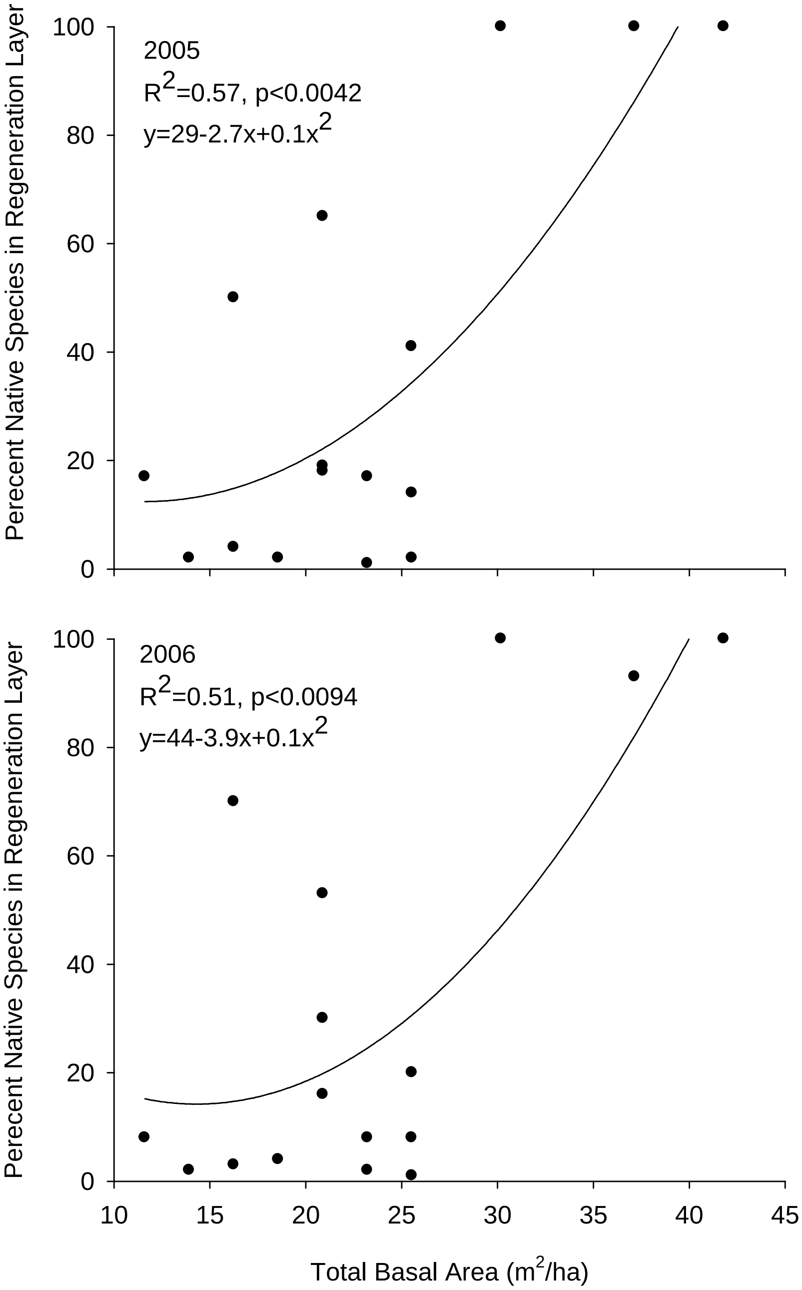

Figure 104. Regression relationships between percent of native vegetation in the regeneration layer and basal area.

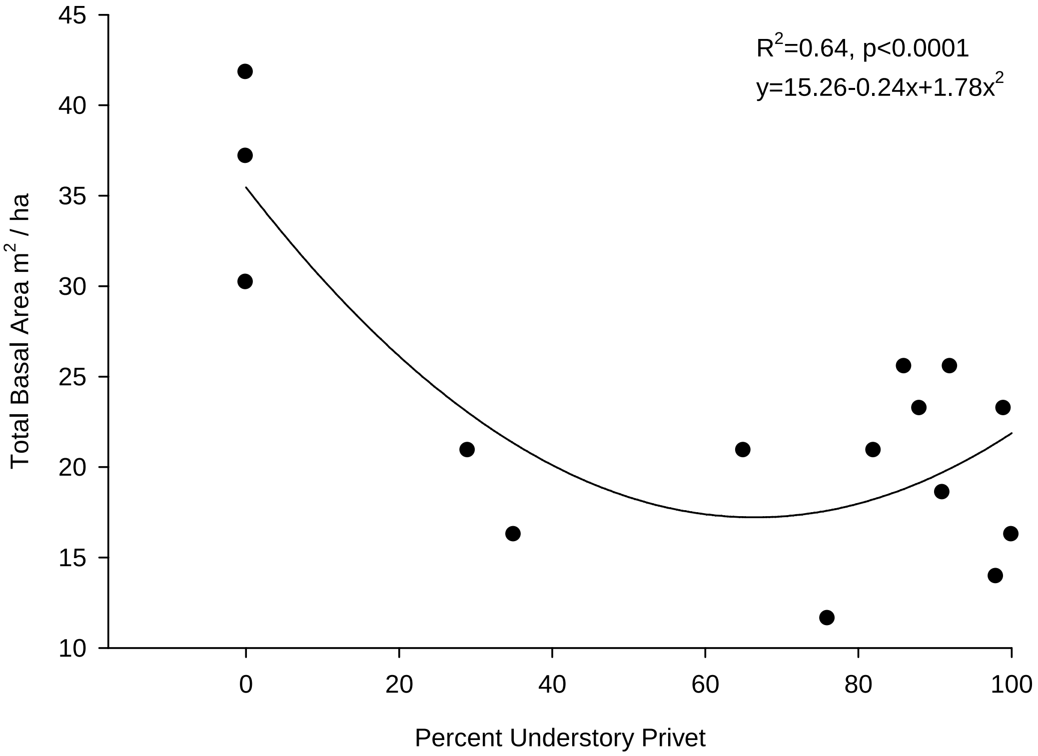

Figure 105. Regression relationships between basal area and percent understory Chinese privet.

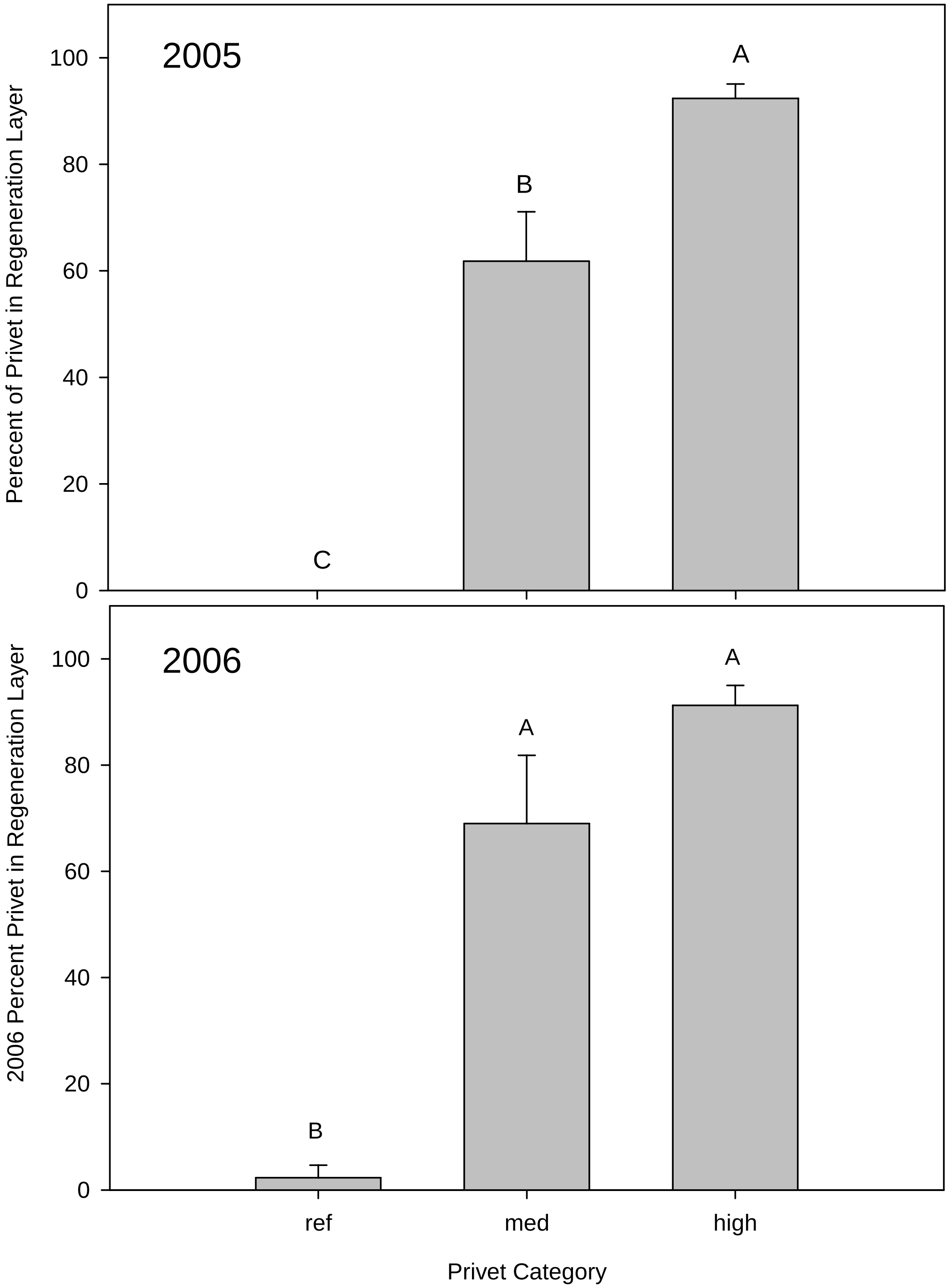

Figure 106. Percent of Chinese privet in the regeneration layer by Chinese privet category. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

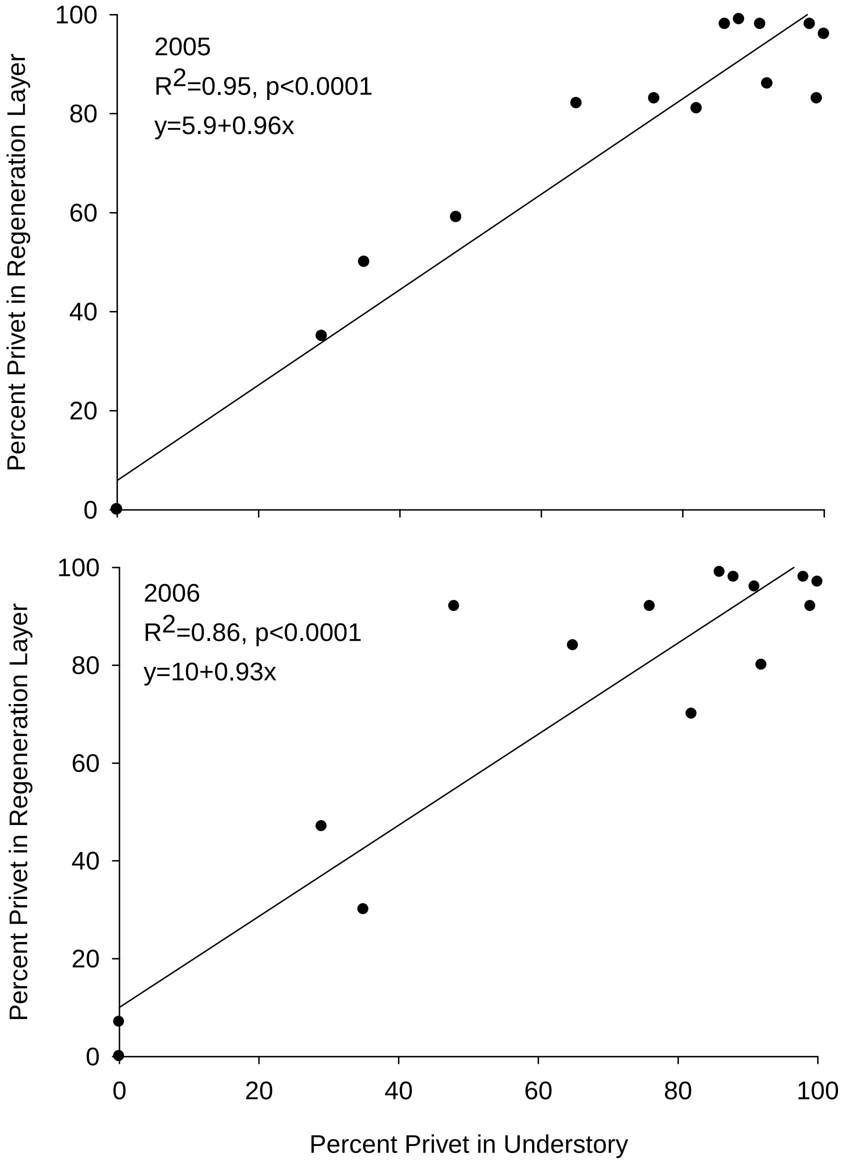

Figure. 107. Significant linear regression relationships between percent of Chinese privet in the regeneration layer and percent of Chinese privet in the understory.

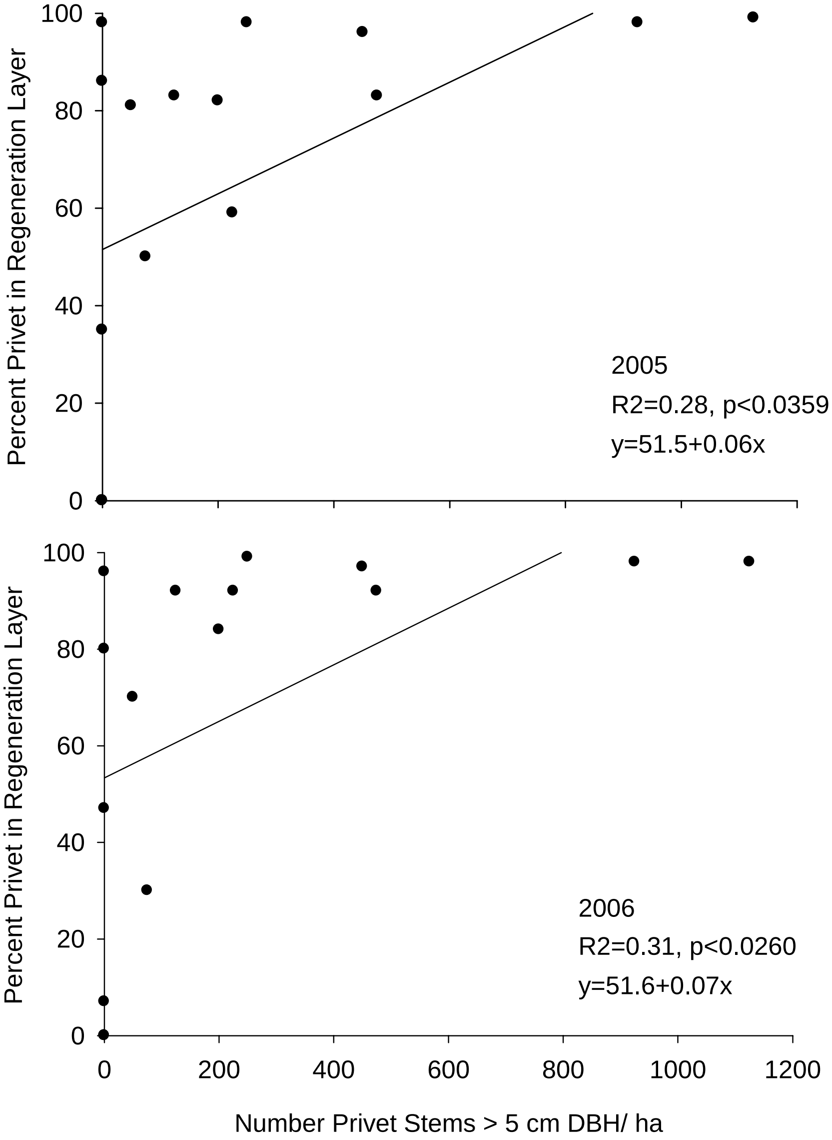

Figure 108. Significant regression relationships between percent of Chinese privet in the regeneration layer and density of Chinese privet stems greater than 5 cm DBH per hectare.

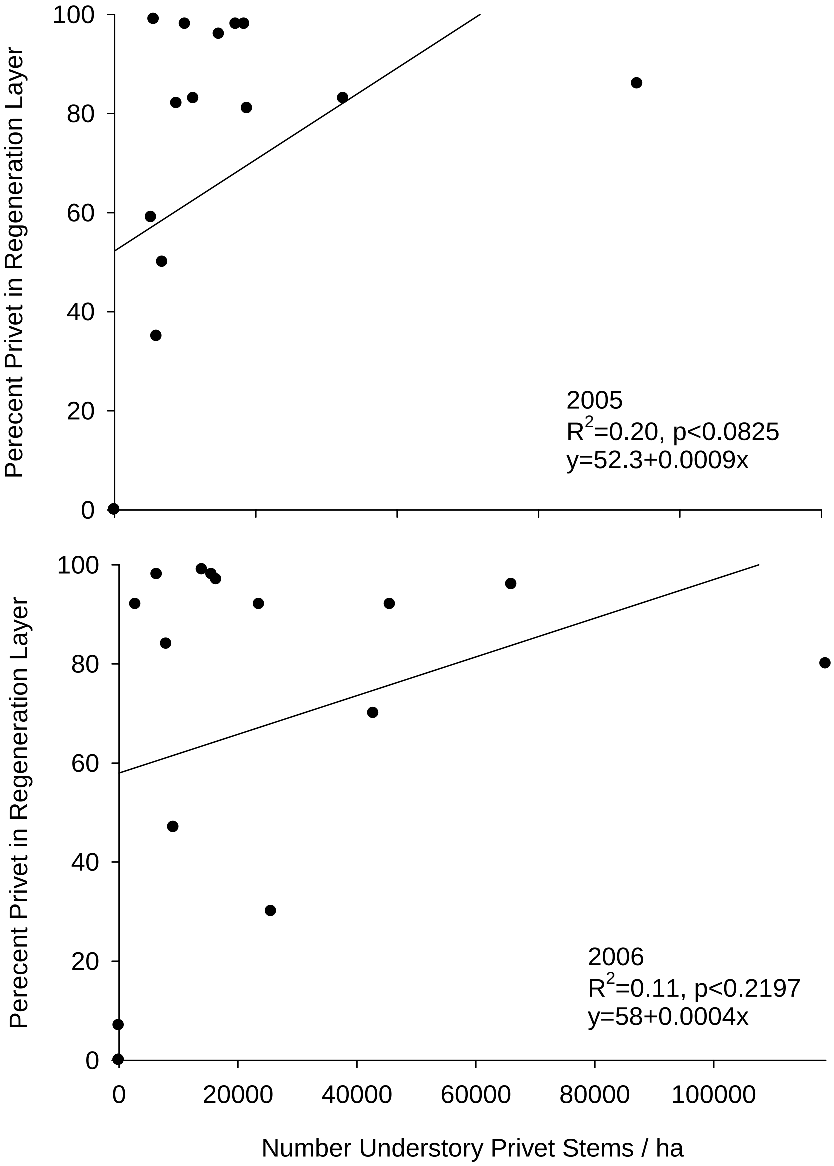

Figure 109. Regression relationships between percent of Chinese privet in the regeneration layer and density of Chinese privet stems in the understory.

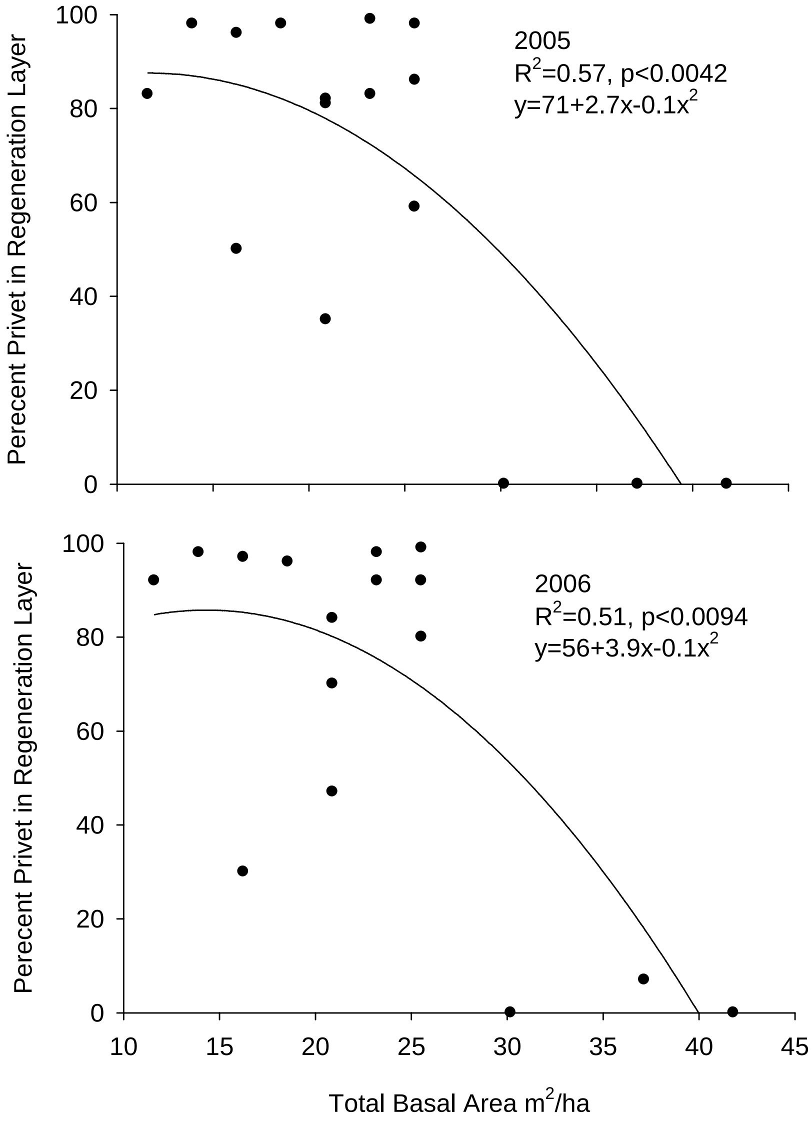

Figure 110. Regression relationships between percent of Chinese privet in the regeneration layer and basal area.

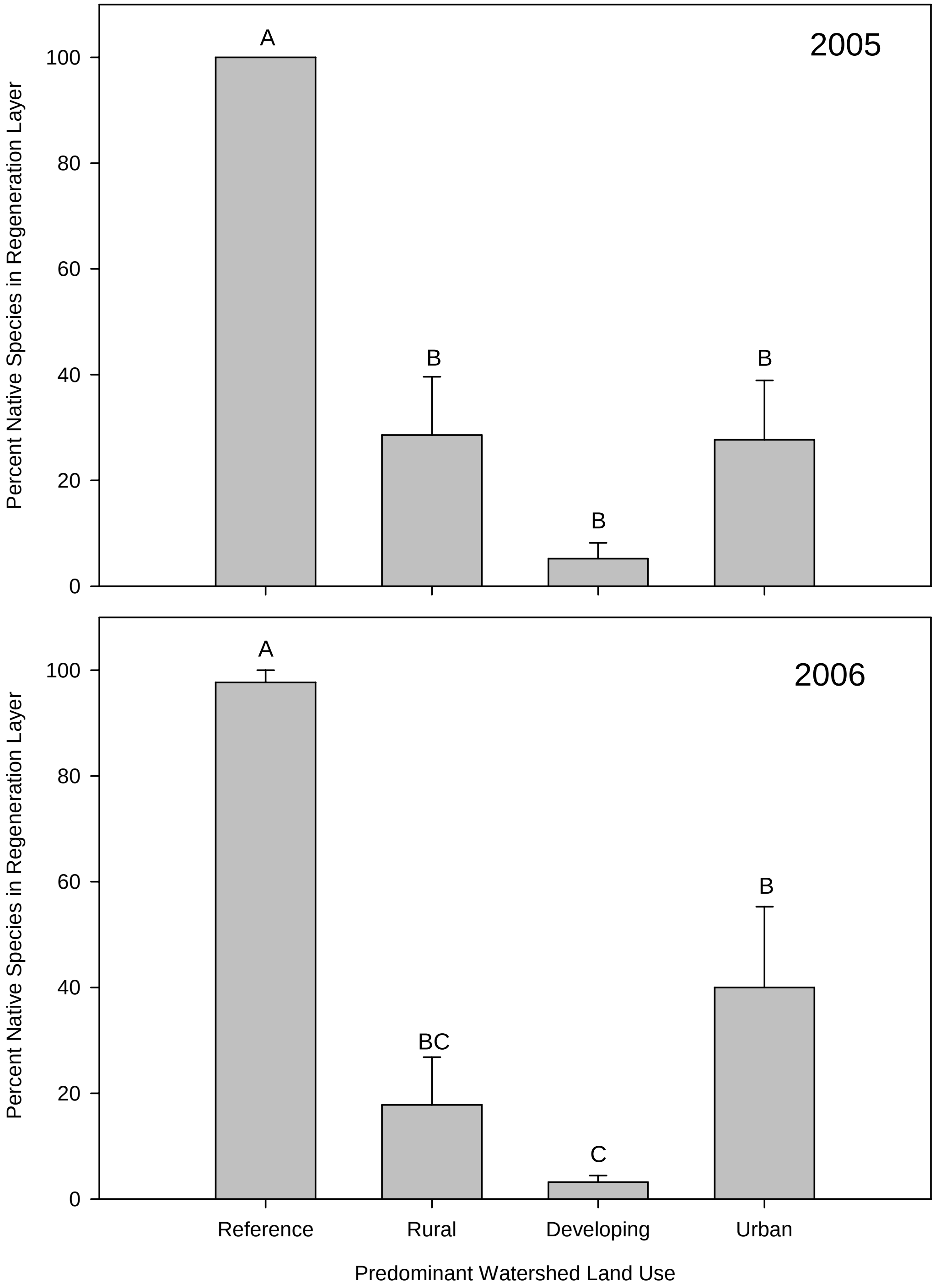

Figure 111. Percent of native vegetation in the regeneration layer by predominant watershed land use. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

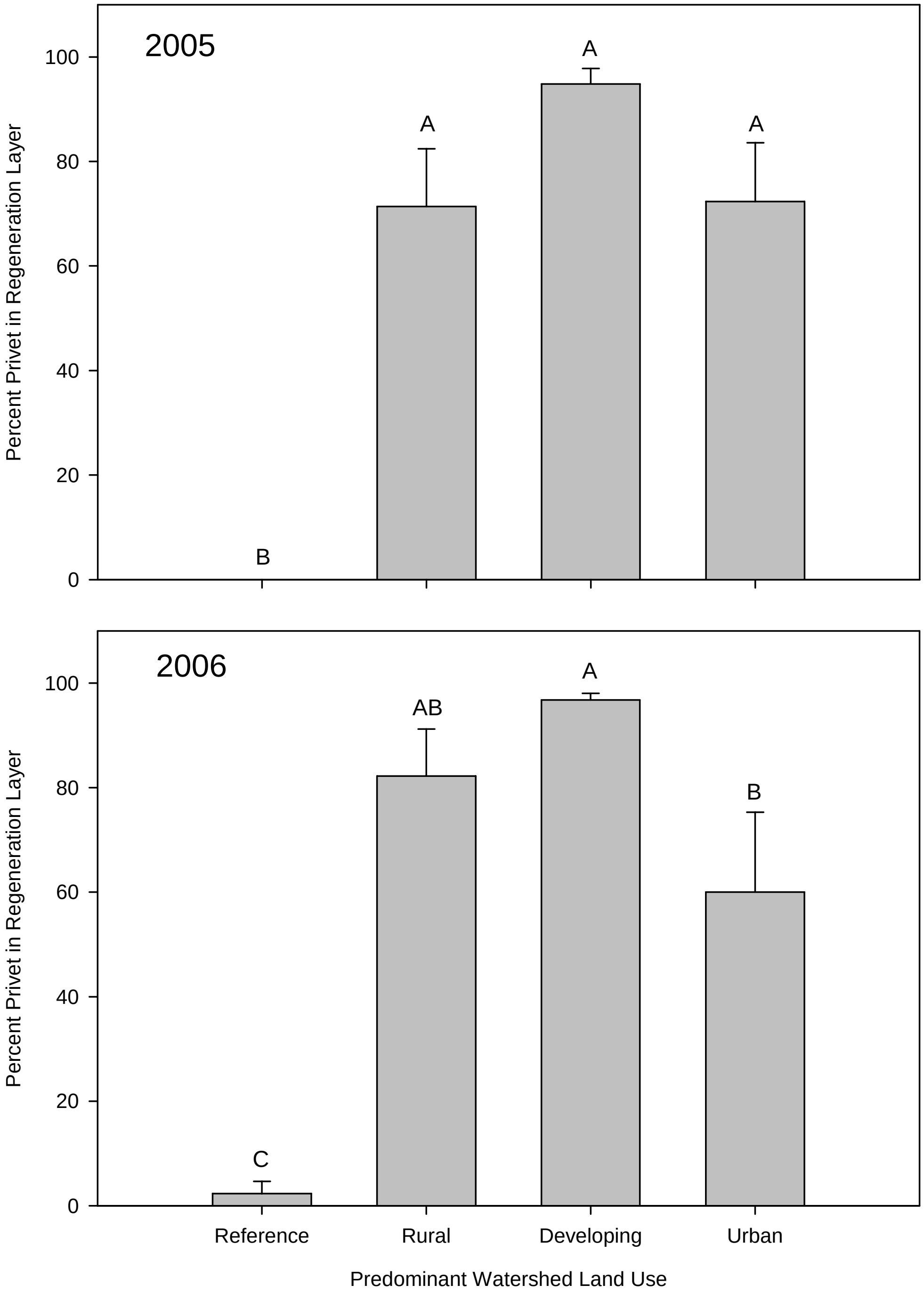

Figure 112. Percent of Chinese privet in the regeneration layer by predominant watershed land use. Means with different letters differ significantly by Tukey HSD (α=0.10). Vertical bars indicate standard errors.

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CHAPTER V

SUMMARY AND CONCLUSIONS

Study Objectives

The goal of this research was to better understand the influence of Chinese privet (*Ligustrum sinense* Lour.) on riparian forests of the Southern Piedmont, specifically above- and belowground productivity, carbon sequestration, and native plant regeneration. Study objectives were to: 1) determine how increasing densities of Chinese privet influence above- and belowground net primary production, 2) examine Chinese privet's impact on carbon sequestration in riparian systems, and 3) establish the influence of Chinese privet on native vegetation regeneration.

Synthesis

Overall, the results suggest that processes and functions such as net primary productivity (NPP), carbon sequestration, and native plant regeneration are influenced by the invasive, nonnative shrub, Chinese privet. Above- and belowground NPP trends were similar during periods of plentiful rainfall with increased levels of total productivity in riparian forests observed with Chinese privet constituting 25-79% of the total understory. The elevated total NPP in the medium category was driven primarily by belowground NPP (BNPP) trends. BNPP was the only productivity measure that was significantly less on reference plots compared to the other categories ($F=6.69$, $p<0.0112$). Also, there was a significant, positive regression relationship between BNPP and percent of understory Chinese privet (R^2=0.53, p<0.0112).

During periods of lower than average rainfall, aboveground NPP (ANPP) measures were significantly related to percent of Chinese privet in the understory. Total litterfall (R^2=0.58, p<0.0058) and leaf litter (R^2=0.49, p<0.0183) exhibited a trend towards increased productivity in the Medium range of Chinese privet invasion. However, reproductive litter increased with increasing understory Chinese privet (R^2=0.42, p<0.0367) and was significantly lower in the Reference category compared to the Medium and High categories during the drought period (F=4.30, p<0.0391).

The lack of a significant difference in BNPP during the less than average rainfall period may be attributed to a decrease in the fine roots produced by Chinese privet in the top 11 cm of soil. Chinese privet was observed to be shallow rooted in the riparian forests of the current study and could have decreased BNPP in response to a lack of soil moisture, whereas, the more deeply rooted native vegetation of the Reference plots was able to access deeper soil moisture which allowed for maintenance of fine root BNPP. Conversely, the significant relationship between litterfall productivity measures in periods of drought could be attributed to a 'lag effect' in which plentiful rainfall in previous years supported productivity of leaf and reproductive litterfall. Reproductive litterfall may have also increased during the drought period due to a 'now or never' response. This response has been observed in periods of stress when plant resources are allocated to reproductive structures to increase opportunities for future generation establishment when environmental conditions are improved for plant growth and development.

Carbon sequestration is closely linked to NPP and the concentration of carbon in plant tissues such as leaf litterfall, stems, and roots. Carbon concentrations of plant tissues in the current study were not significantly different among Chinese privet categories. For this reason, NPP trends reflected carbon sequestration trends. There was significantly more total carbon sequestered in Medium (25-79% of total understory stems) and High (>80% of total understory stems) Chinese privet categories compared to that of the Reference category (0% of total understory stems) during the period of plentiful rainfall. Belowground carbon sequestration was the strongest influence on total carbon sequestration and was significantly less in the Reference category than in the Medium and High categories. Total carbon sequestration had a significant quadratic regression relationship with percent understory Chinese privet during periods of plentiful rainfall ($R^2=0.49$, $p<0.0179$). There was less sequestration in riparian forests that had low Chinese privet invasion and high Chinese privet invasion. Riparian forests that were characterized in the medium range of Chinese privet invasion had higher sequestration rates.

The shifting of NPP and carbon sequestration trends along a continuum of Chinese privet invasion is partially linked to the influence of Chinese privet on native species regeneration. Native species regeneration showed a strong, negative linear relationship as the proportion of Chinese privet in the understory ($R^2=0.95$, $p<0.0001$) increased. The eventual loss of native species, especially large native trees that occupy the canopy stratum, may translate into decreased overall standing crop biomass, NPP, and carbon sequestration rates. In the current study, most of the standing crop biomass and carbon was allocated to the stems of large, native trees and there was no difference among Chinese privet categories in terms of aboveground woody NPP. Suppression of native species regeneration will likely enhance domination of riparian forests by a Chinese privet mid-story with lower rates of total NPP. This could further result in a shift in carbon sequestration trends that are less than riparian forests that retain a more diverse forest structure (regeneration layer, herbaceous layer, understory, mid-story, and canopy). For example, the High privet category plots in the current study displayed suppressed native species regeneration, suppressed herbaceous layers and less dense understories than the Reference or Medium plots, suggesting a trend toward decreased species richness and less diverse forest structure.

In summary, although there is an increase in NPP and carbon sequestration in riparian forests invaded by 25-79% understory Chinese privet in the current study, plots with high levels of Chinese privet invasion (>80% of total understory) exhibited not only decreased NPP and carbon sequestration, but also suppressed native plant regeneration. As succession proceeds, long-term negative impacts will likely be related to the loss of species richness and shifting of forest structure from diverse strata that include layers such as regeneration, understory, mid-story and large, native canopy trees to a less diverse system composed primarily of mid-story Chinese privet trees.

Future Directions

This dissertation investigated the influence of Chinese privet on net primary productivity, carbon allocation and sequestration, and native plant regeneration in riparian systems of the southern Piedmont. However, the spread of Chinese privet occurs across many physiographic regions ranging from Texas to Massachusetts (USDA Plant

Database 2008). Additional research on the extent of Chinese privet influence in different regions could be of help in prioritizing management needs. The interaction between stream carbon cycling and Chinese privet may also provide interesting insights into the role of an invasive, nonnative plant on in-stream processes and downstream impacts. Finally, exploring the recovery of system processes and functions following the removal of Chinese privet may aid in better prediction of long-term positive impacts of that removal on habitat diversity, NPP, and carbon sequestration in riparian forests of the southern Piedmont.